2015

Top-down and bottom-up tools for integrated pest management in Northeastern hop production

Lily Calderwood
University of Vermont

TOP-DOWN AND BOTTOM-UP TOOLS FOR INTEGRATED PEST MANAGEMENT IN NORTHEASTERN HOP PRODUCTION

A Dissertation Presented

by

Lilian B. Calderwood

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fullfillment of the Requirements
for the Degree of Doctor of Philosphy
Specializing in Plant and Soil Science

May, 2015

Defense Date: March 23, 2015
Dissertation Examination Committee:

Heather Darby, Ph.D., Co-Advisor
Josef Gorres, Ph.D., Co-Advisor
Alison Brody, Ph.D., Chairperson
William Lamp, Ph.D.
Cynthia J. Forehand, Ph.D., Dean of the Graduate College

ABSTRACT

The demand for locally sourced hops from Northeastern microbreweries began the recent resurgence in local hop production. The farming community has increased acreage and improved the quality of hops grown and processed in the Northeast region over the past five years. There was a sharp increase in the number of Northeast hop producers from six in 2009 to over 175 in 2014. Hop growers in the Northeast are new to the crop and have limited experience with pest identification and management. This dissertation encompasses three research projects that were conducted over the 2012-2014 growing seasons. These projects were the first critical steps taken to develop arthropod integrated pest management (IPM) tactics for Northeastern hop growers.

First, the arthropod community in seven Vermont hop yards was evaluated. The objectives of Chapter 2 are to 1) present current hop pest biology and management strategies, 2) report the phenology of arthropod pests observed over three growing seasons, 3) report abundance and peak date for each pest, and 4) document natural enemy abundance in Vermont hop yards. The survey indicates that in cool, wet seasons hop aphid (*Phorodon humuli* Schrank) is expected to be a pest of concern. Two-spotted spider mite (*Tetranychus urticae* Koch) is expected to be a pest of concern in hot, dry conditions. Potato leafhopper (*Empoasca fabae* Harris) is an unpredictable pest of special concern for first year hop plants. When hop aphid or potato leafhopper are sprayed for with broad-spectrum insecticide, two-spotted spider mite secondary outbreak can be expected.

Second, the abundance of major arthropod pests and their natural enemy groups were evaluated under drive row flowering cover crop treatments. The objectives of this study were to 1) measure the effect of cover crops on natural enemy group abundance, 2) measure the effect of cover crops on the three major Northeastern hop pests, and 3) measure the effect of cover crop presence on hop yield and quality. Natural enemy groups and pests were positively correlated yet cover crop treatments had no significant effect on natural enemy abundance. Red clover cover crop treatments served as a trap crop for potato leafhopper. No significant difference in hop yield or quality was observed between flowering cover crop treatments.

Finally, potato leafhopper is a documented but understudied regional pest of hops. The objectives of this study were to 1) measure the physiological response of eight hop cultivars to adult potato leafhopper feeding and 2) measure hop leaf recovery from potato leafhopper injury. Gas exchange (net photosynthesis and transpiration) and chlorophyll content were measured to quantify injury by adult potato leafhopper to first year hop leaves in field and greenhouse studies. Cultivars did not vary significantly in their physiological response to potato leafhopper feeding. Injury significantly reduced gas exchange measures in the field ($P < 0.05$) and greenhouse ($P < 0.05$) and when leafhoppers were removed, gas exchange was restored.

ACKNOWLEDGEMENTS

I extend my sincere thanks to everyone who helped to make this project possible. I would especially like to thank my mentor Dr. Heather Darby for taking me under her constantly flying wing. The research presented here is a portion of the knowledge I gained from working on at least 15 other agronomic projects as a member of Heather's UVM Extension Northwest Crops and Soils Team. My projects would not have been possible without the energy, muscle, and dedication of this team which included Katie Blair, Conner Burke, Savanna Crossman, Julija Cubins, Erica Cummings, Flint Darby-Herman, Hannah H. Doyle, Scott Lewins, Rosalie Madden, Susan Monahan, Julian Post, Rhianna Sommers, Dana Vesty, Emily Whalen, and Sara Ziegler. Thank you to Roger Rainville of Borderview Farm in Alburgh, VT and the University of Vermont greenhouse staff for their participation and endless practicality. As Hannah reminded me many times, "There is no "I" in Ph.D.". There is... but teamwork makes the dream work.

Thank you to the Department of Plant and Soil Science and Dr. Josef Gorres for three years teaching assistantship funding. The comradery of my graduate student cohort was unprecedented. Dr. William O. Lamp from the Entomology Department at the University of Maryland generously shared his entomological expertise and leafhopper colony. Dr. Alison Brody, inspired me to maintain excellence in ecological research. Statistician, Alan Howard deserves applause for the hours that we spent analyzing data.

The research herein would not have been possible without funding from Northeast SARE, the Northeastern IPM Center, and the US EPA. Additional support came from University of Vermont Hatch program. My inspiration for this work and career spurs from the Calderwood-Carlaw family, Dr. Jude Boucher, and Earthwatch Institute.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION

1.1 Integrated Pest Management

Integrated pest management (IPM) is a dynamic and applied science. The term was coined by Van den Bosch and Stern (1962) and continues to evolve today in definition and practice (Baiwa and Kogan 2002). Ecosystem and human health were highlighted as the primary reason to use non-chemical means to manage pests. As the "Green Revolution" progressed into the 1960s and 1970s IPM became a product based practice where a use anything and everything mentality was adopted. Researchers saw IPM as one program with a list from 1-5 that would solve a pest issue, end of story (Baiwa and Kogan 2002). By the 2000s a physical, chemical, and biological systems approach to ecologically based pest management was fostered. Currently a shift is underway on farms and in research from pest control to the management of pest populations using chemical-based pesticides as a last resort. Because farms are ecosystems, we cannot control pests permanently. We can manage their populations below economically damaging levels while reducing the amount of pesticide used.

Sustainable pest management systems are those that implement cultural controls and biological organisms first and consider all pests (insects, disease, and weeds), soil, and the surrounding landscape as parts of the pest management puzzle. Narrow spectrum pesticides can be very effective in IPM when other practical methods in a given IPM toolbox do not maintain pests below an economic injury level (National Research Council 1996). Parts of the US are now approaching pest management in these ways but chemical control remains a dominant "quick fix" in many cropping systems (Lewis et al 1997). In order to maintain arthropod pest populations at

sustainable levels many cultural tools have been developed.

For example, alfalfa strips are used as a trap crop in strawberry production as a more attractive host to the strawberry pest, tarnished plant bug (*Lygus hesperus* Knight). Once the tarnished plant bug population reaches threshold abundance on alfalfa, pests are removed with tractor-mounted vacuums (Swezey et al. 2007). Northeastern berry growers currently struggle to manage the invasive spotted wing drosophila *(Drosophila suzukii* (Matsumura)). Management tools do not exist yet. Using a combination of apple cider vinegar, sugar, and yeast traps the IPM community including farmers and researchers are now able to monitor this exploding pest collaboratively (Gurbinger 2014, Burrack et al. 2012). There is no better IPM example than that of Asian irrigated rice. A combination of scientific and social tactics was implemented to strengthen rice systems to manage pests without pesticides. Biologically, fish were added to irrigation water for fertilization and staggered planting dates were established to maintain natural enemy habitat through harvest. Pesticide use increased resistance development of brown planthopper to resistant rice cultivars. Multi-media Extension outreach and education efforts brought the rice farming community together and pesticide use was reduced from 80% to 20% without yield loss in 1993 (Mattson 2000). The National Research Council cited biological control, cultivar resistance and tolerance, and narrow-spectrum pesticides as the major pest management tools of the next century (National Research Council 1996).

1.2 Top-down and Bottom-up Methods of IPM

Basic ecological theories developed in the 1960s inform our current understanding of trophic interactions. Hairston et al. (1960) suggested that herbivores are not controlled by their food source (plants) but by other trophic level interactions. Ehlrich

and Raven (1964) provided coevolution evidence that plant defense is a critical part of herbivore control. The Washington state rocky intertidal ecosystem provided evidence of food web changes in response to predator removal. When starfish were removed from an intertidal rock, some primary producers were pushed out of the food web resulting in a cascade of ecological changes (Paine 1966).

Top-down pest management is a predator-prey relationship. Predatory and parasitic natural enemy arthropods put "top-down" population pressure on herbivores by killing them. Agricultural pests have fast, overlapping generation times that can reach outbreak population levels without predators or parasitoids in the system (Van Driesche et al. 2008). Providing habitat in modern agriculture systems can provide overwintering sites and supplementary food resources for resident natural enemies. This is considered conservation biological control (Lu et al. 2014). Plants are immobile yet are not neutral bystanders in an agricultural field. Plants are in a constant arms race with arthropod and disease pests which has resulted in a diverse array of plant defenses. These defenses put "bottom-up" pressure on herbivores with complex chemical and physical mechanisms. Cultivar resistance and tolerance are considered bottom-up pest management tools.

1.3 Research Context

The Northeastern states of New York and Vermont produced hops commercially 150 years ago. Vermont production peaked when the state produced 289,690 kg (638,657 lbs) in 1860 (USDA Ag Census 1860). A combination of hop downy mildew (*Pseudoperonospora humuli*) Miyabe and Takah (G. W. Wilson), expanding western production, and prohibition later in the 1920s contributed to the decline of 20th century Northeastern hop industry. The United States ranks second to Germany

as the largest producer of hops in the world. Washington, Oregon and Idaho have the highest American acreage, making the Pacific Northwest the major hop growing region of the USA. (Turner et al. 2011, Almaguer et al. 2014). Over the past 5 years the local food movement has expanded into the beverage market. There are more than 35 breweries in Vermont that have increased the demand for local hops and malt. Northeastern 2013 production of the crop was recognized on a national level in 2014 by USA Hops indicating that there were 10.1 and 60.7 ha reported (25 and 150 ac) of hops in Vermont and New York, respectively (2013 USA Hops Annual Report). Hop yards in the Northeast are considered small scale and range in size from 0.1 to 7.2 ha.

Hops, grown commercially for brewing, are the flowers of female *Humulus lupulus* L. plants. Hop plants are a fast growing perennial bine that produces 5 m of annual growth in height, weighing between 5 and 8 kg when harvested in August - September. Female plants grow up coir strings to the top of a 5-5.5 m trellis system. There are two rhizomes planted per hill. Two strings are stapled into the ground at each hill in the spring and 3-4 bines are trained up each string. Hops are sensitive to photoperiod and are able to grow at latitudes between 25 and 70° (Mahaffee 2009). Shoots emerge in early spring, popping out of the snow in some Northeastern locations. The hop trellis system is designed to maximize vegetative growth before June 21 when day length begins to shorten. After the summer solstice the plants enter their reproductive phase. At this time vertical growth slows and side arm growth is initiated. Hop buds, called burrs, grow on side arms, becoming cones in early August. Plants are productive for approximately 10 years and reach peak production by their third year. Because hop plants grow so quickly they present a copious amount of new growth for phytophagous arthropods (Neve 1991). Hops are plagued by several arthropod and disease pests and are traditionally heavily managed with insecticides (Turner et al. 2011).

The overall goal of the work completed for this dissertation was to provide educational hop pest and natural enemy material for new growers and conduct regionally specific IPM research for hop production in the Northeast. Hop pests and natural enemies in seven Vermont hop yards are documented and described in Chapter 2. This regional perspective provides a necessary baseline of regional hop arthropod communities. In Chapter 3, arthropod abundance under flowering and non-flowering cover crop treatments is measured. This study addresses the presence of top-down pest pressure in a Vermont hop yard. Finally, Chapter 4 dives in more detail into a specific pest, potato leafhopper. Hop leaf gas exchange response to potato leafhopper injury was measured between eight hop cultivars. Research on hop cultivar susceptibility and resistance to potato leafhopper is ongoing and preliminary results are presented in Appendix A.2. There are hop variety trial, downy mildew, and weed control research reports on the UVM Extension Northwest Crops and Soils website.

CHAPTER 2

SURVEY OF NORTHEASTERN HOP PESTS AND THEIR NATURAL ENEMIES

2.1 Introduction

Hops have not been grown commercially in the Northeast for 150 years. Vermont production peaked in 1860 when the state produced 289,690 kg of dried hops (Kennedy 1860). A combination of the spread of hop downy mildew (*Pseudoperonospora humuli*) Miyabe and Takah (G. W. Wilson), the expansion of production in western states, and the passing of prohibition laws later in the 1920s contributed to the decline of 19th century Northeast hop industry. Today, Washington, Oregon and Idaho remain the dominant hop production states of the US. However, hop production in nontraditional regions is growing and now accounts for over 2% of the total acreage (US Hops Association, 2014). Over the past 5 years commercial production of hops has made resurgence in the Northeast and is mainly fueled by the local food movement. In Vermont alone, more than 35 breweries are seeking more local ingredients including but not limited to hops. As acreage increases, regionally specific pest challenges have become apparent and growers are looking for relevant scouting and management strategies.

Integrated pest management (IPM) programs are crop, pest, and region specific. Arthropod communities are a reflection of climate, landscape, and management practices (Schweiger et al. 2005). The Pacific Northwestern states of Washington, Oregon, and Idaho comprise the traditional hop production region of the US. There are clear differences in climate and landscape between the Pacific Northwest and the resurging Northeast. Therefore, it is important that Northeast hop IPM is developed to reflect

regional arthropod community abundance and phenology.

Two-spotted spotted spider mite (*Tetranychus urticae* Koch) (Acari:Tetranychidae) and hop aphid (*Phorodon humuli* (Schrank)) (Hemiptera: Aphididae), have been documented and researched extensively as the economically damaging arthropod pests in the Pacific Northwest and European hop growing regions (James 2003, Mahaffee et al. 2009, Woods et al. 2014). To our knowledge, arthropod communities in hop yards were last reported for the Northeast region in the 1940s when hop production was prevalent within this region. Reports from the Cornell Agricultural Experiment Station document hop aphid, two spotted spider mite, potato leafhopper (*Empoasca fabae* Harris) (Hemiptera: Cicadellidae), and hop downy mildew as major pests in New York hop yards (Magie 1942 and 1944).

In an effort to provide farmers and other relevant stakeholders with current pest management strategies it is important first to identify predominant pests and subsequent natural enemies. The objectives of this publication were to 1) present current hop pest biology and management strategies, 2) report the phenology of arthropod pests observed in Vermont hop yards over three growing seasons (2012-2014), 3) report abundance and peak date for each pest and 4) document natural enemy abundance in Vermont hop yards.

2.2 Biology and Management of Major Northeastern Hop Pests

2.2.1 Two-spotted spider mite (*Tetranychus urticae* Koch)

Two-spotted spider mites overwinter in the crown of hop plants, woody debris, and trellis pole crevasses as diapausing adult females. As soon as temperatures warm in the spring, females emerge, migrate to new growth, feed, and lay up to 16 eggs/day. Five to eight generations of spider mite are observed during the hop growing season

in the Pacific Northwest. Two-spotted spider mites are a mid-late season pest that thrives in hot and dry environmental conditions. Spider mites develop from egg to adult in 7-10 days at 28-30°C (Mahaffee et al. 2009). Two-spotted spider mite development is strongly correlated with temperature (Raworth 1994, Wermelinger et al. 1990). Scouting for spider mites on the underside of leaves is an important practice given the potential for rapid population increase in the right conditions (Jeppson et al. 1975, Weihrauch 2004).

2.2.1.1 Symptoms

Two-spotted spider mites are small, transparent mites. Eggs and nymphs are white to clear in color while adults can appear white to yellow in color with two dark spots on the back (Fig. 2.1). Females are the largest stage of this mite with a length of approximately 0.5 mm. Males are approximately 0.2mm. This pest feeds with piercing sucking mouthparts on leaf and cone mesophyll cells. The first signs of damage are pin-prick sized brown spots called "stippling" (Fig. 2.2). Adults and eggs first develop on the underside of leaves in the space between leaf veins. As the population grows, webbing will appear and brown stippling will expand, eventually turning whole leaves brown in desiccation. Foliar damage reduces plant vigor while spider mite feeding on cones can drastically reduce the marketability of the hop product via desiccation which causes cones to shatter (Mahaffee et al. 2009).

Figure 2.1: Two-spotted spider mite adults, nymphs, and eggs.

Figure 2.2: Characteristic two-spotted spider mite "stippling" damage at a low mite infestation level.

2.2.1.2 Management

Insecticides are the traditional management tactic used to control two-spotted spider mite populations below economically damaging levels in hop production. Spray applications are based on economic thresholds ranging from 1-2 mites/leaf in June and 5-10 mites/leaf in July in Washington State (Strong and Croft 1995) to 60 mites/leaf in German hop yards (Wright and Cone 1999 and Weihrauch 2004). Economically damaging levels of two-spotted spider mite are a repercussion of spraying certain broad spectrum insecticides and fungicides (James 2002, James 2003, Gent et al. 2009, Woods et al. 2012). Two-spotted spider mite is a pest of hops whether broad-spectrum insecticides are sprayed or not. However, economic damage to hop yield and quality from this pest is seen with the application of pesticides aimed at reducing other arthropod pests. For example, spring application of imidicloprid is a successful method of reducing hop aphid populations but natural enemies of hop aphid and two-spotted spider mite are also eliminated. This provides an opportunity for secondary pests (two-spotted spider mite) to reach uncontrollable outbreak levels (James and Price 2002, James 2003). Additionally, James and Price (2002) identified increased female spider mite fecundity when exposed to imidicloprid. Resident natural enemy communities regulate spider mite populations on un-sprayed hops (Huffaker et al. 1969, James et al. 2001, Woods et al. 2014). Due to two-spotted spider mite product resistance, research on spider mite pest management in commercial production is evolving toward the conservation of antagonistic arthropods and narrow spectrum insecticides (James 2003).

Hop cultivars have different susceptibility levels to two-spotted spider mites and high farnesol concentration in leaves has been suggested as a possible mechanism behind their preference (Regev and Cone 1975). Peters and Berry (1980) report

variation in the density of leaf trichomes on different hop cultivars. It was observed that two-spotted spider mite development time was higher on leaves with higher leaf trichome density (Peters and Berry 1980). Ground cover between hop rows weather flowering or not will reduce dusty conditions, favorable for two-spotted spider mite. Flowering vegetation increases moisture and provides shelter and alternative food resources for predators of two-spotted spider mite (Grasswitz and James 2009, Lu et al. 2014). Spider mites can be controlled by an assemblage of natural enemy arthropods, viruses, and pathogens (Jeppson et al. 1975), Stethorus punctum spp. (Coleoptera: Coccinellidae) (James 2003a) and Orius spp. (Hemiptera: Anthocoridae) have been identified as effective predators of this pest commonly found in hop yards (Grasswitz and James 2009).

2.2.2 Damson Hop Aphid (*Phorodon humuli* Schrank)

Cool, wet growing seasons are favorable for the damson-hop aphid. Hop aphid alternates between hop as the summer host and Prunus spp. (Rosales: Prunaceae) as winter hosts. Hop aphids have a holocyclic life cycle where adult, winged females (alate) give birth to live nymphs which develop into wingless (apterous) males and females in addition to alate female reproductive adults. Hop aphids overwinter as eggs on Prunus spp. and adult, wingless females hatch in the spring, laying up to four generations of apterous females and alates. Recently hatched alatae fly from Prunus spp. to hop in early spring when temperatures reach 13°C. Up to ten generations of apterous hop aphid on hop per season are observed in the Pacific Northwest depending on weather conditions and management practices. As photoperiod shortens toward the end of the season, apterous females produce alates which return to Prunus spp. in the fall, lay alate males and females which subsequently lay overwintering eggs (Mahaffee et al. 2009, Wright et al. 2005).

In Spain, peak hop aphid date is typically in mid-July (Lorenzana et al. 2013) while in Washington, USA peak populations are observed in late August and continue into early September (Campbell and Cone 1994). The abundance of alternate Prunus spp. hosts in European landscape have been observed to increase the number of migrant females in the spring in comparison to migrant populations in Washington, USA where there are fewer surrounding Prunus spp. (Campbell and Cone 1994). While foliar feeding can reduce plant productivity at high population levels, hop aphids cause serious economic damage to hop yield and quality when present in cones.

2.2.2.1 Symptoms

These soft bodied, pear shaped insects are found on the underside of hop leaves and range in color from white to light green in color. Hop aphids are often found on the upper and lower leaf surfaces of new hop growth (Fig. 2.3). Hop aphids have piercing sucking mouthparts which are used to feed on the phloem of hop plants. On hop, aphids are smaller than on *Prunus* spp, the summer host plant. Hop aphids secrete a sugary substance commonly referred to as "honeydew" that provides the perfect habitat for sooty mold, an Ascomycete fungi, to grow in hop cones (Wright et al. 2005, Mahaffee et al. 2009, Lorenzana et al. 2010). With high aphid population levels during cone development and at harvest time, fuzzy looking grey-black colored mold can be found when hop cones are pulled apart. This sooty mold is the indirect impact that aphids have on hop quality (Fig. 2.4).

Figure 2.3: Alate hop aphids on new hop growth.

Figure 2.4: Hop cone infested with hop aphids and sooty mold.

2.2.2.2 Management

Hop aphid population ecology and has been studied and economic thresholds have been determined (Campbell 1977, Lorenzana et al. 2009, Wright et al. 2005). In the Pacific Northwest it is recommended to hold off from spraying insecticides against hop aphid until an economic threshold of 8-10 hop aphids per leaf is reached (Lorenzana et al. 2009). An economic threshold specific to the Northeast region for hop aphids does not yet exist. Biological control of hop aphid including parasitoids (Wright and James 2001) and predators (Campbell and Cone 1994) are an effective management tool. Hop aphids are reported to thrive on plant parts highest in nitrogen and in hop yards with higher levels of nitrogen (Gent et al. 2009a). Because hop plants grow quickly and can reach a height of 5m in one growing season (Neve 1991), they are heavy feeders of nitrogen. A nutrient management plan with specific nitrogen applications is recommended to reach optimal yield and quality but also to manage pests at sustainable levels.

Hop cultivars vary in their susceptibility to hop aphid (Campbell 1983, Dorschner and Baird 1988, Weihrauch and Moreth 2005). 'Cascade' is reported as highly susceptible to hop aphid in the Pacific Northwest (Dorschner and Baird 1988). The mechanisms behind the variation in hop aphids by cultivar are likely a combination of plant nutrition and chemical leaf composition. Cultivars with high essential oil content are more attractive to hop aphids. In particular, high levels of cariophyllene and farnesene have been highlighted as attractive essential oils to hop aphids (Kralj et al. 1998).

2.2.3 Potato Leafhopper (*Empoasca fabae* Harris)

Severe injury to hop plants from potato leafhopper feeding has been observed in Vermont. Hop as a host for potato leafhopper has not been reported or studied since the 1940s (Magie 1944) because it is a regional pest and hops have not been grown in Eastern states since the early 1900s. These true bugs have an appetite for more than 200 broad leaf plants (DeLong 1971). Potato leafhopper is a migratory insect, native to the Eastern USA. Adult females can arrive to northern Vermont anytime between May and August making it an unpredictable pest. Adults overwinter in southern states. Spring wind currents carry this species of leafhoppers north. Typically, adult females arrive to Mid-Western states first and Northeastern states last (Sidumo et al. 2005).

Upon arrival, females feed and lay eggs in hop leaf and stem tissue. Potato leafhoppers can develop at temperatures between 10 and 24°C (Simonet and Pienkowski 1980, Sher and Shields 1991). On alfalfa, nymphs hatch between three and ten days after oviposition. Apterous nymphs go through five instars over the course of 10-14 days before finally molting into an alate adult. In another 7-10 days females will begin oviposition (DeLong 1971). On average it takes three weeks for an egg to develop into an adult (Hogg 1985). Depending on spring arrival time and temperature potato leafhoppers will have 2 or 3 generations per season at northern latitudes.

2.2.3.1 Symptoms

Potato leafhoppers are light green, wedge shaped insects. Adults are 3.0 mm in length while first instar nymphs can be 0.5 mm long (Fig 2.5). Damage from this pest is called "hopperburn" and described as "V" shaped leaf chlorosis where the outer edges and tip turn yellow which further develops into brown leaf necrosis

(Fig. 2.6). Potato leafhoppers feed with piercing-sucking mouthparts on or phloem depending on the plant host (DeLong 1971). From observations it appears as though potato leafhopper feeds on hop phloem. Either the leafhopper or the plant immune system restricts phloem flow to the leaf edges resulting in leaf edge yellowing and curling. Visual hopperburn is not present until after significant leafhopper feeding has occurred. Multiple studies suggest that these symptoms are the result of host plant physiological response to potato leafhopper feeding. This response is documented by the reduction in photosynthesis in alfalfa (*Medicago sativa* L.) (Lamp et al. 2007) and grape (*Vitis vinifera* L.) (Lamp et al. 2011, Lenz et al. 2012). An overall decrease in photosynthesis was measured on eight hop cultivars in 2014 (see Chapter 4).

Figure 2.5: Potato leafhopper nymphs of different 1st, 3rd, 4th, and 5th instars on the underside of a hop leaf. Small yellow spots on leaves are lupulin glands, not arthropods.

Figure 2.6: Leaf chlorosis and necrosis damage caused by potato leafhopper feeding called “hopperburn”.

2.2.3.2 Management

Potato leafhopper IPM programs involve monitoring of the population weekly. In alfalfa, sweep netting and sticky traps are used to assess leafhopper populations (Degooyer et al. 1998). In hops, scouting the underside of several leaves from each cultivar is recommended. Potato leafhoppers are visible with the naked eye and have a signature side-to-side scuttling movement. There is evidence that copper sulfate fungicides (Bordeaux mixture), primarily used for hop downy mildew control, were indirectly used to manage potato leafhopper populations in the 1800s (Magie 1944). Copper hydroxide based sprays are currently the most widely used products to manage hop downy mildew in the Northeast. As mentioned above, the impact of fungicides on two-spotted spider mite, hop aphid and natural enemies has been investigated in the Pacific Northwest (James 2002, James 2003, Gent et al. 2009, Woods et al. 2012). The natural enemy assemblage for potato leafhopper is similar to that of hop aphid (Table 1) and spraying for potato leafhopper, another soft-bodied insect, is likely to have similar secondary outbreak repercussions.

Potato leafhoppers are known to be repelled by glandular trichomes produced at different densities on alfalfa (Shockley and Backus 2002), potato (Kaplan et al. 2008) and dry bean (Gonzales et al. 2004) cultivars. Scouting efforts preliminarily indicate that different hop cultivars are more susceptible to potato leafhopper feeding than others. Further research should identify which hop cultivars are more and less susceptible to this emerging pest and explore mechanisms behind cultivar susceptibility.

2.2.4 Hop Downy Mildew (*Pseudoperonospora humuli*) Miyabe and Takah (G. W. Wilson)

Although hop downy mildew incidence was not included in this arthropod survey, the biology and management of this pathogen are of great importance as it rears its head again in Northeastern hop yards. The pathogen has been positively confirmed in numerous yards in NY, MA, and VT by the UVM diagnostic lab and at times by Dr. David Gent of Oregon State University. Hop downy mildew is caused by the oomycete pathogen P. humuli. Spring in the Northeast is often cool and wet providing a perfect habitat for the spread of hop downy mildew. The pathogen overwinters as mycelium in ground leaf litter and on hop crowns (Skotland and Johnson 1983). Research on Eastern downy mildew strains is of particular need. It is unclear weather oospores are an overwintering stage of the disease cycle in Eastern states (Magie 1942, Skotland and Johnson 1983). Given moist conditions in the spring, sporangia are carried by wind and rain containing zoospores, the primary innoculum. Zoospores enter hop leaves through leaf stomata, germinate and produce more sporangia, which release secondary inoculum zoospores that infect additional plants. Hop downy mildew zoospores can arrive to a hop yard via wind currents or in already infected rootstock. The crowns that harbor zoospores and oospores over the winter and give rise to infected shoots in the spring, have systemic downy mildew. These shoots are called primary basal spikes (Fig. 2.8) because they release the first innoculum of the season. When downy mildew is systemic the pathogen lives in the hop yard year round and will continue to spread unless meticulously managed.

2.2.4.1 Symptoms

Early spring (March-May) pale green-yellow shoots with short internodes are primary basal spikes. Secondary inoculum infects already trained bines in late spring forming areal spikes. Both basal and areal spikes have a "Christmas tree" appearance in comparison to healthy hop bines (Figs. 2.8 and 2.9). Chlorotic, stunted bines that fall away from strings are also a symptom of secondary inoculum. Foliar lesions are present on the leaves of both basal and areal spikes. Lesions are sections of leaf cells that form angled brown spots on the underside of leaves (Fig. 2.7). On severely infected spikes, the entire underside of leaves will be covered in brown sporangia producing more zoospores (Mahaffee et al. 2009). This hop specific disease reduces hop moisture content and impacts the appearance of hop cones which directly reduces the quality of hops delivered to brewers. Hop cones infected with downy mildew are prone to early ripening, browning, uneven drying in the oast, a shorter shelf life, and less desirable brewing characteristics, all of which affect the marketability of the product (Mahaffee et al. 2009, Skotland and Johnson 1983). Fungicide sprays can cause spotting on hop leaves called phytotoxicity (Fig. 2.10) in hot and humid weather conditions. Severe fungicide burn can result in plant desiccation. Scouting observations indicate that certain hop cultivars are more susceptible to copper based fungicides than others.

Figure 2.7: Hop downy mildew foliar lesions on the underside of a hop leaf.

Figure 2.8: Hop downy mildew primary basal spike with short internodes, chlorosis, and necrosis.

Figure 2.9: Hop downy mildew areal spike with short internodes and chlorosis.

Figure 2.10: Phytotoxicity from application of copper-based fungicide. Cultivars vary in their susceptibility and symptoms are most severe at high humidity and temperature.

2.2.4.2 Management

It is difficult to reduce disease in an already infested hop yard. A combination of resistant cultivars, hop yard sanitation, and fungicides are used to reduce infestation levels of hop downy mildew. No hop cultivar is currently 100% resistant. When the more susceptible cultivars contract the disease the resistant cultivars are exposed and remain subject to economic losses from reduced yield and cone quality. The most resistant cultivars include Fuggle, Newport, Perle, Spalter, Wye Challenger, Hallertauer Gold, Hallertauer Magnum and Hallertauer Tradition (Gent et al. 2009b).

"Crowning" or spring pruning is an important spring management practice where late winter or early spring crown growth is mechanically or chemically removed. In the Pacific Northwest, Gent et al. (2012) provides evidence for the reduction in hop downy mildew infection. Hop yards that were pruned twice showed the lowest disease severity and growers were able to apply one fewer fungicide application. Crowning date and number influenced yield of 'Willamette' in this study (Gent et al. 2012). Research is needed on the impact of crowning on harvest date and yield for the shorter growing season of the Northeast region. Later maturing cultivars in Europe have reduced yield when cut back at later dates (Goenia and Micibski 1972). After crowning, scouting for basal spikes should take place. If basal spikes are present they should be removed from the hop yard immediately. Sanitation of hop yard clippers and pruning tools is a critical and easy way to reduce the risk of disease spread (Skotland and Johnson 1983, Gent et al. 2012).

Pruning must be paired with fungicide applications for hop downy mildew management (Hunger and Horner 1982, Mahaffee et al. 2009). A variety of products and application times are currently exercised in Northeastern hop yards in hopes of controlling this disease. According to our 2014 pesticide survey, which included grower

responses from Vermont, New York, and Massachusetts, the most commonly sprayed fungicides are copper based. A mean of four fungicide applications are sprayed per season with some farms 12 applications of a copper-based fungicide per season. In Europe, 10-16 fungicide applications are common practice. It is clear from research in Washington and Oregon that making the timing of fungicide sprays more precise can reduce the number of fungicide applications per season. Using a forecasting system to calculate emergence of the first systemically infected spikes of downy mildew reduced the amount of fungicide sprayed in the Pacific Northwest without increasing disease severity (Gent et al. 2010).

Powdery mildew is a second disease of economic importance in other growing regions of the world but has not been reported yet in the Northeast region. We would be remised not to mention that weeds are another major pest that requires management in Northeast hop yards.

2.3 Natural Enemy Arthropods of Importance

An assemblage of generalist and specialist natural enemy arthropods reduce pest abundance in hop yards (Campbell and Cone 1994, James 2003a, James 2003b, Gardiner et al. 2003, Gent et al. 2009, Grasswitz and James 2009, Grasswitz and James 2011, Woods et al. 2014).

2.3.1 Parasitoid Wasps

Parasitic hymenopterans are very small wasps abundant in diverse agricultural landscapes. These fast and minute insects are rarely seen in the field with the naked eye. Therefore visual scouting is not a parasitoid wasp monitoring technique. Several species are known parasitoids of potato leafhopper and hop aphid and their presence

in hop yards has been documented (Grasswitz and James 2009, Wright and James 2001). *Anagrus* spp. are particularly known for their parasitism of potato leafhopper eggs (Lovinger et al. 2000) while a suite of additional parasitoid species play a role in field pest biocontrol. Assemblages of several parasitoid species have been shown to keep field crop aphid populations in check (Sigsgaard 2002). The magnitude of parasitoids as biological control agents in hops has not been studied (Grasswitz and James 2009). However, Wright and James (2001) reared 802 parasitoids from 83 hop aphids collected on *Prunus* spp. (alternative hop aphid host) in Washington state. The most abundant species reared was *Lysiphlebus testaceipes* (Cresson). Grasswitz and James (2011) identified nine generalist parasitoid species in Pacific Northwest hop yards when assessing parasitism on hop looper (*Hypena humuli* Harris), a minor Lepidopteran pest of hops. The parasitoids found in this study were not *H. humuli* specialists indicating that there are parasitoids in hop yards with a range of hosts.

Communities of generalist predators can be a major player in pest control in agricultural landscapes (Symondson et al. 2002). The following generalist predator natural enemies are members of naturally occurring arthropod communities.

2.3.2 Spiders and Predatory Mites

There are over 30,000 species of spider. This diverse group of arthropods primarily feeds on other insects making them excellent members of predatory guilds (Riechert and Lockley 1984). A diversity of these generalist predators, are present in healthy agricultural ecosystems. In alfalfa, spiders are highlighted predators of potato leafhopper (Harwood and Obrycki 2007). Predatory mites (Acari: Phytoseiidae) including *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus californicus* McGregor, *Neoseiulus fallacis* Garman, *Amblyseius andersoni* (Chant), *Galendromus occidentalis* Nesbitt have controlled two-spotted spider mite populations in Pacific Northwest (James 2002

and James et al. 2003) and UK (Barber et al. 2003) hop yard field studies. In general, spiders can be seen with the naked eye. Predatory mites are also visible but their minute size and ability to move very quickly makes them difficult to document in the field.

2.3.3 Predatory True Bugs

In the Anthocoridae family of true bugs (Hemiptera), the *Orius* genus is reported as an effective generalist predator of hop aphids (Lorenzana et al. 2010). According to studies in alfalfa, minute pirate bugs are effective predators of potato leafhopper (Wieser Erlandson and Obrycki 2010). Damsel bugs (Nabidae: Hemiptera) and big eyed bugs (Geocoridae: Hemiptera) are present in Pacific Northwest hop yards (Grasswitz and James 2011) and are observed occasionally in Northeastern hop yards.

2.3.4 Lacewings

Green lacewings are effective consumers of soft bodied insects in Pacific Northwest hop yards (James 2006, Lorenzana et al. 2013). James (2006) demonstrated that the goldeneyed lacewing (*Chrysopa aculata* Say) populations were increased with the placement of methyl salicylate baited sticky cards. Lacewing larvae were observed to feed on four potato leafhoppers per day at high pest densities under lab conditions (Weiser Erlandson and Obrycki 2010).

2.3.5 Lady Beetles

The Coccinellidae family of beetles includes many generalist predators. *Hippodamia convergens* Guérin-Méneville, *Harmonia axyridis* Pallas, and the native *Coleomegilla maculata* De Geer are just three predatory lady beetle species found in hop yards (James 2003a, Campbell and Cone 1994). Lady beetles are well known for their con-

sumption of soft bodied arthropod pests and certain species are mass reared for release in some farm landscapes. Lady beetle larvae have a voracious appetite for aphids and will consume more individual pests than the adult life stage (Koch 2003). *H. axyridis* has been reported to feed on two-spotted spider mites and hop aphids in hop yards (James 2003b). *C. maculata* are specifically reported to feed on potato leafhoppers in alfalfa systems. The Western *Stethorus punctum picipes* (Casey), commonly known as the spider mite destroyer is a small lady beetle that feeds on spider mites (James 2003a). *Stethorus punctum punctum* (LeConte) is the spider mite destroyer of the Eastern USA and is conserved for biological control in apple production (Felland and Hull 1996).

Table 2.1: Natural enemy groups that predate or parasitize the three major Northeastern hop arthropod pests. Pests are listed as species while natural enemy groups are listed with a common name and scientific taxon.

Pest	Natural Enemy Common Name	Natural Enemy Taxon
Tetranychus urticae	Predatory mites	Phytosiidae
	Spider mite destroyer	*Stethorus punctum* spp.
	Minute pirate bugs	Anthocoridae
Phorodon humuli	Minute pirate, big eyed, and damsel bugs	Anthocoridae, Geocoridae, Nabidae
	Green & brown lacewings	Chrysopidae & Hemerobiidae
	Lady beetles	Coccinellidae
	Parasitoid wasps	Parasitica
	Syrphid flies	Syrphidae
Empoasca fabae	Minute pirate, big eyed, and damsel bugs	Anthocoridae, Geocoridae, Nabidae
	Green & brown lacewings	Chrysopidae & Hemerobiidae
	Lady beetles	Coccinellidae
	Parasitoid wasps	Parasitica
	Spiders	Spiders

2.4 Arthropod Scouting Methodology

Seven hop yards in Vermont were scouted every other week June-August for three years (2012-2014). In 2012 there were very few hop yards in Vermont and those chosen for this survey were those with growers willing to participate. Hop yards varied in acreage, cultivar diversity, and management practices. As more farmers started growing hops and we were able to expand our reach, the number of hop yards sampled increased as the survey continued. (Table 2.2).

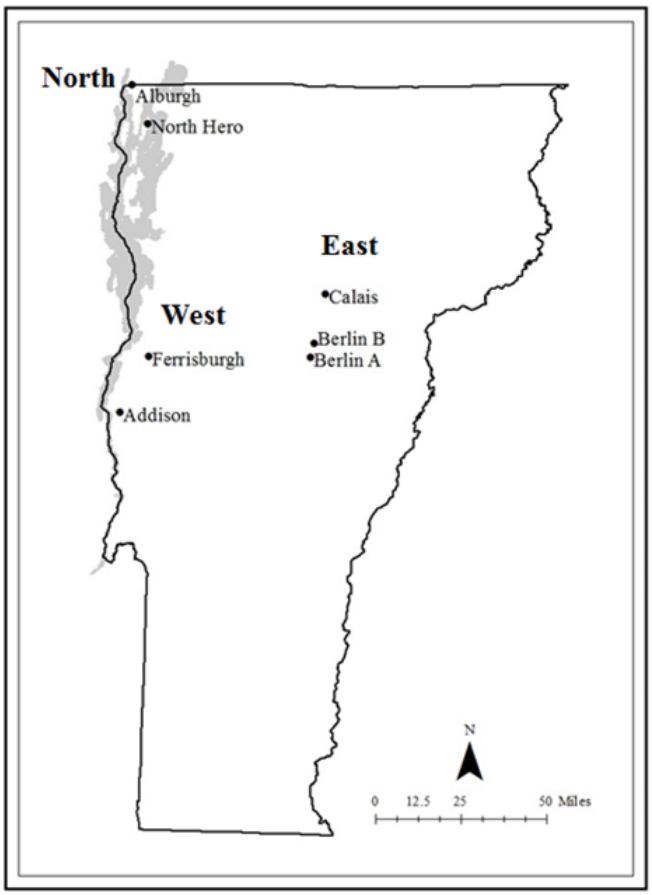

Figure 2.11: Hop yard scouting sites in Vermont. The "North" micro region includes Alburgh and North Hero yards, "West" includes Addison and Ferrisburgh yards, and "East" includes Calais, Berlin A, and Berlin B yards.

Table 2.2: Hop yards scouted in Vermont. Small yards had <60 hills, medium farms had 60-200 hills, and large yards had >200 hills. "Certified Organic" yards were certified organic, “Organic Practice” yards were not certified but use organically certified management while "Non-organic" yards practiced a range of management tactics.

Farm	Years Scouted	# Cultivars	Farm Size	Micro Region	Management
Addison	2012, 2013, 2014	7	Large	West	Certified Organic
Alburgh	2012, 2013, 2014	24	Large	North	Certified Organic
Berlin A	2012, 2013, 2014	3	Medium	East	Non-organic
Calais	2013, 2014	1	Small	East	Organic Practice
North Hero	2013, 2014	4	Small	North	Organic Practice
Berlin B	2014	5	Medium	East	Non-organic
Ferrisburgh	2014	5	Large	West	Non-organic

Scouting took place every other week for a total of 6 collection dates at each location annually. A group of five to seven plants was considered a plot. Three leaves on one plant per plot were sampled during each visit between ground level and 2m above ground. Both top and bottom leaf surfaces were visually examined with optivisor lenses (Donegan Optical Company Inc., Lenexa, KS). Arthropods were identified and counted in the field. Pests were identified to species level while natural enemies were identified to the level at which an ecological role could be assigned (Table 1). Parasitoid wasps and predatory mites are not reported due to the visual, disruptive sampling method used. Statistical comparisons were not presented because it was the goal to show community variation by location and management practices. The data presented are a representation of the arthropod community found in Northeastern hop yards. Season sums were calculated for each arthropod taxon. Pest peak date mean was also calculated. Pest : natural enemy (P:NE) ratios were calculated by dividing pest season sum by natural enemy group season sum.

Beyond farm location, variables impacting arthropod presence including farm size, management practice, and microclimate region were assigned to each farm. Small, medium, or large size was assigned to each farm. Small yards had $<$60 hills ($<$120 plants), medium yards had 60-200 hills (120-400 plants), and large yards had $>$200 hills ($>$ 400 plants). "Organic" yards had an organic certification while "Non-organic" yards practiced a range of management tactics between organic and conventional and were not certified organic. The “North” micro region included Alburgh and North Hero farms, “West” included Addison and Ferrisburgh farms, and “East” includes Calais, Berlin A, and Berlin B farms.

Cumulative degree days (DD) were calculated from March, 1 – August, 31 for each microclimate region using the Cornell Network for Environmental and Weather

Applications (NEWA) database for each year of the study. The Chazy, NY (grower) weather station was used for "North" farms, the Shoreham, VT station was used for "West" farms, and the Calais, VT station was used for "East" farms. Base temperatures of 10°C, 13°C, and 10°C were used for two-spotted spider mites, hop aphid, and potato leafhopper respectively. Two-spotted spider mite and hop aphid base temperatures were chosen based on Mahaffee et al. (2009) and Lorenzana et al. (2013). Potato leafhopper base temperature was the lower development threshold for adult female oviposition (Sher and Shields 1991). Migration date influences potato leafhopper populations in the Northeast. The DDs reported for potato leafhopper were calculated for development after arrival in Vermont.

2.5 Scouting Results

Larger yards have a higher total number of pest and natural enemy individuals. However, there were hot spots of pests present on small and medium sized yards. With higher numbers of pests, the natural enemy community increased in abundance. Aphid and potato leafhopper natural enemy assemblages were similarly composed of generalist predators. The "East" micro region had fewer growing degree-days each year of this study at both 10°C and 13°C base temperatures. Calais and Berlin are mountain locations having elevations of 338 m and 268 m, respectively. Alburgh, North Hero, Addison, and Ferrisburgh are at elevations between 27 m and 32 m along Lake Champlain. Calais and Berlin yards had lower pest levels yet they are also small and medium sized yards.

Table 2.3: Monthly and total Alburgh, VT rainfall (cm) in 2012, 2013, and 2014.

	Alburgh Rainfall (cm)				
Year	May	June	July	August	Season Total
2012	1.1	-1.2	-0.9	-2.5	-3.5
2013	12.2	23.4	4.8	6.1	46.5
2014	12.4	15.5	13.1	10.1	51.1

Table 2.4: Growing degree days at 10°C and 13°C base temperatures.

			Cumulative DD	
Year	Farm	Micro Region	10°C[a]	13°C[b]
2012	Alburgh	North	2720	2061
	Addison	West	2259	1601
	Berlin A	East	1854	1246
2013	Alburgh	North	1976	1375
	North Hero	North	1976	1375
	Addison	West	2154	1547
	Calais	East	1740	1547
	Berlin A	East	1740	1547
2014	Alburgh	North	1878	1288
	North Hero	North	1878	1288
	Addison	West	2027	1417
	Ferrisburgh	West	2027	1417
	Calais	East	1599	1031
	Berlin A	East	1599	1031
	Berlin B	East	1599	1031

[a]Two-spotted spider mite and potato leafhopper base temperature was 10°C.
[b]Hop aphid base temperature was 13°C.

2.5.1 Two-spotted Spider Mite

Two-spotted spider mite populations were highest in 2012 and 2014. In 2012 the spider mite peak date was in early August in all locations. The number of spider mite generations cannot be concluded form these data but there is an overall late season population increase in all hop yards. North and West locations had a similar early August peak date in 2014 while Eastern locations exhibited two-spotted spider mite peaks in late August (Table 2.5 and Fig. 2.3). Peak dates in Table 6 indicate that spider mite destroyer populations mirrored or lagged behind two-spotted spider mite populations. This pattern was especially clear on large yards and in years with high two-spotted spider mite populations (Table 2.6). In Addison, the decreased ratio of two-spotted spider mites to spider mite destroyers from 2012 to 2014 indicates that this predator population can become established. Without considering other yard variables, spider mite destroyers appear to have reduced the 2014 two-spotted spider mite population in that location (Table 2.6). Addison, being a large yard, had fewer two-spotted spider mites than Berlin B, a medium sized yard. Ferrisburgh had the highest total number of two-spotted spider mites in 2014 with a very high P:NE ratio (Table 2.6) showing low natural enemy abundance in this large yard.

Table 2.5: Two-spotted spider mite season sum, peak date, and peak date mean (± SEM) by year and farm. Small yards had <60 hills, medium farms had 60-200 hills, and large yards had >200 hills.

Major Pest						
Two-spotted spider mite	Farm	Farm Size	Micro Region	Season Sum	Peak Date	Peak Date Mean
2012	Alburgh	Large	North	3207	8-Aug	27.32 (± 4.38)
	Addison	Large	West	809	6-Aug	0.70 (± .17)
	Berlin A	Medium	East	4	7-Aug	0.13 (± .13)
2013	Alburgh	Large	North	145	12-Aug	2.00 (± .34)
	North Hero	Small	North	0	N/A	0.00
	Addison	Large	West	172	15-Jul	0.91 (± .23)
	Calais	Small	East	0	N/A	0.00
	Berlin A	Medium	East	0	N/A	0.00
2014	Alburgh	Large	North	3206	4-Aug	14.58 (± 1.82)
	North Hero	Small	North	209	21-Jul	7.50 (± 3.85)
	Addison	Large	West	623	6-Aug	4.77 (± .90)
	Ferrisburgh	Large	West	3609	6-Aug	38.39 (± 4.34)
	Calais	Small	East	2	25-Jul	0.25 (± .25)
	Berlin A	Medium	East	63	22-Aug	1.80 (± .69)
	Berlin B	Medium	East	1046	22-Aug	24.38 (± 4.50)

Table 2.6: Spider mite destroyer adult and larvae season sums and peak date with two-spotted spider mite sums and peak dates reported for comparison. Small farms have <60 hills, medium farms have 60-200 hills, and large farms have >200 hills. Pest (P) to natural enemy (NE) ratio is listed. Two-spotted spider mite and spider mite destroyer season sums were used to calculate Pest (P) to natural enemy (NE) ratio.

		Spider mite destroyers		**Two-spotted spider mites**		
Year	Farm	Season Sum	Peak date	Season Sum	Peak Date	P:NE Ratio
2012	Alburgh	121	8-Aug	3207	8-Aug	27:1
	Addison	21	24-Jul	809	6-Aug	39:1
	Berlin A	1	24-Jul	4	7-Aug	4:1
2013	Alburgh	2	24-Jul	145	12-Aug	73:1
	North Hero	0	N/A	0	N/A	N/A
	Addison	28	15-Jul, 29-Jul	172	15-Jul	6:1
	Calais	0	N/A	0	N/A	N/A
	Berlin A	2	N/A	0	N/A	N/A
2014	Alburgh	163	11-Aug	3206	4-Aug	20:1
	North Hero	35	18-Aug	209	21-Jul	6:1
	Addison	52	6-Aug	623	6-Aug	12:1
	Ferrisburgh	36	6-Aug	3609	6-Aug	100:1
	Calais	0	N/A	2	25-Jul	N/A
	Berlin A	0	N/A	63	22-Aug	N/A
	Berlin B	0	N/A	1046	22-Aug	N/A

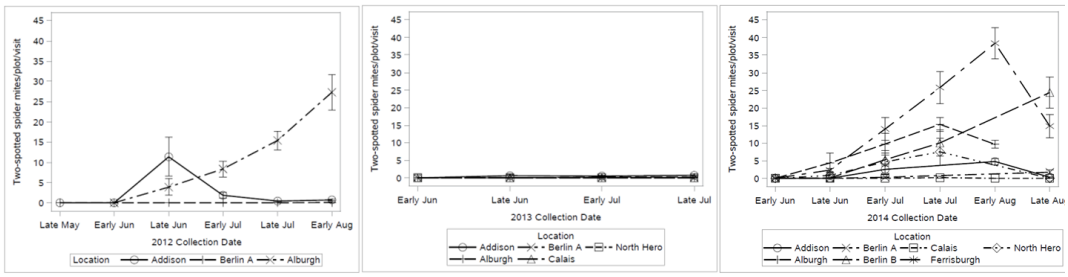

Figure 2.12: Mean number of two-spotted spider mites counted per plot, per hop yard visit in 2012, 2013, and 2014, respectively. Three farms were scouted in 2012, five in 2013, and seven in 2014.

2.5.2 Hop Aphid

Hop aphid populations were highest in 2014 (Fig. 2.7). The wet spring in 2013 and continued precipitation throughout 2014 allowed hop aphids to flourish (Table 2.4 and 2.7). Two hop aphid cycles were observed in 2014. The number of generations was inconclusive. In years of high population levels, hop aphid peak date ranged from early to late August depending on geographic location. As expected, locations with high total pest numbers had the highest peak date means. P:NE ratios were highest in locations and years with high hop aphid populations indicating there could be increased natural enemy presence to aid in pest population management. Similar to two-spotted spider mites, a natural enemy trend was observed. Where predators became established there were lower hop aphid season sums. Specifically in Alburgh, the hop aphid population almost doubled from 2013 to 2014. A higher hop aphid natural enemy population in 2014 decreased the P:NE ratio from 2013 to 2014. In both 2013 and 2014, Addison had the lowest P:NE ratio given relatively high aphid populations. In contrast, Ferrisburgh had the highest hop aphid population of all yards with a high P:NE ratio indicating low natural enemy abundance in this location (Table 2.7). Again, it is difficult to compare hop aphid to potato leafhopper control by natural enemies because these assemblages are very similar (Table 2.1). Although spiders are not included in the hop aphid natural enemy assemblage, it is possible that these generalist predators feed on hop aphids when there is a lack of other prey. Alburgh had the highest spider count of all locations in 2012 and 2014 when the highest number of aphids was observed.

Table 2.7: Hop aphid season sum, peak date, and peak date mean (± SEM) by year and farm. Small yards had <60 hills, medium farms had 60-200 hills, and large yards had >200 hills. Hop aphid and total natural enemy season sums were used to calculate Pest (P) to natural enemy (NE) ratio.

Major Pest							
Hop aphid	Farm	Farm Size	Micro Region	Season Sum	Peak Date	Peak Date Mean	P:NE Ratio
2012	Alburgh	Large	North	172	25-Jul	1.22 (± .55)	1:1
	Addison	Large	West	984	24-Jul	3.18 (± .74)	7:1
	Berlin A	Medium	East	224	7-Aug	3.86 (± .95)	5:1
2013	Alburgh	Large	North	1562	12-Aug	12.93 (± 1.60)	112:1
	North Hero	Small	North	204	9-Jul	5.35 (± 1.73)	26:1
	Addison	Large	West	522	29-Jul	3.00 (± .54)	7:1
	Calais	Small	East	93	6-Aug	5.88 (± 2.13)	N/A
	Berlin A	Medium	East	97	6-Aug	0.80 (± .28)	7:1
2014	Alburgh	Large	North	2864	4-Aug	16.93 (± 3.20)	286:1
	North Hero	Small	North	201	18-Aug	5.81 (± 2.30)	13:1
	Addison	Large	West	1080	27-Aug	7.96 (± 1.51)	29:1
	Ferrisburgh	Large	West	3708	6-Aug	40.53 (± 5.06)	73:1
	Calais	Small	East	365	24-Aug	20.25 (± 3.39)	20:1
	Berlin A	Medium	East	149	22-Aug	4.27 (± .74)	21:1
	Berlin B	Medium	East	1131	22-Aug	30.04 (± 8.50)	63:1

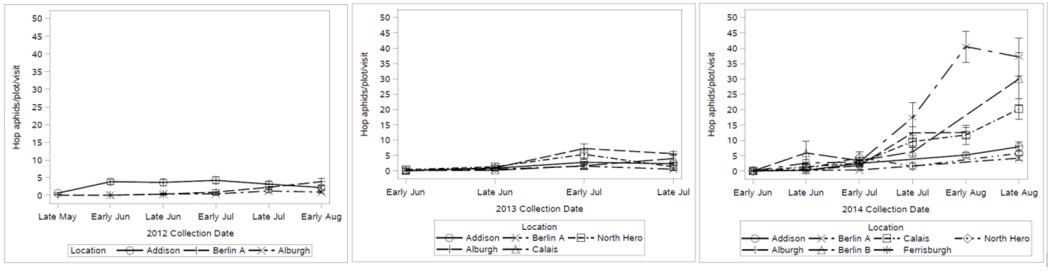

Figure 2.13: Mean number of hop aphids counted per plot, per hop yard visit in 2012, 2013, and 2014, respectively. Three farms were scouted in 2012, five in 2013, and seven in 2014.

2.5.3 Potato Leafhopper

Potato leafhopper populations were highest in 2012 and 2013 across all locations with peak dates in late June and early July. Two generations of potato leafhopper were observed in 2012 and 2013 on multiple farms. This migratory pest arrived late to the Northeast in 2014. A low, later population was therefore observed in 2014 with peak dates throughout July. Eastern sites had very few potato leafhoppers in the 2014 season. Addison was the location with the highest potato leafhopper pressure yet it is also the location with the highest natural enemy abundance. Medium sized Berlin A, had almost the name number of potato leafhoppers as Addison in 2012 with natural enemy presence. In 2013, Berlin A potato leafhopper pest abundance and P:NE ratio dropped indicating natural enemy impact. Potato leafhopper population numbers are less variable by location or farm size than hop aphids or two-spotted spider mites. Because spiders were an abundant natural enemy in all locations, P:NE ratios were low in comparison to hop aphid P:NE values. This indicates that there is an effective generalist natural enemy assemblage for potato leafhoppers. Potato leafhopper was typically an early season pest, attacking new hop growth. This unpredictable pest could potentially arrive before natural enemy population levels are strong.

Table 2.8: Potato leafhopper season sums, peak dates, and peak date means (± SEM) by year and farm. Small yards had <60 hills, medium farms had 60-200 hills, and large yards had >200 hills. Potato leafhopper and total natural enemy season sums were used to calculate Pest (P) to natural enemy (NE) ratio.

Major Pest							
Potato leafhopper	Farm	Farm Size	Micro Region	Season Sum	Peak Date	Peak Date Mean	P:NE Ratio
2012	Alburgh	Large	North	730	29-Jun	6.01 (± .60)	4:1
	Addison	Large	West	588	28-Jun	6.50 (± .97)	3:1
	Berlin A	Medium	East	573	30-Jun	14.70 (± 1.33)	11:1
2013	Alburgh	Large	North	349	24-Jun	3.11 (± .65)	27:1
	North Hero	Small	North	291	24-Jun	6.75 (± 1.73)	12:1
	Addison	Large	West	945	18-Jun	5.65 (± .79)	9:1
	Calais	Small	East	69	9-Jul	4.38 (± 1.44)	6:1
	Berlin A	Medium	East	284	9-Jul	5.67 (± .84)	7:1
2014	Alburgh	Large	North	113	8-Jul	0.59 (± .14)	2:1
	North Hero	Small	North	34	21-Jul	1.12 (± .34)	1:1
	Addison	Large	West	183	11-Jul	0.83 (± .17)	3:1
	Ferrisburgh	Large	West	62	9-Jul	0.65 (± .18)	1:1
	Calais	Small	East	3	25-Jul	0.38 (± .26)	N/A
	Berlin A	Medium	East	6	11-Jul	0.17 (± .10)	N/A
	Berlin B	Medium	East	19	25-Jul	0.33 (± .12)	1:1

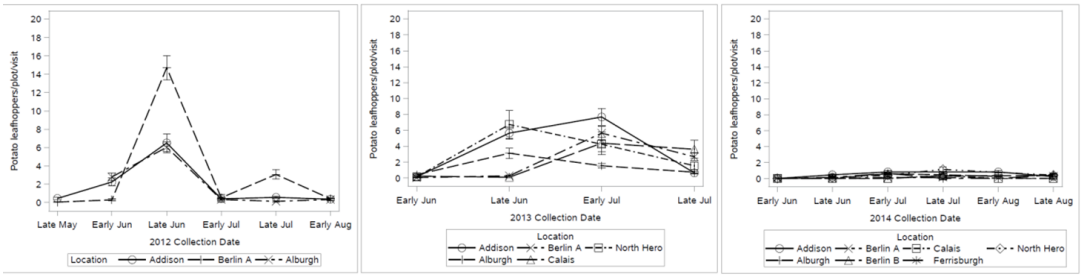

Figure 2.14: Mean number of potato leafhoppers counted per plot, per hop yard visit in 2012, 2013, and 2014, respectively. Three farms were scouted in 2012, five in 2013, and seven in 2014.

2.5.4 Minor Pests

Eastern comma adults and larva were abundant only in 2012 and have not been reported as a problem since. Japanese beetles were reported as a problem on hops in Southern parts of the Northeast region. Low numbers of this pest were observed in 2012. A Japanese beetle hot spot was observed at the Berlin A location in late July through early August of 2013. Hop looper was spotted on all scouted hop yards during at least one year of the survey at low abundance (Table 2.9). The foliar chewing damage that Japanese beetle and Eastern comma larvae incur to hop plants is visually shocking. However, because Japanese beetles are foliar feeders and become a problem in late July or early August, their damage is unlikely to reduce hop yield.

Table 2.9: Eastern comma adult and larvae, hop looper larvae, and Japanese beetle adult season sums. Small yards had <60 hills, medium farms had 60-200 hills, and large yards had >200 hills.

Minor Pests				Season Sum		
	Farm	Farm Size	Micro Region	Eastern comma	Hop looper	Japanese beetle
2012	Alburgh	Large	North	55	7	1
	Addison	Large	West	321	7	5
	Berlin A	Medium	East	100	3	4
2013	Alburgh	Large	North	5	1	1
	North Hero	Small	North	0	0	1
	Addison	Large	West	0	2	7
	Calais	Small	East	0	2	0
	Berlin A	Medium	East	1	7	93
2014	Alburgh	Large	North	0	10	1
	North Hero	Small	North	0	5	0
	Addison	Large	West	0	8	0
	Ferrisburgh	Large	West	0	7	0
	Calais	Small	East	0	5	0
	Berlin A	Medium	East	0	7	0
	Berlin B	Medium	East	0	12	0

Figure 2.15: Eastern comma larva, a minor hop pest.

Figure 2.16: Japanese beetle adults and defoliation. This is a minor pest in Northern hop yards yet a more serious pest in Southern locations.

2.5.5 Generalist Predators

Due to the highly disturbing scouting method used in this survey parasitoid wasps were not recorded and the magnitude of generalist predators was not represented. Chapter 3 contains more in depth documentation of these natural enemy groups. Across all farms lady beetles and spiders were the most abundant generalist predators with a total of 394 and 366 individuals respectively. Lacewings were the next most abundant natural enemy group with a total of 156 individuals followed by syrphid flies with 24 individuals and finally minute pirate bugs with 2 individuals. As expected large farms have the highest natural enemy abundance. However, over the course of three years the smaller North Hero and Calais farms exhibit an increase in the number of total generalist predators. Hop yards that were sampled all three years (Alburgh, Addison, and Berlin A) had the highest generalist natural enemy abundance in 2012 with a total of 390 individuals. In 2013 and 2014 these hop yards had a total of 180 and 162 generalist natural enemies respectively (Table 2.10). The generalist natural enemy populations coincide with high pest abundance in 2012. Hop aphids and potato leafhoppers totaled 2,201 in 2012, 1680 in 2013, and 356 in 2014 in the yards scouted for three years.

Table 2.10: Lady beetle (Coccinellidae) adults and larva, spiders, lacewing (Chrysopidae and Hemerobiidae) adult and larva, syrphid fly (Syrphidae) adults, and minute pirate bug (*Orius* spp.) adults season sums by farm and year. The total number of natural enemies excluding spider mite destroyers is listed. Small yards had <60 hills, medium farms had 60-200 hills, and large yards had >200 hills.

Generalist Predators				Season Sum					
	Farm	Farm Size	Micro Region	Lady beetles	Spiders	Lacewings	Syrphid flies	Minute pirate bugs	NE Total
2012	Alburgh	Large	North	56	39	70	0	0	165
	Addison	Large	West	109	32	31	2	0	174
	Berlin A	Medium	East	33	9	9	0	0	51
2013	Alburgh	Large	North	4	6	3	7	0	20
	North Hero	Small	North	3	17	5	0	0	25
	Addison	Large	West	45	43	17	11	1	117
	Calais	Small	East	0	12	0	0	0	12
	Berlin A	Medium	East	5	29	8	1	0	43
2014	Alburgh	Large	North	8	56	1	0	1	66
	North Hero	Small	North	15	23	0	0	0	38
	Addison	Large	West	34	26	3	0	0	63
	Ferrisburgh	Large	West	41	28	7	3	0	79
	Calais	Small	East	18	9	0	0	0	27
	Berlin A	Medium	East	6	26	1	0	0	33
	Berlin B	Medium	East	17	11	1	0	0	29

2.5.6 Specific Farm Factors

While the season sums and graphical phenology of pest sums and peak date means by location are informative, the effects of cultivar genetic variation, specific management practices, surrounding habitat, previous crop, and hop yard age on pest and natural enemy populations were not accounted for in this survey. There are specific management practices that we believe to have influenced certain pest populations. Alburgh exhibited almost the same total number of spider mites in 2012 and 2014. Pyganic, a pyrethrin broad-spectrum insecticide, was sprayed multiple times at this location for management of potato leafhopper in 2012. This likely caused the late season secondary outbreak of two spotted spider mites at this site (Figure 2.2). Hop quality and yield were negatively affected by this outbreak in 2012. Insecticides have not been applied in the Alburgh hop yard since. The same total number of spider mites in 2014 did not have an impact on hop quality or yield in the unsprayed yard.

2.6 Moving Forward

The patterns observed in this survey are the first published documentation of Northeastern pests and natural enemies since the 1940s. We consider the hop arthropod pests of concern in the Northeast to be two-spotted spider mite, hop aphid and potato leafhopper. We observed similar pest phenology to other hop growing regions for two-spotted spider mites and hop aphids. As documented in the 1940s potato leafhopper is a pest of hop in the Northeast region (Magie 1944).

Arthropod communities are known to change based on climate, landscape, and management practices (Schweiger et al. 2005). Microclimate and hop yard size factors reported here observationally influence pest abundance. As expected, where high pest populations were observed, natural enemies were more abundant. Habitat diversity and surrounding landscape, not reported, are well known variables that increase natural enemy presence (Landis et al. 2000 and Rusch et al. 2010).

Hop yield comes from the top third of plants. Although logistically challenging, we suggest that mid and late season pest monitoring could be improved by sampling the high canopy. Un-baited sticky traps can be used to monitor flying pests and natural enemies. For growers to stay in touch with arthropod populations visual inspection of the underside of leaves should continue as weekly scouting. Because optivisor sampling was the only scouting method used to collect arthropod counts in this survey, flying insects are not completely represented. Parasitoid wasps, not recorded in this survey, are an important and numerous member of hop aphid and potato leafhopper natural enemy assemblages.

Weather was an indicator of pest abundance in Northeastern hops. In a dry, hot year we expect to see high two-spotted spider mite populations yet with cooler temperatures and early or continued precipitation we expect to see high aphid populations

throughout August. Potato leafhopper population prediction will rely on southern reports of presence on other crops, such as alfalfa, that are routinely monitored.

Use of economic threshold levels and insecticides have not been developed for these pests in the Northeast. When making pest control decisions, Eastern Extension professionals reference Pacific Northwest and European economic threshold ranges for two spotted spider mites (10-100 mites/leaf) (Wright and Cone 1999, Weihrauch 2004) and hop aphid (5-70 aphids/leaf) (Lorenzana et al. 2009). The literature suggests that thresholds for these pests vary considerably both locally and regionally (Lorenzana et al. 2009 and Weihrauch 2004). The research hopyard in Alburgh, VT has not exceeded a yard mean of 60 two-spotted spider mites/leaf or a yard mean of 10 hop aphids/leaf during peak pest abundance. These levels have however been reached in pockets of the Alburgh hop yard.

This survey provided evidenced that natural enemies and insecticide applications impact pest populations. Natural enemies were present to varying degrees in Northeast hop yards and once established they appeared to maintain pest populations. This was particularly clear in the Addison hop yard. Insecticides have the opposite effect as they kill natural enemies and increase the risk of a two-spotted spider mite outbreak. This was observed in Alburgh (2012) and Ferrisburgh (2014) yards.

Multiple realms of Northeastern hop IPM require further research. Based on this survey, economic thresholds and region specific IPM tactics should be developed. Among the most pressing issues are potato leafhopper, hop downy mildew, and weed management. In the Alburgh yard a range of cultivar susceptibility to potato leafhopper has been observed. Although some research on natural enemy populations in hop yards has been conducted in commercial growing regions, conservation and augmentative biological control research is warranted for the sustainability of hop production. This survey was the first step toward developing appropriate IPM tactics for mod-

ern day Northeastern hop production. Grower pest management decisions should be based not only on the pest and natural enemy information reported here. As evidenced, it is always important to consider site-specific factors that may influence arthropod populations.

CHAPTER 3

IMPACT OF DRIVE ROW COVER CROPS ON HOP YARD ARTHROPOD PESTS AND THIER NATURAL ENEMIES

3.1 Introduction

Arthropod communities are a reflection of climate, landscape, and management practices (Schweiger et al. 2005). Conservation biological control is one method of increasing top-down pressure on a pest population and can be part of integrated pest management (IPM) programs. The basis for conservation biological control studies is the "enemies hypothesis" proposed by Root (1973) which states that top-down control by natural enemies reduces pest arthropod damage to plants. Arthropod, disease, and weed management is critical to hop yield and quality. Insecticides are the go-to management tool for hop arthropod pest suppression yet the importance of natural enemy ecosystem services in hop yards is recognized by the scientific community (James 2003, Woods et al. 2014).

Nineteenth century US hop production took place in the Northeast region. Today, Pacific Northwestern states dominate hop production in the US. Over the past 10 years the local food movement has expanded into the beverage market initiating the resurgence of hop production to the Northeast. Two-spotted spider mite (TSSM) and hop aphid (HA) are the arthropod pests of economic importance in the Pacific Northwest and are continually managed with insecticides (Turner et al. 2011). The native potato leafhopper (PLH) was a third major arthropod pest in 19th century Northeastern hop production and is also recognized today (Magie 1944). Commercial hop producers worldwide require alternatives to insecticides and the Northeast region in particular requires regionally adapted pest management tools.

While flowering cover crops in perennial systems have increased natural enemy abundance and therefore decreased pest pressure of spider mites and aphids (Altieri and Schmidt 1986, Alston 1994, Tuovinen 1994, Wyss 1995, Gontijo et al. 2013), implementation of cover crops has also been shown to increase pest presence (Meagher and Meyer 1989, Goller et al. 1997). Few studies have investigated the use of cover crops as a pest management tool in hop yards. A three-year Washington State study indicated that incorporating flowering plants between rows of hops attracts effective natural enemy arthropods and reduces populations of TSSM. Spider mite populations were reduced on cover crop plot plants yet aphid populations showed more variable population reduction (Grasswitz and James 2009). Aphid populations were highest on hop plants with a mowed fava bean (*Vicia faba* L.) ground cover in Germany (Goller et al. 1997). The need to reduce herbicide use and manage erosion in hops is also recognized (Lepecki and Berbec 1997). Cover cropping is a logical step toward improving hop production sustainability. However, appropriate cover crop plant species must be identified and efficacy evaluated for successful pest management (Geneau et al 2012 and Gontijo et al. 2013).

Cover crops have not been reported as an IPM tool in Northeastern hop production. Additionally, un-mowed drive row vegetation has not been evaluated for its impact on hop yield and quality. As PLH is not a pest in the Pacific Northwest production region, including this pest in regional habitat management studies is important. In hopes of reducing pesticide use and spider mite secondary outbreak in hop yards, we hypothesized that flowering cover crops of increasing species diversity would increase natural enemy abundance and therefore reduce hop pest abundance in a Northeastern hop yard. Our study had three objectives; 1) measure the effect of drive row cover crops on natural enemy group abundance, 2) measure the effect of drive row cover crops on the three major Northeastern hop pests and 3) measure the

effect of cover crop presence on hop yield and quality. Susceptibility of 'Cascade' and 'Nugget' to the three major arthropod pests is discussed.

3.2 Materials and Methods

3.2.1 Study Site

A certified organic research hop yard was established in the fall of 2010 at Borderview Farm in Alburgh, VT (Vermont Organic Farmers, LLC, Richmond, VT). Six meter tall cedar posts were set on the Benson rocky silt loam soil type, making a finished trellis height of 4.8 m. The entire research hop yard has an area of 0.3 ha. The cover crop trial took place on the southern 0.1 ha of the yard where cultivars 'Cascade' and 'Nugget' alternate rows. The hop yard is surrounded by yearly rotating field crops including wheat, barley, sunflower, canola, and pasture. Along the eastern edge of the hop yard is a 20 x 200 m un-mowed pasture strip with two trees in the *Ulmus* genus. The hop yard is approximately 300 m from a hard wood forest, which includes tree species in the genera *Acer*, *Fraxinus*, and *Betula*. These genera are not alternate hosts of the major arthropod hop pests.

3.2.2 Experimental Design and Management

Cover crop treatments were planted on 15 May 2012 in a split strip plot design replicated three times. The main plot was cover crop treatment and the subplot was cultivar. Cover crop treatments included mowed clover/resident weed control (Control), red clover, *Trifolium pretense* (Clover), and a more diverse mixture including common yarrow, *Achillea millefolium* cv. 'strawberry seduction', beebalm, *Monarda fistulosa*, red clover, and annual sunflower, *Helianthus annuus* cv. 'Durango' (Diverse). Cover crops were planted in the drive row between rows of hops. Hop rows

were mulched with hardwood bark mulch for weed management. In our region, the majority of hop yard drive rows are currently maintained as mowed sod or weeds. Therefore, the Control treatment was mowed clover where weeds were allowed to establish. Red clover was chosen as a cover crop treatment due to interest from hop growers. The mixture of flowering plants in Diverse plots were chosen with the goal of continued flower from June-August and for vertical structural complexity.

Each main plot was 3.65 m by 9.14 m with subplots of 0.9 m by 9.14 m and each hill had two coir strings clipped into the ground and tied to the top of the trellis. Three to four hop bines were trained to each string. Due to the prevalence of hop downy mildew caused by *Pseudoperonospora humuli*, all hop plants in this study were sprayed with copper hydroxide based fungicide (Champ WG Agricultural Fungicide EPA Reg. No. 55146-1) as needed. Insecticides were not applied. All hop plants were treated equally in terms of weed control, fertilizer applications, and other production practices.

The cover crop plots were prepared with a moldboard plow, disked and finished with a spike tooth harrow. Red clover in Control, Clover and Diverse plots were seeded with a 3.08 m Kverneland drill (Kverneland Group, Norway). In the Control and Clover treatments red clover was seeded at a rate of 1.4 kg/ha every 11.4 cm and every 22.8 cm Diverse plots. All clover was planted to a depth of 0.64 cm. Each Diverse plot consisted of ten planted rows to create mixed species treatments. This mix was planted in a random rotating order of yarrow, beebalm, red clover, sunflower rows. Second year plugs of yarrow and beebalm were planted by hand in rows of nine in each Diverse plot (North Creek Nurseries in Oxford, PA). Sunflower seeds were planted by hand in rows of nine in May each season yet only flowered in 2012. Original perennial plugs and red clover stand remained undisturbed for the duration of the three-year study. In all treatments cover crops did not reach full bloom in 2012

the establishment year. In 2013, Clover plots began flowering 5 June and reached full bloom on 27 June. Diverse plots reached full bloom on 24 July. In 2014, Clover began flowering 11 June and reached full bloom 26 June. Diverse plots reached full bloom 21 July.

Hop plants were drip irrigated with 5977 L/ha per week June-August in all years of this study. Hop plants were fertilized on 7 May 2012 and 28 May 2013 with North Country Organics Pro-Booster (10-0-0) and ProGro (5-3-4) for a goal of 13.8 kg/ha plant available N, 8.3 kg/ha P, and 11.0 kg/ha K. In 2013, an additional 11.0 kg/ha of Chilean Nitrate was applied on 18 June. In 2014, hop plants were first amended with Chilean Nitrate to provide 9.2 kg/ha plant available N at training and 8.5 kg/ha plant available N on 27 June. The hop yard was fertigated on 10 June, 28 June, 4 July, 2014 with soy based Ferti-Nitro Plus produced by Ferti-Organic. Each fertigation application was applied to provide 0.55 kg/ha for a total of 1.65 kg/ha N applied via the drip line. There was a total of 19.3 kg/ha plant available N in 2014. Every year 0.36 kg/ha of Boron and 0.92 kg/ha Zinc were applied.

3.2.3 Arthropod Collection

Arthropod collection was performed each week for 12 consecutive weeks over the three seasons. Vacuum sampling was the most effective collection method for TSSM and sticky traps were the most effective collection method for PLH and HA. Vacuum samples were taken from plants and cover crop vegetation. Sticky traps were hung in the hop canopy. Detail sampling was also conducted yet results from this collection method are not reported (see Appendix A). Collection began the first week of June and continued approximately every seven days until harvest began in late August.

3.2.3.1 Vacuum Sampling

Of the three middle hills of each cultivar, two hills were chosen at random each week for vacuum and detail sampling. The order in which plants and plots were vacuumed was randomized weekly. Vacuum sampling was performed mid-day between 10am and 2pm using a reverse leaf blower with a 25 CC 2-cycle gas engine (Poulan PRO BVM210VS, Charlotte, NC). A 20 cm long chiffon bag was attached to the end of the vacuum arm to catch the incoming sample. Each hill was vacuumed up and down for 40 s. The cover crop ground vegetation was also vacuumed for 40 s. This drive row space was sampled by zig-zagging through the ground vegetation while vacuuming. Samples account for 0-3 m height of each hill (as high as we could reach). The vacuum was left on while the mesh bag was removed from the vacuum. The sample was placed into a kill jar containing ethyl acetate and left for 2-5 minutes while the rest of the plot samples were collected. Once all hills and the cover crop treatment had been sampled, arthropod samples in kill jars were transferred into labelled 250 ml glass jars containing 30 ml 70% ethyl alcohol for later lab sorting.

3.2.3.2 Sticky Traps

Sticky traps were un-baited 7.6 x 12.7 cm yellow cards hung between the two strings of the middle plant in each plot, 1.5 m off the ground on coir rope held with wooden close-pins. There was one trap for each variety in each plot hung between bines on the center plant for a total of 18 traps weekly. Traps were hung after vacuum and detail sampling each week and collected before sampling the following week.

3.2.4 Arthropod Identification

Vacuum and sticky trap samples were sorted into pest and natural enemy groups using a Zeiss Stemi DV4 stereo microscope (Carl Zeiss MicroImaging GmbH, Ger-

many). Major pest arthropods were identified to species while natural enemies were identified to functional group. Major pest arthropods included HA, PLH, and TSSM. Natural enemy groups were formed based on previous studies that show predation or parasitism of HA, PLH, and TSSM. Parasitoid families included Mymaridae, Chalcidoidea, Braconidae, Aphelinidae (Lovinger et al. 2000) and were not sorted separately but lumped into one "parasitoid" category. Two spotted spider mite natural enemies included predatory mites (Phytoseiidae), spider mite destroyers (*Stethorus punctum* spp.) and minute pirate bugs (Anthocoridae).

Table 3.1: Natural enemy arthropod groupings for each major hop pest species. Vacuum, and sticky trap specimens were identified to the following classification.

Pest	Natural Enemy Group
Tetranychus urticae (TSSM)	*Stethorus punctum* Anthocoridae
Phorodon humuli (HA)	Anthocoridae, Geocoridae, Nabidae Chrysopidae & Hemerobiidae Coccinellidae Parasitica Syrphidae
Empoasca fabae (PLH)	Anthocoridae, Geocoridae, Nabidae Chrysopidae & Hemerobiidae Coccinellidae Parasitica Spiders

3.2.5 Hop Harvest Yield and Quality

'Cascade' and 'Nugget' were harvested when the cones reached 23% dry matter. Hop bines were cut in the field and harvested within 8 hrs. Bine pre-pick and total cone weights were recorded. Percent dry matter and total cone weights were determined at harvest. Harvested hops were air dried in a 40.5^{o}C oast. Once hops reached 92% dry matter (typically overnight) a representative 100g sample of each cultivar in each plot was collected. Alpha Analytics in Yakima, WA analyzed samples for alpha and beta acid percentage according to the American Society of Brewing Chemists (ASBC Hops 6a).

3.2.6 Data Analysis

Arthropod count data was square root transformed. First, Pearson partial correlations were conducted for each natural enemy group and pest accounting for the effect of collection date (PROC CORR, SAS Institute 2014). Then a linear mixed model with repeated measures (PROC MIXED, SAS Institute 2014) was used to evaluate pest arthropods by cover crop treatment, cultivar, and collection date for each collection method. Vacuum plant, vacuum cover crop, and sticky trap samples were analyzed separately because collection methods did not have the same sampling unit but similar analyses were conducted. Natural enemy group was included in the model as a continuous covariate due to the amount of variation accounted for by this variable. Factors were considered fixed with the exception of replication. Fixed effects included natural enemy group, natural enemy group x treatment, cultivar, cover crop treatment, treatment x cultivar, collection date, cultivar x collection date, and treatment x collection date. Natural enemy group x treatment was removed from the model because it was not significant.

In the vacuum plant model, hop plant was the experimental unit measured repeatedly over time. For the sticky trap model, hop plant was the experimental unit measured repeatedly over time. For the vacuum cover crop vegetation model, cover crop plot was the experimental unit measured repeatedly over time. Years of data collection were not pooled. Statistics for TSSM are reported using the vacuum model and PLH and HA are reported using the sticky trap model.

Hop quality is represented using alpha and beta acid percentage. Yield was calculated using a hop population of 784 hills per acre. Cover crop treatment yield and quality were compared using the general linear model procedure (PROC GLM, SAS Institute 2014). Yield and quality data were run separately and included the same fixed effects: year, cultivar, year x cultivar, cover crop treatment, year x treatment, cultivar x treatment, and year x cultivar x treatment. All statistics were run at the 0.05 level of significance (LOS) and generated using SAS software, Version 9.4 (Copyright 2014 by SAS Institute Inc., Cary, NC, USA).

3.3 Results

3.3.1 Effect of Cover Crop and Cultivar on Arthropod Pests on Hop Plants

The TSSM population was highest in 2012. The slightly cooler, more moist seasons of 2013 and 2014 had lower spider mite populations. There was a positive correlation between TSSM natural enemy group and TSSM in all years (2012: r = 0.29, 2013: r = 0.15, 2014: r = 0.14). When TSSM were most numerous in the hot and dry 2012 season, TSSM natural enemies were a strong predictor of this pest on hop plants (Table 3.2). The effect of cultivar on TSSM was significant in 2012 and 2013 where 'Nugget' had higher abundance than 'Cascade'. The effect of cover crop treatment

and treatment x cultivar did not have a significant effect on the TSSM population. Collection date was significant with populations of TSSM peaking in early to mid-August in all years (Fig. A.12). There was a significant cultivar x date interaction in all three years of the study (Table 3.2). In 2012 and 2013, TSSM was higher on 'Nugget' until late August when the population on 'Nugget' decreased and 'Cascade' increased (Figs. A.1 and A.2). In 2014, TSSM abundance remained higher on Nugget throughout the season (Fig. A.3). There was a significant treatment x date interaction in 2014. The TSSM population remained fairly constant in all treatments until 21 July at which time the TSSM populations increased considerably in the Control and Diverse treatments. The population of TSSM on plants in Diverse plots had a similar peak abundance to the Control yet, steadily decreased into late August. Of all treatments the Clover TSSM population remained consistently lowest (Table 3.2 and Fig. 3.1).

Table 3.2: ANOVA summary statistics for two-spotted spider mites from vacuum samples. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
TSSM	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	15.84 (1, 323)	**< 0.0001**	2.91 (1, 366)	0.09	1.56 (1, 323)	0.21
Cultivar	0.40 (1, 88.6)	0.53	11.25 (1, 98.6)	0.001	10.26 (1, 79.7)	**0.002**
Treatment	1.27 (2, 88.4)	0.29	0.01 (2, 98.2)	0.99	1.98 (2, 78.5)	0.15
Treatment x Cultivar	0.14 (2, 95.9)	0.87	0.80 (2, 105)	0.45	2.25 (2, 82.8)	0.11
Date	25.14 (11, 321)	**< 0.0001**	30.83 (11, 326)	**< 0.0001**	23.71 (11, 310)	**< 0.0001**
Cultivar x Date	4.13 (11, 325)	**< 0.0001**	3.74 (11, 327)	**< 0.0001**	2.64 (11, 312)	**0.003**
Treatment x Date	0.70 (22, 332)	0.84	0.95 (22, 335)	0.53	1.66 (22, 317)	**0.03**

PLH were most abundant in 2012 and 2013 (Fig. A.13). In 2014, PLH arrived late with a population approximately half the size of the previous two years. In all years, natural enemies and PLH were positively correlated on hop plants (2012: r = 0.32, 2013: r = 0.43, 2014: r = 0.40). The effect of cultivar on PLH was significant in 2013 with higher abundance observed on 'Nugget'. Also in 2013, there was a significant effect of treatment where a higher number of PLH were observed on hop plants in Diverse treatments (Fig. 3.2). There was no significant interaction between treatment and cultivar. Collection date was significant with populations of PLH peaking on 10 July in 2012 and 2013. In 2014, PLH peaked on 12 August (Fig. A.13). PLH cultivar x date and treatment x date interactions were not significant.

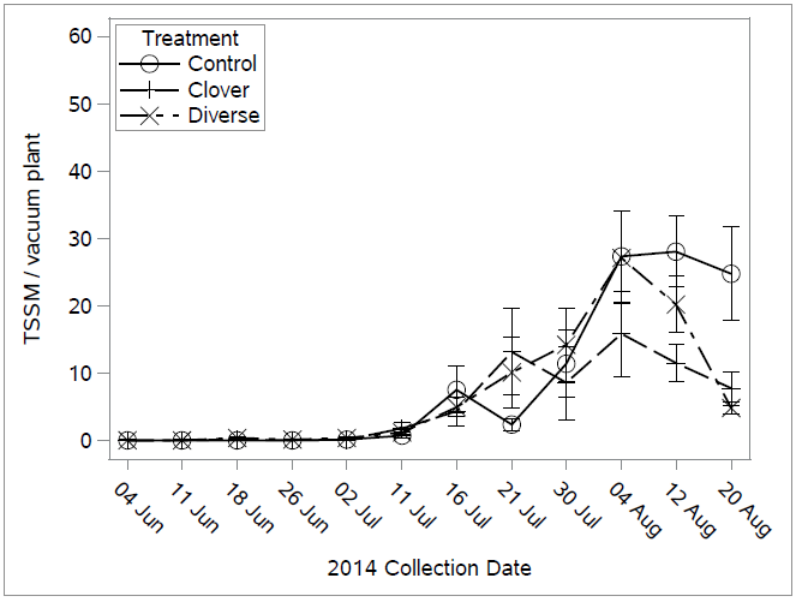

Figure 3.1: Mean TSSM/vacuum sample on hop plants in 2014. There was a significant interaction between treatment and collection date (Table 2). Diverse and Control plots spiked on 4 August. Control TSSM remained high while Diverse TSSM dropped to meet population level in Clover plots. TSSM abundance in Clover plots remained lowest.

Table 3.3: ANOVA summary statistics for potato leafhopper from sticky traps. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
PLH	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	5.92 (1, 131)	**0.02**	15.77 (1, 142)	**0.0001**	5.10 (1, 150)	**0.03**
Cultivar	2.64 (1, 33.3)	0.11	4.51 (1, 63.7)	**0.04**	0.96 (1, 34.5)	0.33
Treatment	0.12 (2, 32.7)	0.89	4.60 (2, 63.8)	**0.01**	0.27 (2, 34.2)	0.76
Treatment x Cultivar	0.45 (2, 33.7)	0.64	.35 (2, 62.8)	0.70	0.02 (2, 36.5)	0.98
Date	34.40 (11, 124)	**< 0.0001**	5.74 (11, 140)	**< 0.0001**	32.70 (11, 143)	**< 0.0001**
Cultivar x Date	0.73 (11, 120)	0.71	0.69 (11,140)	0.75	0.93 (11, 142)	0.51
Treatment x Date	0.41 (22, 122)	0.99	0.70 (22, 142)	0.84	0.69 (22, 143)	0.84

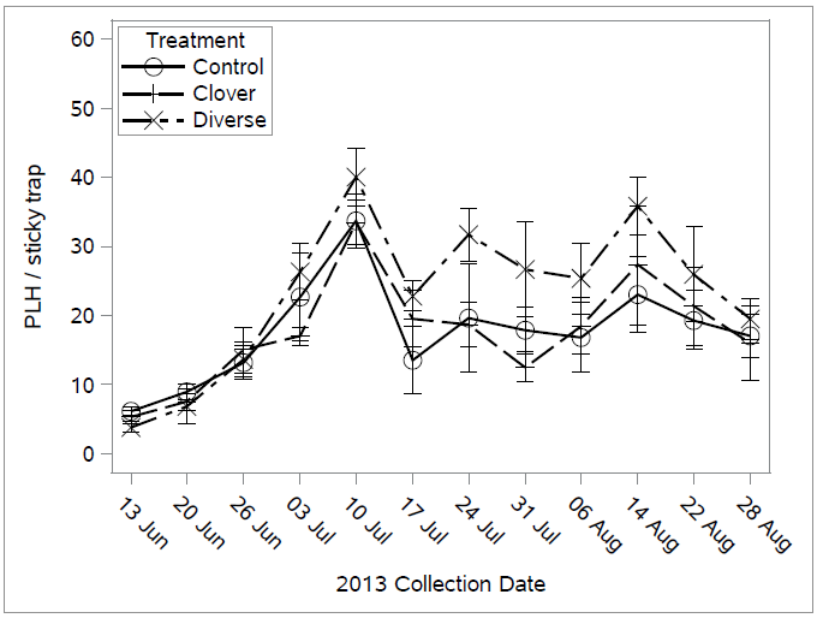

Figure 3.2: Mean PLH/sticky trap on hop plants in 2013 by cover crop treatment. Cultivars are combined. There was a significantly higher number of PLH on hop plants in Diverse plots (P = 0.01).

The HA population was highest in 2014 when weather conditions were cool in spring and consistent precipitation occurred throughout the season. There was a positive correlation between HA natural enemy group and HA in all years (2012: r = 0.27, 2013: r = 0.23, 2014: r = 0.37). Additionally, HA natural enemies were a strong predictor of this pest in 2012 and 2014 (Table 3.4). The effect of cultivar was significant in 2014 with 'Cascade' having higher aphid abundance than 'Nugget'. The effect of cover crop treatment did not have a significant effect on HA populations. There was a significant interaction between treatment and cultivar in 2013. 'Nugget' Control and Clover plants had higher HA abundance yet more HA were observed on 'Cascade' plants in Diverse plots (Fig. A.7). The effect of collection date was significant in all years with HA populations peaking in early to mid-August. In 2013 aphids were less abundant with an earlier peak date in June (Fig. A.14). There was a significant cultivar x date interaction in 2014 where HA were higher on 'Cascade' until late August when HA on 'Nugget' spiked and 'Cascade' HA abundance declined before 'Nugget' (Fig. A.8). Treatment x date was not a significant interaction for HA.

Table 3.4: ANOVA summary statistics for hop aphid from sticky traps. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
HA	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	9.28 (1, 129)	**0.002**	1.74 (1, 156)	0.19	14.58 (1, 161)	**0.0002**
Cultivar	3.76 (1, 45.5)	**0.06**	.04 (1, 50.9)	0.84	7.26 (1, 38.2)	**0.01**
Treatment	0.10 (2, 46.4)	0.91	.27 (2, 50.8)	0.76	1.16 (2, 37.8)	0.32
Treatment x Cultivar	0.48 (2, 47)	0.62	4.47 (2, 51.2)	**0.02**	2.02 (2, 39.4)	0.15
Date	5.41 (11, 119)	**< 0.0001**	10.3 (11, 139)	**< 0.0001**	8.73 (11, 139)	**< 0.0001**
Cultivar x Date	1.21 (11, 117)	0.29	.58 (11, 138)	0.84	1.93 (11, 137)	**0.04**
Treatment x Date	1.12 (22, 117)	0.34	1.27 (22, 141)	0.20	0.81 (22, 139)	0.71

3.3.2 Effect of Cover Crops on Arthropod Pests in Cover Crop Vegetation

In 2013, TSSM natural enemy group and TSSM were positively correlated in cover crop vegetation (r = 0.19). TSSM natural enemies were not a strong predictor of spider mites in cover crop vegetation. The effect of treatment did not significantly impact TSSM abundance. Collection date had a significant effect in 2013 and 2014. There was a significant treatment x date interaction in 2014 where Clover vegetation had the highest mean TSSM population while aphid populations in Diverse plots spiked twice. The Diverse population dropped earlier and remained lower than Control and Clover treatments (Table 3.5, Fig. A.4).

Table 3.5: ANOVA summary statistics for TSSM in cover crop vegetation. F values and significance from linear mixed model with repeated measures are reported at 0.05 LOS.

Effects	2012		2013		2014	
TSSM	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	0.1 (1, 62.9)	0.78	0.01 (1, 48.3)	0.93	0.27 (1, 66.8)	0.60
Treatment	0.1 (2, 14.4)	0.94	2.8 (2, 19.6)	0.09	0.42 (2, 25.6)	0.66
Date	1.1 (11, 55.9)	0.38	2.1 (10, 51.2)	**0.04**	7.1 (11, 57.3)	**<0.0001**
Treatment x Date	0.80 (22, 53.5)	0.71	1.3 (20, 49.2)	0.21	1.9 (22, 54.6)	**0.03**

In all years of the study PLH natural enemy group and PLH were positively correlated (2012: r = 0.63, 2013: r = 0.73, 2014: r = 0.49). Vacuum samples from cover crop plot vegetation indicated that PLH natural enemies were strong predictors of this pest in all years. The effect of treatment was significant in 2012 when PLH mean abundance was highest in Diverse vegetation and in 2013 when PLH abundance was highest in Clover vegetation (Figs. 3.3 and 3.4). The effect of collection date was significant in all years. There was a significant treatment x date interaction in 2014. In this low population year PLH had the highest population in Diverse plots which also decreased earlier than PLH in Control and Clover vegetation. Clover typically reached senescence by early August. The 2014 PLH population arrived after clover senescence and therefore showed a trend toward higher PLH in Diverse plot vegetation (Table 3.6, Fig. 3.5).

Table 3.6: ANOVA summary statistics for PLH in cover crop vegetation. F values and significance from linear mixed model with repeated measures are reported at 0.05 LOS.

Effects	2012		2013		2014	
PLH	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	25.3 (1, 63.5)	**<0.0001**	41.7 (1, 63.3)	**<0.0001**	19.0 (1, 66.2)	**<0.0001**
Treatment	3.8 (2, 17.4)	**0.04**	6.9 (2, 20.1)	**0.0050**	1.5 (2, 21.1)	0.26
Date	6.7(11, 58.8)	**<0.0001**	4.3 (10, 52.5)	**0.0002**	10.5 (11, 60)	**<0.0001**
Treatment x Date	1.6 (22, 56.1)	0.07	1.4 (20, 49.8)	0.17	3.5 (22, 56.6)	**<0.0001**

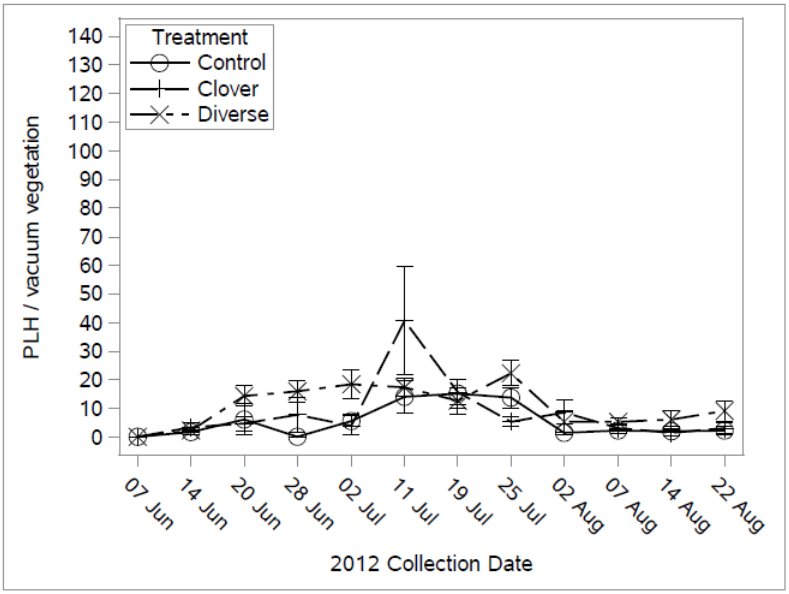

Figure 3.3: Mean PLH/vacuum sample in 2012 cover crop vegetation by treatment. There was significantly higher mean PLH abundance in Diverse cover crop plots in ($P = 0.04$) yet Cover plot vegetation spiked highest.

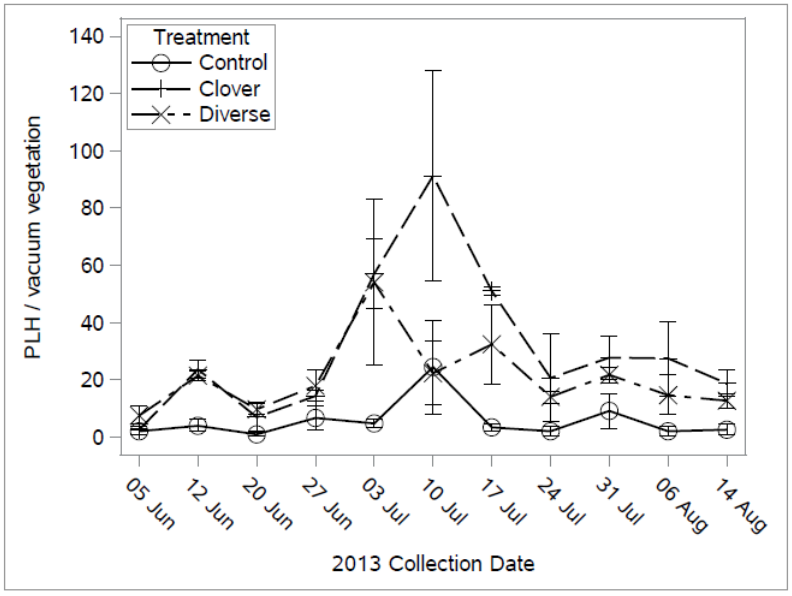

Figure 3.4: Mean PLH/vacuum sample in 2013 cover crop vegetation by treatment. There was a significantly higher number of PLH in Clover cover crop treatments (P = 0.0001).

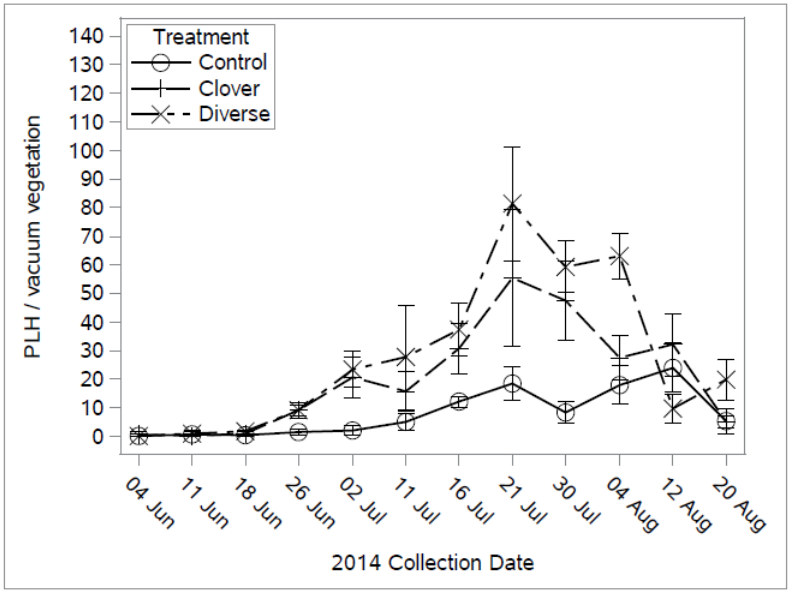

Figure 3.5: Mean PLH/vacuum sample in 2013 cover crop vegetation by treatment. There was a significantly higher number of PLH in Clover cover crop treatments (P = 0.0001).

In all years of the study HA natural enemy group and HA were positively correlated (2012: r = 0.38, 2013: r = 0.60, 2014: r = 0.50). HA natural enemies were a strong predictor of this pest in all years. The effect of treatment on HA was not significant. Collection date had a significant effect on HA populations in 2012 and 2013. There was not a significant interaction between treatment and collection date for HA (Table 3.7).

3.3.3 Hop Harvest Yield and Quality

Year had a significant effect on hop yield. Mean 'Cascade' yield increased over the course of this three-year study from 56.04 kg/ha in 2012 to 134.49 kg/ha in 2014. Mean 'Nugget' yield increased from 77.02 kg/ha to 139.87 kg/ha in 2014. Year also had a significant effect on 'Cascade' and 'Nugget' alpha and beta acids. As expected the effect of cultivar on yield and quality were significant. There was a significant year x cultivar interaction in hop quality as expected due to known differences in quality parameters between the two cultivars. Cover crop treatment did not have an effect on hop yield or quality. Additionally, year x treatment and cultivar x treatment interactions were not significant. The year x cultivar x treatment three way interaction was not significant (Table 8).

Table 3.7: ANOVA summary statistics for HA in cover crop vegetation. F values and significance from linear mixed model with repeated measures are reported at 0.05 LOS.

Effects	2012		2013		2014	
HA	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	5.3 (1, 70.4)	**0.02**	12.6 (1, 64.9)	**0.0007**	11.9 (1, 70.1)	**0.0009**
Treatment	0.01 (2, 23.2)	0.98	2.1 (2, 26.9)	0.14	0.5 (2, 28.8)	0.62
Date	2.2 (11, 58.9)	**0.03**	3.8 (10, 53.7)	**0.0005**	1.4 (11, 59.9)	0.19
Treatment x Date	0.85 (22, 56.3)	0.64	0.6 (20, 51)	0.86	0.5 (22, 56.7)	0.95

Table 3.8: ANOVA summary statistics for yield, alpha acid, and beta acid percent. F values (n,d) and significance values are presented from generalized mixed model at 0.05 LOS.

Effects	Yield		α acid (%)		β acid (%)	
	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Year	28.6 (2, 35)	**< 0.0001**	4.8 (2, 30)	**0.02**	6.7 (2, 30)	**0.004**
Cultivar	8.7 (1,35)	**0.01**	1035.3 (1,30)	**< 0.0001**	348.8 (1,30)	**< 0.0001**
Year x Cultivar	1.7 (2, 35)	0.19	21.1 (2)	**< 0.0001**	11.1 (2, 30)	**0.0002**
Treatment	0.5 (2, 35)	0.62	0.0 (2, 30)	0.99	0.2 (2, 30)	0.82
Year x Treatment	0.4 (4, 35)	0.82	2.1 (4)	0.11	0.2 (4, 30)	0.94
Cultivar x Treatment	0.1 (2, 35)	0.91	1.0 (2, 30)	0.37	0.04 (2, 30)	0.96
Year x Cultivar x Treatment	0.8 (4, 35)	0.50	0.25 (4)	0.91	0.7 (4. 30)	0.63

3.4 Discussion

Our results indicate that flowering cover crop treatments did not increase natural enemy or pest abundance. Where pests were abundant, natural enemies were present. There was a positive correlation between natural enemy groups and pests on hop plants and in cover crop vegetation even after accounting for the effect of collection date. This indicates that natural enemies of the major Northeast arthropod pests were present in the hop yard. Importantly, TSSM and HA that are economically damaging in other production regions did not reach outbreak levels making insecticide application unnecessary in this research hop yard. Our findings are evidence that cover crops in Northeast hop production may serve more specific pest management functions rather than boosting overall natural enemy abundance. Established red clover served as a trap crop for PLH in this study. It is clear that natural enemy populations were present when and where pests were abundant, yet it is unclear which habitat provided this level of top-down pest suppression due to the lack of spatial independence. We suggest that Northeast perimeter and hop yard landscapes may be able to support appropriate levels of natural enemies to control pest populations without added flowering cover crop habitat. Cover crop presence did not have a negative effect on hop yield or quality.

We observed different results in comparison to the Washington state flowering cover crop study. James et al 2009 showed a significant reduction in TSSM and variable reduction in HA populations. In our study TSSM and HA populations did not increase as a result of cover crop presence yet there was little effect of cover crop treatment on TSSM and HA populations on hop plants and in cover crop vegetation. In the case of 2014, lower TSSM abundance was observed on hop plants in Clover and Diverse cover crop plots (Table 3.2, Fig. 3.1). This higher level of TSSM on hop

plants in Control plots may be due to drier conditions where cover crop vegetation was not present or lower natural enemy abundance in Control plots. Cover crop plots were in close proximity to each other and it is likely that natural enemy assemblages spilled over into control plots. Natural enemies of PLH and HA were present and positively correlated with pests in cover crop vegetation. The ability to identify the source of natural enemies is confounded by spatial independence.

Surrounding landscape is a critical factor in understanding where conservation biological control is an appropriate IPM tool (Tscharntke et al. 2007). We suggest that in the Northeast surrounding habitat diversity is more important than cover crop species selection for TSSM and HA natural enemy habitat. It has been stressed that successful conservation biological control hinges on plant species selection (Geneau et al. 2012, Gontijo et al. 2013). While plant species selection is important for natural enemy attraction in some systems, the diverse, research farm landscape that surrounded our research hop yard during this study appears to have provided a level of natural enemy habitat that reduced the need for cover crop habitat between hop rows. In comparison to the Pacific Northwest, landscape diversity in the Northeast region is high. Additionally, hop yard size may have an effect on hop arthropod pest pressure. Western hop yards range in size from 202.3-809.3 ha while Northeastern yards currently range from 0.4 – 8.0 ha. The large, bare soil, monoculture landscape of Western hop yards appears to benefit from the implementation of habitat diversity providing biological control, yet this may not be required in Northeastern hop yards.

Our findings are evidence that cover crops in Northeastern hop production may serve more specific pest management functions rather than boosting overall top-down pest suppression. The non-mowed, fully established clover cover crop plots served as a PLH trap crop. Clover cover crop plots were still establishing in 2012 when PLH were highest in Diverse cover crop plot vegetation. In 2013, PLH numbers were highest

on plants in Diverse plots yet highest in the Clover cover crop vegetation. This indicates that a full stand of clover was preferred by PLH over hop plants and the Diverse polyculture cover crop treatment. While clover was a member of the Diverse treatment mix there was a lower density of clover in Diverse plots. Straub et al. (2012) provided evidence of the same phenomenon in alfalfa where PLH populations were higher in alfalfa monocultures than in mixed species alfalfa stands. Further research should address clover trap crop size and population capacity of a clover trap crop for PLH in hop yards.

Differences in susceptibility of hop cultivars to TSSM have been documented in other growing regions of the world. The minor interactions observed between cultivar and collection date indicate that TSSM had consistently higher abundance on 'Nugget' until the end of the season. At the end of the 2012 and 2013 seasons TSSM 'Nugget' populations decreased while 'Cascade' TSSM populations increased. It is unclear why this swapping phenomenon was observed. Essential oil content of hop leaves, specifically farnesol, was suggested as a possible mechanism of increased susceptibility of hop cultivars to TSSM (Regev and Cone 1975). Further study found a lack of farnesol in hop leaves (Gunson et al. 1981). 'Cascade' and 'Nugget' have different chemical profiles and maturity dates. 'Cascade' reaches maturity before 'Nugget' and therefore we believe that higher TSSM abundance on 'Nugget' is a factor of leaf chemistry or morphology rather than plant phenology. Peters and Berry (1980) report higher TSSM development time on hop leaves with higher leaf trichome density (Peters and Berry 1980).

It is also well documented that hop cultivars have different susceptibility to HA (Campbell 1983, Dorschner and Baird 1988, Weihrauch and Moreth 2005) and the same pattern was observed in our study. HA varied by cultivar in all years with a significantly higher number of HA on 'Cascade' in 2014. High susceptibility of 'Cas-

cade' to HA is consistent with previous research conducted in the Pacific Northwest (Dorschner and Baird 1988). Cultivar susceptibility to HA has been linked to high essential oil content with cariophyllene and farnesene highlighted as HA feeding compounds (Kralj et al. 1998). Further research on the relationship between TSSM and HA pest abundance and leaf chemical and physical defenses should be investigated in hopes of developing more resistant cultivars and reducing insecticide applications. Our research indicated that neither yield nor quality differed between cover crop treatments. Growers have expressed concern about cover crop vegetation trapping moisture and therefore increasing the presence of hop downy mildew. Although this study did not address disease incidence and plots were preventatively sprayed with copper hydroxide fungicide, the presence of downy mildew was observationally clear. Because there was no decrease in yield nor quality, cover crops of the stature used in this study did not trap enough moisture to increase hop downy mildew incidence. However, farms have different microclimates. Alburgh, VT, being a peninsula reaching out into Lake Champlain, is a well-ventilated, windy site for a hop yard. Yearly variation in hop yield and quality parameters seen in both cultivars is likely due to hop plant age. Hop plant yield reaches high performance in year three (Neve 1991). In 2012 the hop yard used in this study was two years old.

Pest management needs of Northeastern hop yards are different from the needs of Pacific Northwest hop yards. Future research should address clover trap crop size and clover carrying capacity for PLH management. Hop leaf chemistry and morphology research would provide a window into "bottom-up", chemical free pest management tools. Although it was not our objective to investigate landscape sources of natural enemies, we were forced to hypothesize in this direction. We believe it is important to quantify how much habitat diversity is required for natural enemy ecosystem services in the Northeast. The quantity and quality of habitat required to

manage pest populations below economic thresholds by natural enemies is not well understood in our region.

In conclusion, flowering cover crop treatments did not increase natural enemy or pest abundance. Where pests were abundant, natural enemies were present. Cover crop presence did not have a negative effect on hop yield or quality. Natural enemy groups and pests were positively correlated on hop plants and in cover crop vegetation. Importantly, TSSM and HA are economically damaging pests in other production regions. These species did not reach outbreak levels in our research hop yard. It is clear that natural enemy populations were present when and where pests were abundant, yet it remains unclear which habitat provided this level of top-down pest suppression due to the lack of spatial independence. Northeast perimeter and hop yard landscapes may be able to support appropriate levels of natural enemies to control pest populations without flowering cover crop implementation. Our findings are evidence that cover crops in Northeast hop production may serve more specific pest management functions than boosting overall natural enemy abundance. Established red clover planted in drive rows served as a trap crop for PLH in this study.

CHAPTER 4

IMPACT OF ADULT POTATO LEAFHOPPER FEEDING ON FIRST YEAR HOP GAS EXCHANGE

4.1 Introduction

Potato leafhopper feeding has been reported to cause significant yield damage to many crops. Most recently potato leafhopper has reduced alfalfa (Medicago sativa L.) yield by 15.7% (Kaplan et al. 2008) and dry bean yield by 20.0% (Phaseolus vulgaris L.) (Lindgren and Coyne 1995). Similarly there is documentation from New York State Agricultural Experiment Stations that potato leafhopper (Empoasca fabae Harris) was a pest of economic importance on hops in 19th and 20th century Northeastern hop production (Magie 1944). In 2012 Dr. Dmitry Dmitriev of the Illinois Natural History Survey confirmed leafhopper specimens from the University of Vermont research hop yard located in Alburgh, VT as E. fabae. Two generations of potato leafhopper have been observed on hops in Alburgh, VT (see Chapter 2). Extension scouting and survey efforts indicate the presence of this pest in hop yards across the northeast.

Hops are fast growing perennials with approximately 5 m of annual growth occurring before 21 June. In response to shorter photoperiod, hops enter the reproductive growth stage (Neve 1991). While arrival date of potato leafhopper to the Northeast varies depending on Southeastern degree-days and northerly trade winds, the pest typically arrives to the region in late spring (Sidumo et al. 2005). Because potato leafhopper is generally an early season pest and causes foliar damage to hops during vegetative development, it is a pest of concern for hop production in this region.

As a cell rupture feeder, potato leafhopper consumes leaf and stem vascular tissue

or mesophyll cells by continually injecting its stylet into host plant tissue (Hunter and Backus 1989, Backus et al. 2005). Potato leafhopper is known to feed on more than 200 plant species (Lamp et al. 1994). Due to this high degree of polyphagy, the species has slightly different methods of feeding on different host plants (Hunter and Backus 1989). A combination of mechanical and saliva release actions cause a cascade of host plant wound responses. Potato leafhopper saliva has long been described as toxic and recent evidence revealed diverse composition of genes in the species saliva provoking further investigation (Delay et al. 2012). One known response is the restriction of phloem and eventual xylem flow to the rest of the leaf (Nielsen et al. 1990), resulting in visual leaf edge yellowing and curling (hopperburn), and stunted internode growth (Backus et al. 2005).

The immediate restriction of photosynthates through vascular tissue impacts the rate at which an injured leaf photosynthesizes (Womack 1984, Flinn et al. 1990, Lamp et al. 2004). Gas exchange measurements including net photosynthesis, transpiration, and stomatal conductance in addition to leaf chlorophyll content have been used to measure potato leafhopper injury impact to alfalfa and grape (Vitis vinifera L.) cultivars (Lamp et al. 2004, 2007, 2011, Lenz et al. 2012). Upon removal of potato leafhoppers physically or with an insecticide spray, alfalfa has been shown to restore gas exchange after 7 d of recovery (Lamp et al. 2007). The visual symptoms of hopperburn, measured with a chlorophyll meter, do not appear until approximately 5 d after injury (Granovsky 1928). At this point the plant may have already begun to recover gas exchange.

Potato leafhoppers are reported to cause the most severe damage to young grape leaves (Lamp et al. 2011) and alfalfa re-growth (Backus et al. 2005). Observations in the region have indicated that in years with high abundance of potato leafhopper death of first year hop plants has occurred. It is unclear if potato leafhoppers actually

prefer young hop plants and if this added preference predisposes young plants to be at greater risk for long term damage. Protecting first year plants would be critical as hop production and success in year one sets the stage for this perennial's subsequent production years.

Plants and herbivores have developed complex chemical and physical defense mechanisms through coevolution (Futuyma 2000). Plant resistance to herbivores is a tool used in agriculture to promote bottom-up pest suppression in integrated pest management programs. A range of cultivar susceptibility to potato leafhopper has been shown in alfalfa, grape, dry bean, and potato (Schaafsma et al. 1998, Gonzales et al. 2004, Kaplan et al. 2008, Lamp et al. 2011). Alfalfa cultivars have been bred for chemical resistance to potato leafhopper (Shockly and Backus 2002). Ranger et al. (2005) indicated disorientation followed by deterrent volatile chemistry as the two lines of plant defense in resistant alfalfa cultivars. Resistant cultivars have more dense leaf and stem glandular trichomes (Elden and McCaslin 1997) in comparison to the more susceptible cultivars. Varying degree of damage has been reported on different cultivars of two and three year old plants. It is unclear if potato leafhoppers differ in their preference for specific hop cultivars.

The objectives of this research were to 1) measure the physiological response of first year hop leaves to adult potato leafhopper feeding, 2) measure first year hop leaf recovery from potato leafhopper injury, and 3) compare the physiological response to potato leafhopper feeding between eight hop cultivars.

4.2 Materials and Methods

4.2.1 Cultivar Selection

Eight USDA bred hop cultivars were selected for the leafhopper studies based on two previous years of field scouting. Field potato leafhopper scouting occurred on second and third year old hop plants in a research variety trial containing 22 hop cultivars in Alburgh, VT. The mean number of leafhoppers per leaf counted in 2012 and 2013 are reported in Figure 4.1. Among available and virus free cultivars, four with a mean less than two and four with a mean greater than two leafhoppers per leaf were chosen for this study. Cultivars chosen for field and greenhouse gas exchange experiments included 'Horizon', 'Cascade', 'Centennial', 'Nugget', as low level leafhopper cultivars and 'Newport', 'Mt. Hood', 'Chrystal', 'Liberty' as high level leafhopper cultivars. Second year plugs were purchased and shipped from Great Lakes Hops, Zeeland, MI on 2 April 2014. Vegetative cuttings were taken from mother plants. The rooting end of each cutting was dipped in water, then in rooting hormone powder (Hormonin 1, OHP, Inc., Mainland, PA), and inserted into a 3.2 cm rootcube (Oasis Rootcubes, Oasis Grower Solutions, Kent, OH). Two weeks later, propagated plants were planted into 7.6 x 12.7 cm plastic pots. Plants for the field experiment were planted in a compost based potting mix (Fort Vee, Vermont Compost Company, Montpelier, VT). Plants for the greenhouse experiment were planted in Fafard 3B potting mix (Fafard 3B, Sun Gro Horticulture, Agawam, MA). Field plants were grown for an additional two weeks in the greenhouse at 21 $\pm$ 5°C and then for one week outside in pots before they were transplanted into the ground. Greenhouse plants were grown in pots for seven weeks in the greenhouse at 21 $\pm$ 5°C before experiments and never fertilized. Mother plants were fertilized once per month with 17-4-17 synthetic fertilizer (Jack's Professional LX, Allentown, PA).

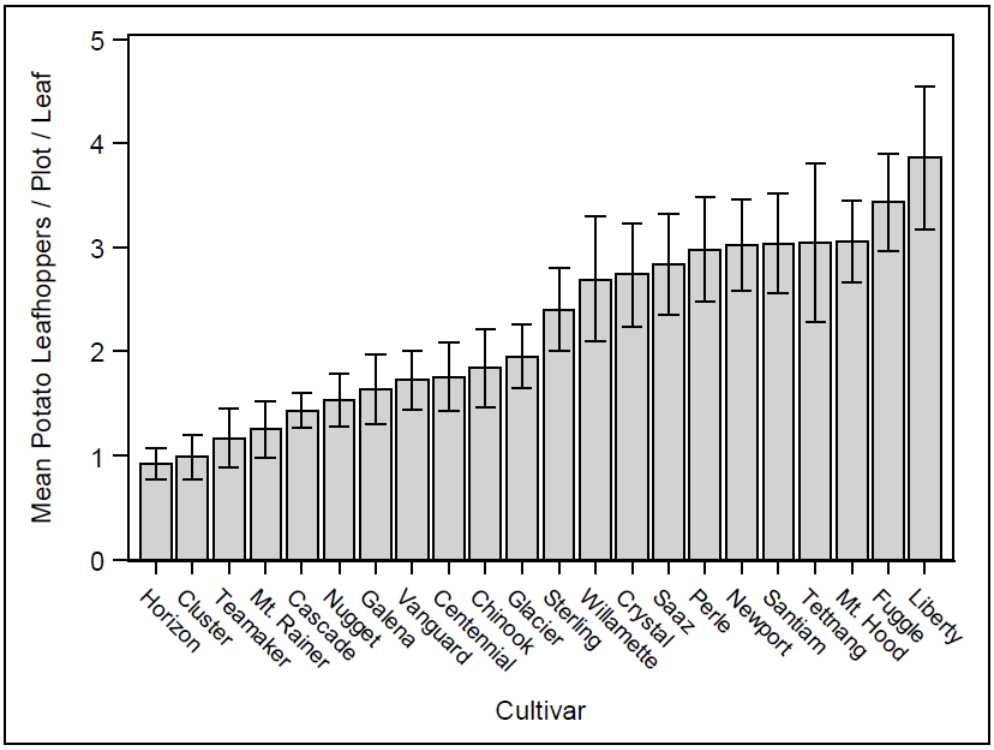

Figure 4.1: The number of potato leafhopper nymphs and adults scouted on hop plants in the field. Values are a mean of 2012 and 2013 potato leafhoppers on second and third year old plants. 'Horizon', 'Cascade', 'Nugget', 'Centennial', 'Crystal', 'Newport', 'Mt. Hood', and 'Liberty' were chosen for further study.

4.2.2 Leafhopper Colony

Potato leafhoppers were collected from an alfalfa field in Grand Isle, VT on August 10, 2013 with a 25 CC 2-cycle gas engine reverse leaf blower (Poulan PRO BVM210VS, Charlotte, NC). They were aspirated, isolated from other field collected insects, and reared on greenhouse grown fava bean, *Vicia faba* var. 'Windsor' (Territorial Seed Co., Cottage Grove, OR). The colony was maintained in several .3 x .3 m mesh cages (S1 Caterpillar Castle, Live Monarch, Boca Raton, FL)in a laboratory room set to 23.8 ± 2 °C under 15:9 (L:D). There were three to four fava bean plants per cage at any given time. Fava bean seeds were planted in Fafard 3B potting mix (Fafard 3B, Sun Gro Horticulture, Agawam, MA). Plants were watered as needed and were not

fertilized.

4.2.3 Field Experiment

A 0.05 ha area was prepared with a moldboard plow, disked, and finished with a spike tooth harrow. On 12 May 2014 a 3 m standard trellis system was constructed on the Benson rocky silt-loam soil type, conventionally managed land. This experimental hop yard was 84 m long x 5.5 m wide. Black 0.9 m wide landscape fabric (Dewitt P3 Pro 5 Weed Barrier Fabric) was stapled down in two rows and holes were cut 0.5 m apart in the fabric before planting. Field plants were planted on 3 June 2014 at Borderview Farm in Alburgh, VT in a split plot randomized complete block design, replicated five times. Each replicate included a "Healthy" control block that was not exposed to potato leafhopper and an "Injured" block that was exposed to adult potato leafhoppers. Each block had two plants/hill of each hop cultivar, for a total of eight hills per plot. Treatment was considered the main plot and cultivar was considered the subplot. After field planting, a drip irrigation system was installed (Drip Irrigation Systems, Growers Supply, Dyersville, IA) and plants were irrigated as needed. The 3.6 m wide drive row was planted with a forage mixture (white and ladino clovers, *Trifolium repens* L. and meadow fescue, *Festuca pratensis* Huds.) using a 3.08 m Kvernaland drill at a rate of 1.4 kg/ha. Drive row ground cover was mowed regularly.

Two leaves of each plant were scouted for two spotted spider mite, hop aphid, and potato leafhopper presence on 1 and 22 July 2014. Two-spotted spider mites and leafhoppers were present in pockets of the experimental hop yard at low levels. All plants were sprayed with Pyganic (Pyganic Crop Protection EC 1.411, MGK, Minneapolis, MN) on 22 July 2014 at a rate of 8.09 fl oz/ha. Naturally occurring pest arthropods were also counted on sampled leaves each collection day.

Net photosynthesis, stomatal conductance, and transpiration were measured using

a LI-6400 Photosynthesis Measurement System (LI-COR Inc., Lincoln, NE). Net photosynthesis and transpiration gas exchange results were more effective than stomatal conductance. Therefore stomatal conductance is reported in Appendix B. A SPAD-501 chlorophyll meter (Konica Minolta Sensing Inc., Japan) was used to measure leaf chlorophyll content. For gas exchange and chlorophyll content measurements, the more vigorous plant per hop hill was selected. On this plant, one of the two leaves of the third leaf pair from the top of the plant was measured. The third leaf-pair is a fully expanded but young hop leaf and has been documented to have trichome density similar to that of leaf-pairs one-seven (Oliveira and Pais 1988). The one sampled leaf per plant was tagged with a silver twist tie, twisted loosely around the leaf pediole. One gas exchange reading was taken per leaf while five SPAD readings were taken per leaf on each collection date. Plants were scouted for two-spotted spider mites, thrips, and aphids before measurements on each collection date. The number of potato leafhoppers left in "Injured" treatment bags was counted when the bag was removed.

LI-6400 and SPAD readings were taken from the same leaf on three dates. The first was a baseline measurement taken on 8 August 2014. Both "Healthy" and to be "Injured" leaves were sampled before any leafhoppers were released. Three, three-five day old adult potato leafhoppers were then aspirated from the colony into 7 x 7cm and 14 x 10 cm white, drawstring mesh bags (Celebrate It Occasions Organza Bags, Michaels, Irving, TX). Hop leaf size varies by cultivar. Two size bags were used to ensure that the bag stayed on each leaf. To attach bags to leaves in "Injured" blocks without losing leafhoppers, a bag was quickly opened, pulled over the hop leaf, and closed. Identical bags were also attached and secured to tagged hop leaves in "Healthy" blocks to account for the influence of the bag on gas exchange. After 3 d of leafhopper exposure LI-6400 and SPAD readings were taken immediately after bags

were removed from leaves on 11 August 2014. The third, collection date measured recovery from potato leafhopper injury and occurred on 29 August 2014, 18 d after bags and leafhoppers were removed. Both LI-6400 and SPAD readings were taken from the same leaf before leafhopper exposure, after leafhopper exposure, and 18 days after leafhopper removal. LI-6400 measurements were taken on sunny days between the hours of 10 am and 2 pm and measured gas exchange under standard levels of CO2 (400 µmol-1) with a leaf area of 6 cm2. The light source was natural light "Sun+Sky". The LI-6400 collected light intensity readings for each gas exchange measurement taken (Fig. 4.2).

4.2.4 Greenhouse Experiment

The field experiment was replicated in the University of Vermont greenhouse in Burlington, VT under the same methods described above. The greenhouse experiment was also conducted in a split plot randomized complete block design, replicated five times. Plants remained in their 7.6 x 12.7 cm plastic pots throughout the duration of their use. Pots were placed randomly within split plot block formation on a south facing greenhouse bench. There were two rounds of this experiment due to plant propagation space limitations. Round one included replications one and two. Round two included replications three, four, and five. In greenhouse experiments LI-6400 and SPAD recovery readings were taken 7 d after potato leafhoppers and bags were removed from leaves.

	Field (± SEM)		Greenhouse (± SEM)	
	3 d	18 d	3 d	7 d
Healthy	1490 (± 39.4)	1613 (± 85.6)	258.1 (± 62.4)	148.6 (± 9.7)
Injured	1452 (± 41.0)	1425 (± 96.1)	257.4 (± 62.4)	146.9 (± 9.8)

Figure 4.2: Light intensity table of means (± SEM). There was no significant difference between treatments in the field or greenhouse.

Plants used in round one were planted on 23 September 2014 and the experiment commenced on 28 October 2014 with baseline LI-6400 and SPAD readings. The second (3 d) and third (7 d) readings were taken on 31 October 2014 and 7 November 2014, respectively. Plants used in the second round were planted on 25 November 2014 and the experiment commenced on 6 January 2015 with baseline LI-6400 and SPAD readings. The second (3 d) and third (7 d) readings were taken on 9 January 2014 and 16 January 2014, respectively. The greenhouse house was climate controlled under the same temperature as the leafhopper colony of 23.8 ± 2 °C and 15:9 (L:D) while plants grew. During experiments the temperature was reduced to 16.6 ± 2 °C in order to keep potato leafhoppers alive inside bags on "Injured" leaves.

4.2.5 Data Analysis

A linear mixed model with repeated measures (PROC MIXED, SAS Institute 2014) was used to evaluate net photosynthesis, transpiration, and chlorophyll in both field and greenhouse hop plants exposed ("Injured") and not exposed ("Healthy") to potato leafhopper. The mean of five SPAD readings per collection date was used for chlorophyll analyses. LI-6400 and SPAD data from the field and greenhouse were analyzed separately. Gas exchange and chlorophyll measurements were analyzed within individual days of data collection. Baseline Measurement and Day 3 Measurement were included in each model to account for the effect of leaf history. The fixed effects for the post exposure measurement (3 d) included the number of potato leafhoppers still alive after bags were removed ("PLH Alive"), the number of two-spotted spider mites on sampled leaves ("TSSM"), Baseline Measurement, Treatment, Cultivar, and Cultivar x Treatment. The fixed effects for the recovery measurement included Day 3 Measurement, Treatment, Cultivar, and Cultivar x Treatment. Light intensity analysis showed no significant difference between treatments and was therefore not

included in models. Cultivar 'Horizon' grew poorly in the field making 18 d recovery readings impossible. Therefore, 'Horizon' was removed from the field 18 d analysis. All statistics were run at the 0.05 LOS and generated using SAS software, Version 9.4 (Copyright 2014 by SAS Institute Inc., Cary, NC, USA).

4.3 Results

4.3.0.1 Field Experiment

After three days of leafhopper feeding, neither the number of leafhoppers left in bags nor the number of two-spotted spider mites counted on sampled leaves had an effect on gas exchange or chlorophyll. Baseline measurements did not have a significant effect on gas exchange or chlorophyll. There was a significant effect of treatment where injured leaves showed a reduction in gas exchange and chlorophyll content. Net photosynthesis was reduced by 32.8% and transpiration was reduced by 53.0%. There was a significant effect of cultivar on gas exchange and chlorophyll content. There was no significant interaction between cultivar and treatment for net photosynthesis or chlorophyll. There was a significant interaction between cultivar and treatment for transpiration (Table 1).

Eighteen days after potato leafhoppers were removed, the day 3 measurement had a significant effect on gas exchange and chlorophyll. There was no significant effect of treatment on gas exchange or chlorophyll indicating that leaves recovered from leafhopper injury. Cultivar did not have a significant effect on gas exchange. There was a significant effect of cultivar on chlorophyll content where injured leaves had lower chlorophyll content. This is likely due to high 'Liberty' values (Fig. A.21). There was no significant interaction between cultivar and treatment (Table 1).

Table 4.1: Field ANOVA summary statistics of gas exchange and chlorophyll on single leaves of eight cultivars exposed to potato leafhoppers for 3 d and 18 d after leafhopper removal.

Effects	Days After Exposure	Net Photosynthesis[a]		Transpiration[b]		Chlorophyll[c]	
Field		F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
PLH Alive	3	0.1 (1, 56)	0.72	1.8 (1, 56)	0.19	2.5 (1, 54)	0.12
TSSM		0.0 (1, 54.8)	0.92	0.0 (1, 56)	0.99	1.5 (1, 54)	0.22
Baseline Measurement		0.8 (1, 55.5)	0.37	0.2 (1, 55.3)	0.68	5.3 (1, 56)	**0.02**
Treatment		13.8 (1, 55.8)	**0.0005**	35.6 (1, 55.8)	< **0.0001**	3.8 (1, 56)	**0.0005**
Cultivar		3.5 (7, 52.9)	**0.003**	3.9 (7, 52.5)	**0.002**	5.1 (7, 56)	**0.004**
Cultivar x Treatment		0.8 (7, 52.7)	0.56	3.5 (7, 52.3)	**0.004**	1.2 (7, 56)	0.29
Day 3 Measurement	18	4.5 (1, 47)	**0.04**	12.7 (1, 46.1)	**0.001**	35.0 (1, 45)	< **0.0001**
Treatment		0.8 (1, 47)	0.38	0.3 (1, 45.5)	0.58	3.1 (1, 45)	0.08
Cultivar		1.3 (6, 47)	0.28	1.1 (6, 43.2)	0.40	3.7 (6, 45)	**0.005**
Cultivar x Treatment		0.9 (6, 47)	0.51	1.1 (6, 43.3)	0.39	0.6 (6, 45)	0.68

[a] Units are µmol Co_2 $m^{-2}s^{-1}$

[b] Units are mmol H_2O $m^{-2}s^{-1}$

[c] Units are SPAD

Horizon' is not included in 18 d.

Table 4.2: Field means (± SEM) of gas exchange and chlorophyll on single leaves of eight cultivars exposed to potato leafhoppers for 3 d and 18 d after leafhopper removal. Significance is noted where "Healthy" treatment mean was significantly higher than "Injured" at the 0.05 LOS.

Field	Treatment	3 Day Injury Mean (± SEM)	18 Day Recovery Mean (± SEM)
Net Photosynthesis	Healthy	9.10 (± 0.57)*	14.46 (± 0.84)
Transpiration	Healthy	2.17 (± 0.11)*	1.68 (± 0.12)
Chlorophyll	Healthy	32.93 (± 0.61)*	41.60 (± 0.76)
Net Photosynthesis	Injured	6.12 (± 0.61)*	15.69 (± 0.87)
Transpiration	Injured	1.02 (± 0.12)*	1.75 (± 0.12)
Chlorophyll	Injured	31.17 (±0.67)*	39.67 (± 0.76)

*Indicates mixed model treatment significance at the .05 level.

Horizon' is not included in18 day Field means.

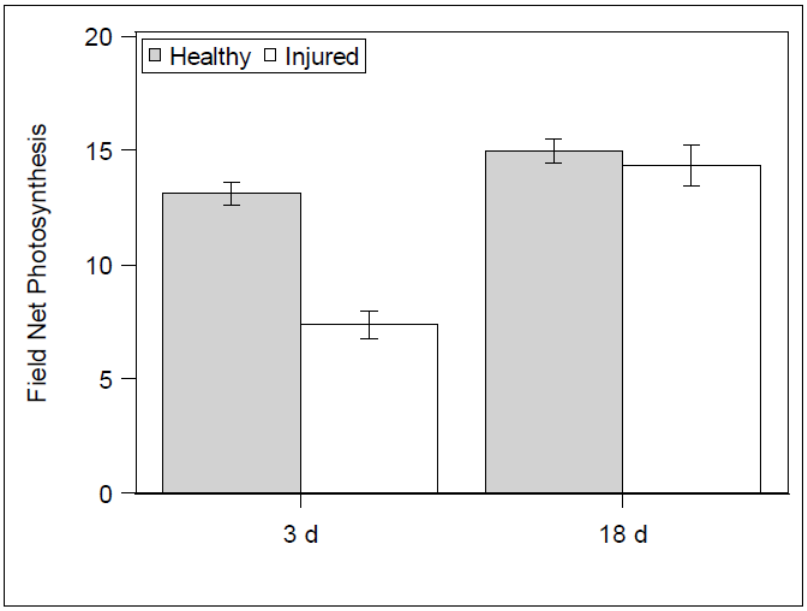

Figure 4.3: Mean field net photosynthesis (µmol Co_2 $m^{-2}s^{-1}$) by treatment after 3 d of exposure to three adult potato leafhoppers and 18 d after feeding injury.

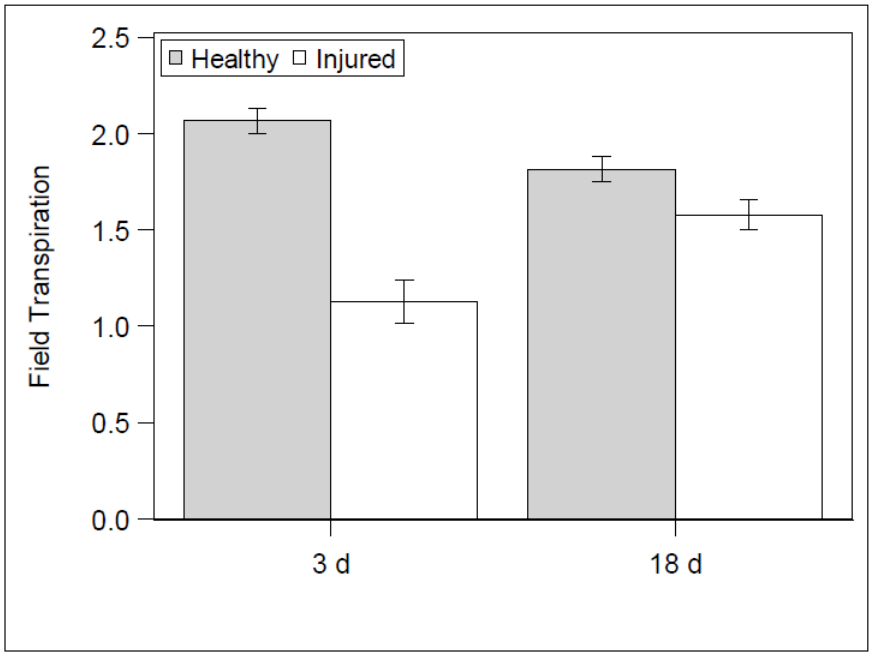

Figure 4.4: Mean field transpiration (mmol H_2O $m^{-2}s^{-1}$) by treatment after 3 d of exposure to three adult potato leafhoppers and 18 d after feeding injury.

4.3.1 Greenhouse Experiment

After three days of leafhopper feeding, neither the number of leafhoppers left in bags nor the number of two-spotted spider mites counted on sampled leaves had an effect on gas exchange or chlorophyll. Baseline measurements did not have a significant effect on net photosynthesis. Baseline measurement did have a significant effect on transpiration and chlorophyll. There was a significant effect of treatment where Injured leaves showed a reduction in gas exchange. Net photosynthesis was reduced by 55.9% and transpiration was reduced by 65.6%. There was no significant effect of treatment on chlorophyll content. There was no significant effect of cultivar on gas exchange. There was a significant effect of cultivar on chlorophyll content where Healthy leaf pigment was slightly lower than Injured. There was no significant interaction between cultivar and treatment for gas exchange or chlorophyll (Table 3).

Seven days after potato leafhoppers were removed there was no significant effect of day 3 measurement on gas exchange. There was a significant effect of day 3 history on chlorophyll content. There was not a significant effect of treatment on net photosynthesis indicating that leaves restored gas exchange. Treatment did have a slightly significant effect on transpiration where Injured leaves remained lower than Healthy leaves. Treatment also had a significant effect on chlorophyll where Injured leaves had lower chlorophyll content likely due to hopperburn. Cultivar did not have a significant effect on gas exchange. There was a significant effect of cultivar on chlorophyll content likely due to low 'Liberty' values. There was no significant interaction between cultivar and treatment for gas exchange. However, there was a significant interaction between cultivar and treatment for chlorophyll, also likely due to low 'Liberty' values (Table 3, Fig. A.27).

Table 4.3: Greenhouse ANOVA summary statistics of gas exchange and chlorophyll on single leaves of eight cultivars exposed to potato leafhoppers for 3 d and 7 d after leafhopper removal.

Effects	Days After Exposure	Net Photosynthesis[a]		Transpiration[b]		Chlorophyll[c]	
Greenhouse		F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
PLH Alive	3	0.1 (1, 53.8)	0.74	0.4 (1, 54.7)	0.53	0.01 (1, 53)	0.92
TSSM		2.5 (1, 56.7)	0.12	2.8 (1, 57)	0.10	1.02 (1, 53)	0.32
Baseline Measurement		0.1 (1, 54)	0.74	15.6 (1, 56.6)	**0.0002**	30.2 (1, 54.9)	< **0.0001**
Treatment		9.4 (1, 54)	**0.003**	32.6 (1, 54.8)	< **0.0001**	0.1 (1, 54.1)	0.74
Cultivar		1.3 (7, 53.3)	0.26	1.1 (7, 53.7)	0.36	2.3 (1, 51.9)	**0.04**
Cultivar x Treatment		0.6 (7, 53.1)	0.75	1.2 (7, 53.2)	0.35	1.9 (7, 51.6)	0.09
Day 3 Measurement	7	0.0 (1, 53)	0.97	0.4 (1, 53)	0.51	29.3 (1, 51)	< **0.0001**
Treatment		0.0 (1, 53)	0.90	4.0 (1, 53)	**0.05**	9.6 (1, 51)	**0.003**
Cultivar		1.3 (7, 53)	0.27	1.35 (7, 53)	0.24	2.8 (7, 51)	**0.04**
Cultivar x Treatment		0.6 (7, 53)	0.73	0.8 (7, 53)	0.60	2.6 (7, 51)	**0.02**

[a] Units are μmol $Co_2 m^{-2} s^{-1}$

[b] Units are mmol $H_2O\, m^{-2} s^{-1}$

[c] Units are SPAD

Table 4.4: Greenhouse means (± SEM) of gas exchange and chlorophyll on single leaves of eight cultivars exposed to potato leafhoppers for 3 d and 7 d after leafhopper removal. Significance is noted where "Healthy" treatment mean was significantly higher than "Injured" at the 0.05 LOS.

Greenhouse	Treatment	3 Day Injury Mean (± SEM)	7 Day Recovery Mean (± SEM)
Net Photosynthesis	Healthy	2.65 (± 0.43)*	0.82 (± 0.37)
Transpiration	Healthy	0.96 (± 0.08)*	0.50 (± 0.04)
Chlorophyll	Healthy	28.01 (± 0.97)	29.88 (± 0.74)*
Net Photosynthesis	Injured	1.17 (± 0.43)*	0.89 (± 0.45)
Transpiration	Injured	0.33 (± 0.08)*	0.36 (± 0.05)
Chlorophyll	Injured	28.47 (± 1.03)	26.33 (± 0.87)*

*Indicates mixed model treatment significance at the .05 level.

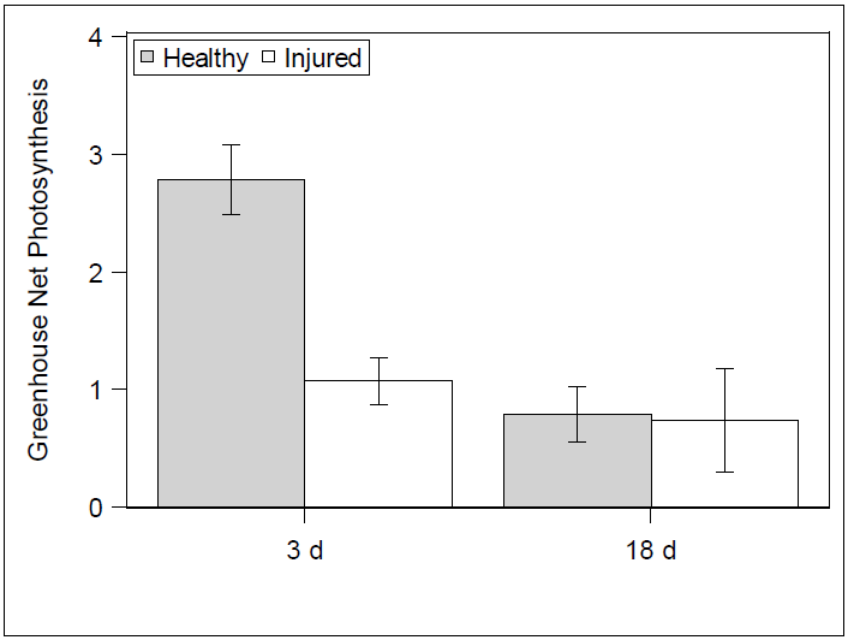

Figure 4.5: Mean greenhouse net photosynthesis (µmol Co_2 $m^{-2}s^{-1}$) by treatment after 3 d of exposure to three adult potato leafhoppers and 7 d after feeding injury.

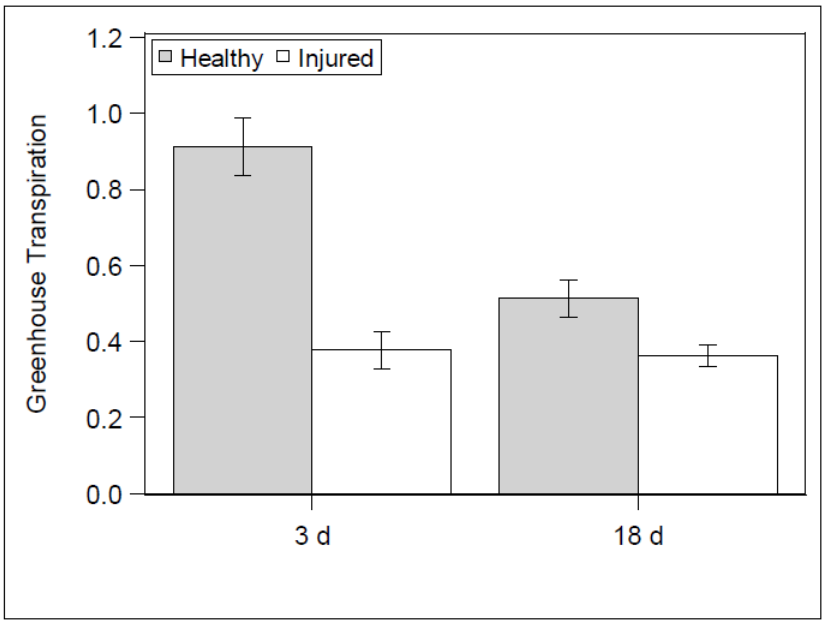

Figure 4.6: Mean greenhouse transpiration (mmol H_2O $m^{-2}s^{-1}$) by treatment after 3 d of exposure to three adult potato leafhoppers and 7 d after feeding injury.

4.4 Discussion

The primary objective of this research were to measure the physiological response of first year hop leaves to adult potato leafhopper feeding and determine if these leaves are able to recover from the injury. Potato leafhopper feeding on one year old plants reduced net photosynthesis by 32.8% in the field and 53.0% in the greenhouse. If three days of exposure to three leafhoppers resulted in 50% reduction in gas exchange it is plausible to think that repeated exposure even at low levels of leafhoppers could lead to death of a plant with limited foliage growth such as that of first year plants .

Under the second objective of this research, when leafhoppers were removed, gas exchange was restored. This finding suggests that if potato leafhoppers were removed, plants could recover from the damage incurred. The current option for potato leafhopper removal is broad-spectrum insecticide application. Hop research conducted in the Pacific Northwest indicates high risk of yield and quality loss from secondary outbreaks of two-spotted spider mites when broad-spectrum insecticide sprays are applied to control hop aphid (Phorodon humuli Schrank) (James and Price 2002, James 2003). In efforts to control potato leafhopper Vermont, growers have sprayed broad-spectrum products. This action has also resulted in two-spotted spider mite secondary outbreak. It will be important to further our understanding of economic thresholds for potato leafhoppers in first year plants to limit application of pesticides that may have other indirect effects.

The final objective of this experiment was to compare the physiological response to potato leafhopper feeding between eight hop cultivars. Hop cultivars did not vary in physiological response to adult potato leafhopper feeding on leaves of first year plants. Regardless of cultivar, potato leafhopper feeding reduced gas exchange significantly in field and greenhouse experiments. Variation in cultivar resistance to

potato leafhopper damage has been observed in older hop plants (Fig. 4.1). It is unclear if first year hop plants have different cues that influence leafhopper feeding preference over older plants. Host plant color has been shown to be the mechanism behind potato leafhopper feeding preference in dry bean (Bullas-Appleton 2004). In addition, this experiment did not provide the leafhoppers with a cultivar choice, forcing leafhoppers to feed the leaf presented. If provided a choice between cultivars in a hop yard potato leafhoppers may show preference for some cultivars over others. Shockley and Backus (2002) provided supportive evidence where potato leafhoppers settled on resistant alfalfa cultivars when no alternative is presented.

Cultivars of other host plants range in resistance to potato leafhopper and we suggest further research on hop leaf morphology and chemistry in order to understand hop cultivar resistance to potato leafhopper (Shockly and Backus 2002, Lefko et al. 2000). The abaxial side of hop leaves have two types of glandular trichomes: peltate and bulbous. Both are present on hop cone bracts and leaves with the highest concentration in hop cones (Oliveira and Pais 1988). Peltate trichomes are commonly referred to as lupulin glands. Female hop cones are harvested for essential oil and bittering compounds secreted by both trichome types for beer brewing. Therefore, hundreds of hop cultivars have been bred for their variation in hop cone lupulin gland chemical composition (Almaguer et al. 2014). These breeding choices may have an effect on bottom-up pest suppression.

Many new hop yards in the Northeast are adjacent to perennial mixed stands of grass and legumes. There have been several reports to Extension of potato leafhopper migration to hop yards directly after cutting nearby perennial forage. While adult potato leafhoppers survived on fava bean, alfalfa, and grape, potato leafhopper nymphs preferred fava bean over alfalfa and grape (Lamp et al. 2011). Choice experiments should address potato leafhopper preference between alfalfa, clover, and hop.

Cover and trap crop habitat management is feasible given the layout of hop yards. Evidence is provided in Chapter 3 for potato leafhopper preference for red clover over hop. If a preferred host plant was planted in or surrounding hop yards adjacent to harvested alfalfa fields, potato leafhopper damage to hops could be reduced and insecticide applications avoided.

The current option for potato leafhopper removal is broad-spectrum insecticide application. Hop research conducted in the Pacific Northwest indicates high risk of yield and quality loss from secondary outbreaks of two-spotted spider mites when broad-spectrum insecticide sprays are applied to control hop aphid (James and Price 2002, James 2003). In efforts to control potato leafhopper Vermont, growers have sprayed broad-spectrum products. This action has also resulted in two-spotted spider mite secondary outbreak. In agreement with the National Research Council (1996), cultivar resistance and habitat management schemes are the future of pest management. This work sets the stage for economic threshold development and studies that address hop cultivar resistance to potato leafhopper.

CHAPTER 5

COMPREHENSIVE BIBLIOGRAPHY

Almaguer, C., Schonberger, C., Gastl, M., Arendt, E., Becker, T. 2014. *Humulus lupulus* - a story that begs to be told. A review. J. Brew. Distilling 120, 289-314.

Alston, D. 1994. Effect of apple orchard floor vegetation on density and dispersal of phytophagous and predaceous mites in Utah. Agric. Ecosyst. Environ. 50, 73-84.

Backus, E., Serrano, M., and Ranger, C. 2005. Mechanisms of hopperburn: an overview of insect taxonomy, behavior, and physiology. Annu. Rev. Entomol. 50, 125-151.

Bajwa, W. and M. Kogan. 2002. Compendium of IPM Definitions: what is IPM and how is it defined in the Worldwide Literature? IPPC Publication No. 998. Integrated Plant Protection Center, Oregon State University. Corvallis, OR.

Barber, A., Campbell, C., Crane, H., Lilley, R. 2003. Biocontrol of two-spotted spider mite *Tetranychus urticae* on dwarf hops by the Phytoseiid mites *Phytoseiulus persimilis* and *Neoseiulus californicus*. Biocontrol Sci.Technol. 13, 275-284.

Bavec, F., Ceh Breznik, B., and Breznik, M. 2003. Hop yield evaluation depending on experimental plot area under different nitrogen management. Plant Soil Environ. 4, 163-167.

Bugg, R., and Dutcher, D. 1993. *Sesbania-exaltata* (Rafinesque-Schmaltz) Cory (Fabaceae) as a warm season cover crop in pecan orchards - effects on aphidophagous Coccinellidae and pecan aphids. Biol. Agric. Hort. 9, 215-229.

Bullas-Appleton, E., Otis, G., Gillard, C., & Schaafsma, A. 2004. Potato leafbopper (Homoptera : Cicadellidae) varietal preferences in edible beans in relation to visual and olfactory cues. J. Environ. Entomol. 33, 1381-1388.

Burrack, H., Smith, J., Pfeiffer, D., Koeher, G., and Laforest, J. 2012. Using volunteer-based networks to track *Drosophila suzukii* (Diptera: Drosophilidae) an invasive pest of fruit crops. J. Int. Pest Mgmt. 4, 1-5.

Campbell, C. 1983. Antibiosis in hop (*Humulus lupulus*) to the damson-hop aphid, *Phorodon humuli*. Entomol. Exp. Appl. 33, 57-62.

Campbell, C. 1977. Distribution of damson-hop aphid (*Phorodon humuli*) migrants on hops in relation to hop variety and wind shelter. Annal. Appl. Biol. 87, 315-325.

Campbell, C. and Cone, W. 1994. Influence of predators on population development of *Phorodon humuli* (Homoptera: Aphididae) on hops. Pest Manag. Samp. 23, 1391-1396.

DeLong, D. 1971. The bionomics of leafhoppers. Annu. Rev. Entomol. 16, 179-210.

Delay, B., Mamidala, P., Wijeratne, A., Wijeratne, S., Mittapalli, O., Wang, J., & Lamp, W. (2012). Transcriptome analysis of the salivary glands of potato leafhopper, Empoasca fabae. J. Insect Physiol., 58, 1626-1634.

Degooyer, T., Pedigo, L., and Rice, M. 1998. Evaluation of grower-oriented sampling techniques and proposal of a management program for potato leafhopper (Homoptera, Cicadellidae) in alfalfa J. Econ. Entomol. 91, 143-149.

Dorschner, K., and Baird, C. 1988. Susceptibility of hop to *Phorodon humuli*. Exp. Appl. Entomol. 49, 245-250.

Ehrlich, P., and Raven, P. (1964). Butterflies and plants: a study in coevolution. Soc. Study Evol., 18, 586-608.

Elden, T. and McCaslin, M. 1997. Potato leafhopper (Homoptera: Cicadellidae) resistance in perennial glandular-haired alfalfa clones. Plant Res. 90, 842-847.

Felland, C., and Hull, L. 1996. Overwintering of *Stethorus punctum punctum* (Coleoptera: Coccinellidae) in apple orchard ground cover. J. Environ. Entomol. 25, 972-976.

Flinn, P., Hower, A., and Knievel, D. 1990. Physiological response of alfalfa to injury by *Empoasca fabae* (Homoptera: Cicadellidae). Environ. Entomol. 19, 176-181.

Futuyma, D. 2000. Some current approaches to the evolution of plant-herbivore interactions. Plant Sp. Biol. 15, 1-9.

Hop Growers of America. 2014. US hop acreage estimate. Yakama, WA. 1-2.

Geneau, C., Felix, W., Luka, H., Daniel, C., Balmer, O. 2012. Selective flowers to enhance biological control of cabbage pests by parasitoids. Basic and Appl. Ecol. 13, 85-93.

Gent, D.H., James, D., Wright, L., Brooks, D., Barbour, J., Dreves, A., Fisher, G., Walton, V. 2009a. Effects of powdery mildew fungicide programs on two-spotted spider mite (Acari: Tetranychidae), hop aphid (Hemiptera: Aphididae), and their natural enemies in hop yards. Hort. Entomol. 102, 274-286.

Gent, D., Barbour, J., Dreves, A., James, D., Parker, R., Walsh, D. (Eds). 2009b. Field guide for integrated pest management in hops. Vol. 1. Oregon State University, University of Idaho, U.S. Department of Agriculture - Agricultural Research Service, and Washington State University.

Gent, D. H., Nelson, M. E., Grove, G. G., Mahaffee, W. F., Turechek, W. W., Woods, J. L. 2012. Association of spring pruning practices with severity of powdery mildew and downy mildew on hop. Plant Dis. 96, 1343-1351.

Goenia, A., and Micibski, B. 1972. The influence of term of rootstock cutting on the spring infestation of hop with *Peronospora*. Rocz. Nauk Roln., 2, 7-22.

Goller, E., Nunnenmacher, L., Goldbach, H. 1997. Faba beans as a cover crop in organically grown hops: influence on aphids and aphid antagonists. Biol. Agric. Hort. 15, 279-284.

Gontijo, L., Beers, E., and Snyder, W. 2013. Flowers promote aphid suppression in apple orchards. Biol. Control. 66, 8-15.

Gonzales, J., Coyne, D., Lindgren, D., Schaaf, D., Eskridge, K. 2004. Heritability of the resistance to potato leafhopper in dry bean. Hort. Sci. 39, 1578-1580.

Grasswitz, T., and James, G. 2009. Influence of hop yard ground flora on invertebrate pests of hops and their natural enemies. J. Appl. Entomol. 133, 210-221.

Grasswitz, T., & James, D. 2011. Phenology and impact of natural enemies associated with the hop looper (*Hypena humuli*) in Washington State, USA. Int. J. Pest Manag, 57, 329-339.

Gurbinger, V. 2014. 2014 spotted wing drosophila update. Vermont Cooperative Extension Bulletin, University of Vermont, Burlington, VT.

Gunson, F., & Hutchins, R. (1981). Absence of farnesol in strawberry and hop foliage. J. Chem. Ecol. 8, 785-795.

Hairston, N., Smith, F., and Slobodkin, L. 1960. Community structure, population control, and competition. Am. Nat. 94, 421-425.

Harwood, J. and Obrycki, J. 2007. Web-site selection strategies of linyphiid spiders in alfalfa: implications for biological control. BioControl. 52, 451-467.

Huffaker, C., Vrie, M., and McMurty, J. 1969. The ecology of tetranychid mites and their natural control. Annu. Rev. of Entomol. 14, 125-174.

Hunger, R., and Horner, C. 1982. Control of hop downy mildew with systemic fungicides. Plant Dis. 66, 1157-1159.

Hunter, W., and Backus, E. 1989. Mesophyll-feeding by potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae): results from electronic monitoring and thin layer chromatography. Environ. Entomol. 18, 465-472.

James, D., and Coyle, J. 2001. Which pesticides are safe to beneficial insects and mites? Agr. Environ. News. 178, 12-14.

James, D. 2002. Selectivity of the acaricide, befenazate, and aphicide, pymetrozine, to spider mite predators in Washington hops. Int. J. Acarol. 28, 175-179.

James, D. 2003. Pesticide susceptibility of two Coccinellids (*Stethorus punctum picipes* and *Harmonia axyridis*) important in biological control of mites and aphids in Washington hops. Biocontrol Sci. Techn. 13, 253-259.

James, D. 2003b. Toxicity of imidacloprid to *Galendromus occidentalis*, *Neoseiulus fallacis* and *Amblyseius andersoni* (Acari: Phytoseiidae) from hops in Washington State, USA. Exp. Appl. Acarol. 31, 275-281.

James, D. 2006. Methyl salicylate is a field attractant for the goldeneyed lacewing, *Chrysopa oculata*. Biocontrol Sci. Technol. 16, 107-110.

James, D., Castle, S., Grasswitz, T., Reyna, V. 2005. Using synthetic herbivore-induced plant volatiles to enhance conservation biological control: field experiments in hops and grapes, 192-205. In Proceedings, Second International Symposium on Biological Control of Arthropods, Davos, Switzerland.

James, D. and Price, T. 2002. Fecundity in two spotted spider mite (Acari: Tetranychidae) is increased by direct and systemic exposure to imidicloprid. J. Econ. Entomol. 95, 729-732.

James, D., and Price, T. 2004. Field-testing of methyl salicylate for recruitment and retention of beneficial insects in grapes and hops. J. Chem. Ecol. 30, 1613-1628.

James, D., Price, T., and Wright, L. 2003. Mites and aphids in Washington hops: candidates for augmentative or conservation biological control, 189-194. In Proceedings, First International Symposium on Biological Control of Arthropods, Honolulu, HI.

James, D. 2003a. Pesticide susceptibility of two Coccinellids (*Stethorus punctum picipes* and *Harmonia axyridis*) important in biological control of mites and aphids in Washington hops. Biocontrol Sci. Technol.13, 253-259.

James, D. 2003b. Toxicity of imidacloprid to *Galendromus occidentalis*, *Neoseiulus fallacis* and *Amblyseius andersoni* (Acari: Phytoseiidae) from hops in Washington State, USA. Exp. Appl. Acarol. 31, 275-281.

James, D. and Price, T. 2002. Fecundity in two spotted spider mite (Acari: Tetranychidae) is increased by direct and systemic exposure to imidicloprid. J. Econ. Entomol. 95, 729-732.

Jeppson, L., Keifer, H., Baker, E. 1975. Mites injurious to economic plants. University of California Press, Berkeley and Los Angeles, CA. Kaplan, I., Dively, G., & Denno, R. 2008. Variation in tolerance and resistance to the leafhopper *Empoasca fabae* (Hemipetera: Cicadellidae) among potato cultivars: implications for action thresholds. J. Econ. Entomol. 101, 959-968.

Kennedy, J. 1860. Eighth Census of Agriculture, Vermont. United States Department of Agriculture. Washington, DC. Kralj, D., Kac, M., Dolinar, M., Zolnir, M., Kralj, S. 1998. Marker-assisted hop (Humulus lupulus L.) breeding. Monat. Brauw. 7, 111-119.

Lamp, W. O., Miranda, D., Culler, L., Alexander, L. 2011. Host suitability and gas exchange response of grapevines to potato leafhopper (Hemiptera: Cicadellidae). J. Econ. Entomol. 104, 1316-1322.

Lamp, W. O., Alexander, L., and Nguyen, M. 2007. Physiological response of glandular-haired alfalfa to potato leafhopper (Hemiptera: Cicadellidae) injury. J. Environ. Entomol. 36, 195-203.

Lamp, W., Nielsen, G., Fuentes, C., and Quebedeaux, B. (2004). Feeding site preference of potato leafhopper (Hemiptera: Cicadellidae) on alfalfa and its effect on photosynthesis. J. Agric. Urban Entomol. 21, 25-38.

Lamp, W. O., Nielsen, G., and Danielson, S. 1994. Patterns among host plants of potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae). J. of the Kansas Entomol. Soc. 67, 354-368.

Lamp, W., Nelson, M., and Dively, G. 1991. Insect pest-induced losses in alfalfa: patterns in Maryland and implications for management. J. Econ. Entomol. 84, 610-618.

Landis, D., Wratten, S., and Gurr, G. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45, 175-201.

Lenz, M., Isaacs, R., Flore, J., Howell, G. 2012. Photosynthetic performance of Pinot gris (*Vitis vinifera* L.) grapevine leaves in response to potato leafhopper (*Empoasca fabae* Harris) infestation. Amer. J. Enol. Vitic. 63, 357-366.

Lewis, W., van Lenteren, J., Phatak, S., and Tumlinson, J. (1997). A total ecosystem approach to sustainable pest management Proc. Natl. Acad. Sci. 94, 12243-12248.

Lindgren, D., and Coyne, D. 1995. Injury and yield of leafhopper-infested dry beans. J. Amer. Soc. Hort. Sci. 120, 839-842.

Lipecki, J., and Berbec, S. 1997. Soil management in perennial crops: orchards and hop gardens. Soil Till. Res. 43, 169-184.

Lorenzana, A., Hermoso-de-Mendoza, M., Seco, M., Casquero, P. 2013. Population dynamics and integrated control of the damson-hop aphid *Phorodon humuli* (Schrank) on hops in Spain. Span. J. of Agric. Res. 11, 505-517.

Lorenzana, A., and Hermoso, A. 2010. Population development of *Phorodon humuli* and predators (*Orius* spp.) within hop cones: influence of aphid density on hop quality. Crop Prot. 29, 832-837.

Lorenzana, A., Hermoso de Mendoza, A., and Seco, M. 2009. Thresholds for management of *Phorodon humuli* (Hemiptera: Aphididae) on hops. J. Entomol. Sci. 44, 198-208.

Lovinger, A., Liewehr, D., & Lamp, W. 2000. Glandular trichomes on alfalfa impede searching behavior of the potato leafhopper parasitoid. Biol. Control, 18, 187-192.

Lu, Z.-X., Zhu, P.-Y., Gurr, G., Zheng, X., Read, D., Heong, K., Yang, Y., Xu, H. 2014. Mechanisms for flowering plants to benefit arthropod natural enemies of insect pests: prospects for enhanced use in agriculture. Insect Sci. 21, 1-12.

Magie, R. O. 1944. Disease and insect control on hops; technical bulletin 708. New York State Agricultural Experiment Station. Cornell University. Geneva, NY.

Magie, R. O. 1942. The epidemiology and control of downy mildew on hops; technical bulletin 267. New York State Agricultural Experiment Station, Cornell University. Geneva, NY.

Mahaffee, W., S. Pethybridge and D. Gent (Eds). 2009. Compendium of hop diseases and pests. APS Press, St. Paul, MN.

Martinez, D., and Pienkowski, R. 1982. Laboratory studies on insect predators of potato leafhopper eggs, nymphs, and adults. Environ. Entomol. 11, 361-362.

Mattson, P. (2000). Insect pest management in tropical Asian irrigated rice. Annu. Rev. Entomol. 45, 549-574.

National Research Council. 1996. Ecologically based pest management: new solutions for a new century. National Academy Press, Washington, DC.

Neve, R. 1991. Hops. Chapman and Hall, London, United Kingdom.

Nielsen, G., Lamp, W., and Stutte, G. 1990. Potato leafhopper (Homoptera: Cicadellidae) feeding disruption of phloem translocation in alfalfa. J. Econ. Entomol. 83, 807-813.

Oliveira, M., and Pais, M. 1988. Glandular trichomes of *Humulus lupulus* var. Brewer's Gold: ontogeny and histochemical characterization of the secretion. Nord. J. Bot. 8, 349-359.

Paine, R. (1966). Food web complexity and species diversity. Am. Nat., 100, 65-75.

Peters, K., and Berry, R. 1980. Effect of hop leaf morphology on two spotted spider mite. J. Econ. Entomol., 73, 235-238.

Ranger, C., and Hower, A. 2001. Role of the glandular trichomes in resistance of perennial alfalfa to the potato leafhopper (Homoptera: Cicadellidae). J. Econ. Entomol. 94, 950-957.

Raworth, D. (1994). Estimation of degree-days using temperature data recorded at regular intervals. Popul. Ecol. 23, 893-899.

Regev, S., & Cone, W. 1975. Chemical differences in hop varieties vs. susceptibility to the two spotted spider mite. Environ. Entomol. 4, 697-700.

Riechert, S., & Lockley, T. 1984. Spiders as biological control agents. Annu. Rev. Entomol., 29, 299-320.

Rieux, R., Simon, S., and Defrance, H. 1999. Role of hedgerows and ground cover management on arthropod populations in pear orchards. Agric. Ecosyst. Environ. 73, 119-127.

Root, R. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol. Monog. 43, 94-125.

Rusch, A., Valantin-Morison, M., Sarthou, J., Roger-Estrade, J. 2010. Biological control of insect pests in agroecosystems: effects of crop management, farming systems, and semi-natural habitats at the landscape scale. A review. Adv. Agron. 109, 219-259.

Sarthou, J., Badoz, A., Vaissiere, B., & Chevallier, A. 2014. Local more than landscape parameters structure antural enemy communities during their overwintering in semi-natural habitats. Agric. Ecosyst. Environ. 194, 17-28.

SAS Institute Inc. 2014. SAS/STAT software 9.4. SAS Institute Cary, NC.

Schaafsma, A., Cardona, C., Kornegay, J., and Wylde, A. 1998. Resistance of common bean lines to the potato leafhopper (Homoptera: Cicadellidae). J. Econ. Entomol. 91, 981-986.

Schweiger, O., Maelfait, J., Windgerden, W., Hendrickx, F., Billeter, R., Spellmans, M. 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J. Appl. Ecol. 42, 1129-1139.

Seefelder, S., Ehrmaier, H., Schweizer, G., and Seigner, E. 2000. Genetic diversity and phylogenetic relationships among accessions of hop, *Humulus lupulus*, as determined by amplified fragment length polymorphism fingerprinting compared with pedigree data. Plant Breeding 119, 257-263.

Sher, R., and Shields, E. 1991. Potato leafhopper (Homoptera: Cicadellidae) oviposition and development under cool fluctuating temperatures. Environ. Entomol. 20, 1113-1120.

Shockley, F., and Backus, E. 2002. Repellency to the potato leafhopper (Homoptera: Cicadellidae) by erect glandular trichomes on alfalfa. Physiol. Chem. Ecol. 31, 22-29.

Sidumo, A. J., Shields, E., and Lembo, A. 2005. Estimating the potato leafhopper *Empoasca fabae* (Homoptera: Cicadellidae) overwintering range and spring premigrant development by using geographic information system. J. Econ. Entomol. 98, 757-764.

Silva, E., Franco, J., Vasconcelos, T., and Branco, M. 2010. Effect of ground cover vegetation on the abundance and diversity of beneficial arthropods in citrus orchards. Bull. Entomol. Res. 100, 489-499.

Simon, S., Bouvier, J.-C., Debras, J.-F., Sauphanor, B. 2009. Biodiversity and pest management in orchard systems. A review. Agron. Sustain. Dev. 30, 139-152.

Simonet, D., and Pienkowski, R. 1980. Temperature effect on development and morphometrics of the potato leafhopper. J. Environ. Entomol. 9, 798-800.

Sigsgaard, L. 2002. A survey of aphids and aphid parasitoids in cereal fields in Denmark, and the parasitoids' role in biological control. J. Appl. Entomol. 126, 101-107.

Skotland, C., and Johnson, D. 1983. Control of downy mildew of hop. Amer. Phytopathol. Soc. 1183-1185.

Smith, M., Arnold, D., Eikenbary, D., Rice, N., Shiferaw, A., Cheary, B., Carroll, B. 1995. Influence of ground cover on beneficial arthropods in pecan. Biol. Control 6, 164-176.

Stajner, N., Satovic, Z., Cerenak, A., and Javornik, B. 2008. Genetic structure and differentiation in hop (*Humulus lupulus* L.) as inferred from microsatellites. Euphytica

161, 301-311.

Staudter, K. and Krakowski, A. 2014. Vermont beer; history of a brewing revolution. American Palate, Charleston, SC, USA.

Straub, C., Simasek, N., Gapinski, M., Dohm, R., Aikens, E., Muscella, S. 2013. Influence of non-host plant diversity and natural enemies on the potato leafhopper, *Empoasca fabae*, and pea aphid, *Acyrthosiphon pisum*, in alfalfa. J. Pest Sci. 86, 235-244.

Strong, W. B., and Croft, B. A. 1995. Inoculative release of Phytoseiid mites (Acarina: Phytoseiidae) into the rapidly expanding canopy of hops for control of *Tetranychus urticae* (Acarina: Tetranychidae). Environ. Entomol. 24, 446-453.

Swezey, S., Nieto, D., and Bryer, J. (2007). Control of Western tarnished plant bug *Lygus hesperus* Knight (Hemiptera: Miridae) in California organic strawberries using alfalfa trap crops and tractor-mounted vacuums. Environ. Entomol., 36, 1457-1465.

Symondson, W., Sunderland, K., and Greenstone, M. 2002. Can generalist predators be effective biocontrol agents? Annu. Rev. Entomol. 47, 561-594.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T., Kleijn, D., Rand, T., Tylianakis, J., Nouhuys, S., Vidal, S. (2007). Conservation biological control and enemy diversity on a landscape scale. BioControl 43, 294-309.

Tuovinen, T. 1994. Influence of surrounding trees and bushes on the phytoseiid mite fauna on apple orchard trees in Finland. Agric. Ecosyst. Environ. 50, 39-47.

Turner, S., Benedict, C., Darby, H., Hoagland, L., Simonson, P., Sirrine, R., Murpy, K. 2011. Challenges and opportunities for organic hop production in the United States. Agron. J. 103, 1-10.

USA Hops. 2013. Variety Manual. Hop Growers of America, Moxee, WA.1-36.

Van den Bosch, R., and Stern, V. (1962). The integration of chemical and biological control of arthropod pests. Annu. Rev. Entomol., 7, 367-386.

Van Driesche, R., Hoddle, M., and Center, T. 2008. Control of pests and weeds by natural enemies; an introduction to biological control. Blackwell Publishing, Malden, MA.

Wan, N., Ji, X., and Jiang, J. 2014. Testing the enemies hypothesis in peach orchards in two different geographic areas in Eastern China, the role of ground cover vegetation. PLoS One 9, 1-11.

Weihrauch, F. 2004. A new monitoring approach for the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) in hop culture. J. Plant Dis. and Protect. 111, 197-205.

Weihrauch, F., and Moreth, L. 2005. Behavior and population development of *Phorodon humuli* (Schrank) (Homoptera: Aphididae) on two hop cultivars of different susceptibility. J. Insect Behav. 18, 693-705.

Weiser Erlandson, L., and Obrycki, J. 2010. Predation of immature and adult *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae) by three species of predatory insects. J. Kansas Entomol. Soc. 83, 1-6.

Womack, C. 1984. Reduction in photosynthetic and transpiration rates of alfalfa caused by potato leafhopper (Homoptera: Cicadellidae) infestations. J. Econ. Entomol. 77, 508-513.

Woods, J., James, D., Lee, J., and Gent, D. 2011. Evaluation of airborne methyl salicylate for improved conservation biological control of two-spotted spider mite and hop aphid in Oregon hop yards. Exp. Appl. Acarol. 55, 401-416.

Woods, J., Dreves, A., James, D., Lee, J., Walsh, D., and Gent, D. 2014. Development of biological control of *Tetranychus urticae* (Acari: Tetranychidae) and *Phorodon humuli* (Hemiptera: Aphididae) in Oregon hop yards. J. Econ. Entomol.107, 570-581.

Woods, J., Dreves, A., Fisher, G., James, D., Wright, L., and Gent, D. 2012. Population Density and Phenology of *Tetranychus urticae* (Acari: Tetranychidae) in hop is linked to the timing of sulfur applications. Environ. Entomol. 41, 621-635.

Wright, L., and James, D. 2001. Parasitoids of the hop aphid (Homoptera: Aphidae) on *Prunus* during the spring in Washington state. J. Agr. Urban Entomol. 18, 141-147.

Wright, L., Cone, W., and James, D. 2005. Sources of spring and fall hop aphid, *Phorodon humuli* (Schrank), (Homoptera: Aphidae) migrants in south central Washington. J. Entomol. Soc. BC. 102, 21-26.

Wright, L., and Cone, W. 1999. Binomial sequential sampling plans for adult

female two-spotted spider mites (Acari: Tetranychidae) on hops. J. Econ. Entomol. 92, 1335-1343.

Wyss, E., Niggli, U., Nentwig, W. 1995. The impact of spiders on aphid populations in a strip-managed apple orchard. J. Appl. Entomol. 119, 473-478.

Appendices

APPENDIX A

APPENDICES

A.1 Chapter 3

A.1.1 Sampling Method Comparison

Table A.1: Pest season sums regardless of cover crop treatment in hop canopy by collection method (Vacuum, Sticky trap, Detail) and combined (Total).

2012	Vacuum plants	Sticky traps	Detail	Total
TSSM	6811	613	4887	7424
PLH	5402	3574	1177	8976
HA	1440	1103	1043	2543
2013	Vacuum	Sticky traps	Detail	Total
TSSM	1869	90	193	1959
PLH	4477	4215	137	8692
HA	1653	753	1276	2406
2014	Vacuum	Sticky traps	Detail	Total
TSSM	2961	18	1213	2979
PLH	2214	2537	1497	4751
HA	1523	1043	98	2566

Table A.2: Most abundant natural enemy season sums by collection method (Vacuum, Sticky trap, Detail) and combined (Total).

2012	Vacuum plants	Sticky traps	Detail	Total
Parasitica	1788	8172	0	9960
Spiders	668	127	34	795
Orius spp.	217	1296	6	1513
Stethorus spp.	308	552	223	860

2013	Vacuum plants	Sticky traps	Detail	Total
Parasitica	1731	6067	0	7798
Spiders	797	108	22	905
Orius spp.	78	258	0	336
Stethorus spp.	281	442	23	723

2014	Vacuum plants	Sticky traps	Detail	Total
Parasitica	1549	4087	0	5636
Spiders	1286	103	50	1389
Orius spp.	37	266	0	303
Stethorus spp.	155	263	76	418

Table A.3: Peak date and mean number of individuals/sample or sticky trap (± SEM) for each major hop pest. Values are from the most representative collection method (plants vacuumed or sticky traps) for each pest and year.

Pest	Year	Peak date	Mean (± SEM)	Collection method[a]
TSSM	2012	7-Aug	47.8 (± 3.1)	vacuum
	2013	21-Aug	21.3 (± 3.3)	vacuum
	2014	4-Aug	23.3 (± 3.8)	vacuum
PLH	2012	10-Jul	43.3 (± 3.8)	sticky trap
	2013	10-Jul	35.7 (± 2.1)	sticky trap
	2014	12-Aug	41.8 (± 5.3)	sticky trap
HA	2012	2-Aug	11.8 (± 2.8)	sticky trap
	2013	20-Jun	6.6 (± .74)	sticky trap
	2014	12-Aug	15.2 (± 2.1)	sticky trap

[a]Vacuum sampling was the most effective collection method for TSSM. Sticky traps were the most effective collection method for PLH and HA.

A.1.2 Detail Arthropod Sampling

In addition to sticky trap and vacuum sampling, naked eye counts of arthropods on leaves after vacuuming was conducted. This sampling was called detail sampling. Three leaves were scouted top and bottom with optivisor glasses on each vacuumed plant, each vacuum collection date in the 2012-2014 collection seasons. Arthropods were summed on a per plot bases by cultivar. As expected, detail sampling did not capture the abundance that vacuum samples and sticky traps offer.

Table A.4: Pest : natural enemy ratios for each collection year by vacuum and sticky trap collection methods. Natural enemy populations built over time. Treatments are pooled together.

	Pests : Natural Enemies (Total Count)	
	Vacuum Samples	Sticky Traps
2012	4.19:1	0.50:1
2013	2.55:1	0.72:1
2014	2.12:1	0.74:1

Table A.5: ANOVA summary statistics for detail sampled two-spotted spider mites. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
TSSM	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	0.1 (1, 156)	0.71	11.5 (1, 131)	**0.0009**	0.3 (1, 161)	0.58
Cultivar	0.01 (1, 46.5)	0.90	0.1 (1, 56.1)	0.80	5.3 (1, 53.5)	**0.03**
Treatment	1.3 (2, 45.8)	0.28	3.1 (2, 56.8)	**0.05**	0.4 (2, 53.3)	0.69
Treatment x Cultivar	0.6 (2, 47.2)	0.53	0.2 (2, 54.9)	0.81	0.5 (2, 54.3)	0.60
Date	22.6 (11, 40)	**< 0.0001**	31.3 (10, 123)	**< 0.0001**	11.5 (11, 140)	**< 0.0001**
Cultivar x Date	0.77 (11, 139)	0.67	0.2 (10, 123)	1.00	0.86 (11, 139)	0.58
Treatment x Date	1.16 (22, 142)	0.29	0.6 (20, 127)	0.90	1.2 (22, 142)	0.28

Table A.6: ANOVA summary statistics for detail sampled potato leafhopper. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
PLH	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	0.1 (1, 148)	0.70	0.6 (1, 150)	0.45	0.0 (1, 160)	0.99
Cultivar	6.9 (1, 37.2)	**0.01**	7.0 (1, 56.7)	**0.01**	0.4 (1, 67.4)	0.54
Treatment	0.2 (2, 37.4)	0.83	0.4 (2, 57)	0.70	0.9 (2, 67)	0.40
Treatment x Cultivar	0.4 (2, 39.3)	**< 0.0001**	1.8 (2, 56.3)	0.17	0.9 (2, 66.7)	0.42
Date	58.3 (11, 141)	**< 0.0001**	9.3 (10, 128)	**< 0.0001**	6.5 (11, 142)	**< 0.0001**
Cultivar x Date	3.5 (11, 141)	**0.0003**	1.3 (10, 128)	0.22	0.9 (11, 141)	0.51
Treatment x Date	0.6 (22, 142)	0.95	0.95 (20, 130)	0.52	0.5 (22, 143)	0.97

Table A.7: ANOVA summary statistics for detail sampled hop aphid. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
HA	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	4.0 (1, 156)	**0.04**	0.0 (1, 149)	0.88	0.3 (1, 155)	0.58
Cultivar	2.9 (1, 49)	0.09	6.3 (1, 52.9)	**0.01**	0.0 (1, 44.5)	0.95
Treatment	0.1 (2, 49.1)	0.87	0.3 (2, 53)	0.72	2.4 (2, 44.7)	2.40
Treatment x Cultivar	1.1 (2, 50.7)	0.34	0.15 (2, 53.4)	0.86	2.4 (2, 46.3)	0.10
Date	17.9 (11, 141)	**< 0.0001**	43.9 (10, 126)	**< 0.0001**	20.7 (11, 140)	**< 0.0001**
Cultivar x Date	2.14 (11, 141)	**0.02**	1.2 (10, 126)	0.33	0.5 (11, 139)	0.91
Treatment x Date	1.3 (22, 143)	0.21	1.3 (20, 128)	0.22	0.8 (22, 142)	0.85

A.1.3 Two-spotted Spider Mite Sticky Trap Data

In an effort to present results from a consistent arthropod collection method, two-spotted spider mite sticky trap data are not in Chapter 3.

Table A.8: ANOVA summary statistics for two-spotted spider mites collected on sticky traps. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
TSSM	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	0.1 (1, 152)	0.72	2.7 (1, 162)	0.10	0.7 (1, 149)	0.41
Cultivar	0.8 (1, 56.7)	0.37	0.4 (1, 63.5)	0.53	0.1 (1, 60.8)	0.72
Treatment	1.7 (2, 55.6)	0.18	3.4 (2, 64.4)	**0.04**	0.3 (2, 58.8)	0.75
Treatment x Cultivar	0.9 (2, 56.3)	0.39	0.0 (2, 62.1)	0.97	0.1 (2, 57.4)	0.89
Date	40.5 (11, 139)	**< 0.0001**	43.4 (11, 142)	**< 0.0001**	2.9 (11, 137)	**<0.0001**
Cultivar x Date	0.3 (11, 138)	0.98	0.27 (11, 141)	0.98	0.6 (11, 136)	0.80
Treatment x Date	1.0 (22, 139)	0.46	1.9 (22, 143)	**0.01**	0.79 (22, 139)	0.73

A.1.4 Aphid and Potato Leafhopper Vacuum Sampling Data

In an effort to present results from a consistent arthropod collection method, potato leafhopper and hop aphid vacuum data are not in Chapter 3. The vacuum data for hop aphids in 2013 is a better representation of the population with a peak date of 21-Aug and mean of 12. Overall, the aphids collected were apterous which provides an argument for using vacuum data because aphids could not fly to sticky traps. The aphids recorded on sticky traps must have been blown to them.

Table A.9: ANOVA summary statistics for potato leafhopper from vacuum samples. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012		2013		2014	
PLH	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	41.0 (1, 377)	**< 0.0001**	74.7 (1, 353)	**< 0.0001**	52.4 (1, 348)	**< 0.0001**
Cultivar	5.0 (1, 89.6)	**0.03**	1.8 (1, 87.2)	0.17	1.0 (1, 103)	0.33
Treatment	1.2 (2, 89.7)	0.32	.24 (2, 84.2)	0.79	0.9 (2, 95.4)	0.39
Treatment x Cultivar	0.4 (2, 97.1)	0.69	2.1 (2, 90.4)	0.13	3.8 (2, 99.4)	**0.02**
Date	71.6 (11, 322)	**< 0.0001**	10.2 (11, 326)	**< 0.0001**	17.5 (11, 315)	**< 0.0001**
Cultivar x Date	1.0 (11, 320)	0.42	3.8 (11, 326)	**< 0.0001**	1.4 (11, 318)	0.17
Treatment x Date	1.3 (22, 329)	0.19	1.7 (22, 331)	**0.02**	1.8 (22, 323)	**0.02**

Table A.10: ANOVA summary statistics for hop aphid from vacuum samples. F values and significance from linear mixed model with repeated measures is reported at the 0.05 LOS for 2012, 2013, and 2014.

Effects	2012 (Vacuum)		2013 (Vacuum)		2014 (Vacuum)	
HA	F (n, d)	Sig.	F (n, d)	Sig.	F (n, d)	Sig.
Natural Enemy Group	16.6 (1. 350)	**< 0.0001**	20.4 (1, 381)	**< 0.0001**	40.6 (1, 366)	**< 0.0001**
Cultivar	1.6 (1, 72.9)	0.21	7.0 (1, 110)	**0.01**	2.9 (1, 117)	0.09
Treatment	0.1 (2, 73.1)	0.89	1.3 (2, 104)	0.28	0.5 (2, 111)	0.59
Treatment x Cultivar	0.0 (2, 79.4)	0.99	2.2 (2, 109)	0.12	0.0 (2, 113)	0.99
Date	5.9 (11, 322)	**< 0.0001**	27.6 (11, 328)	**< 0.0001**	20.6 (11, 321)	**< 0.0001**
Cultivar x Date	0.7 (11, 323)	0.70	1.6 (11, 326)	0.10	1.5 (11, 321)	0.14
Treatment x Date	0.7 (22, 327)	0.84	0.9 (22, 336)	0.65	0.8 (22, 328)	0.62

A.1.5 Pest Interaction Figures

There were interesting but minor interactions in Chapter 3 ANOVA tables.

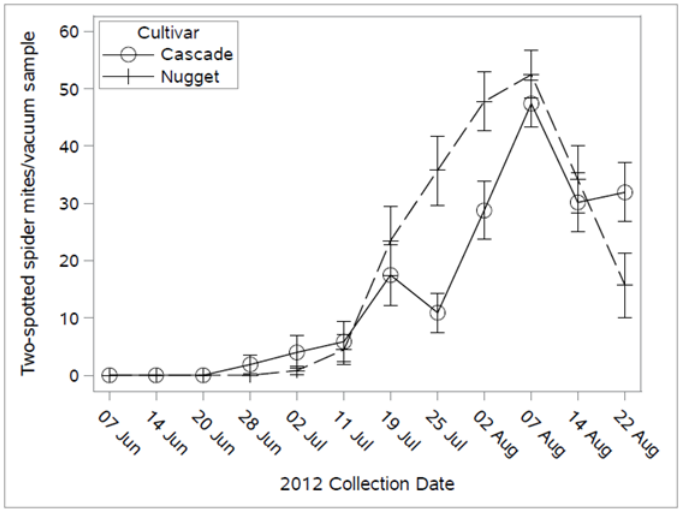

Figure A.1: Cultivar and date for TSSM/vacuum sample in 2012 ($P < 0.0001$). TSSM was higher on 'Nugget' until late August when the population on 'Nugget' decreased and 'Cascade' increased.

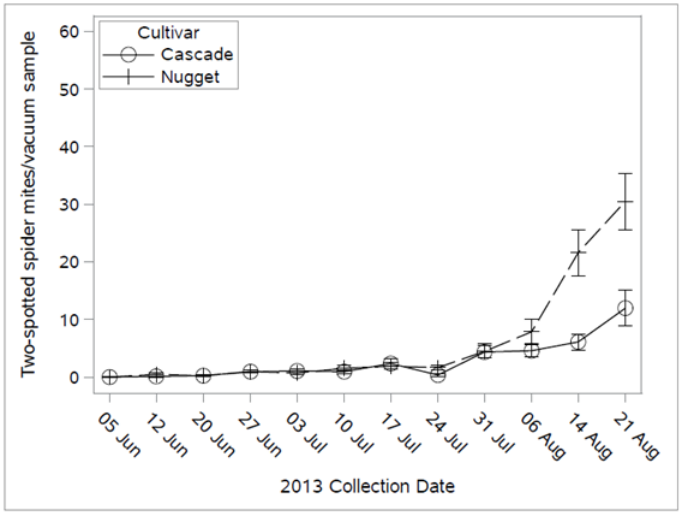

Figure A.2: Cultivar by date for TSSM/vacuum sample in 2013 ($P < 0.0001$). TSSM was higher on 'Nugget' until late August when the population on 'Nugget' decreased and 'Cascade' increased.

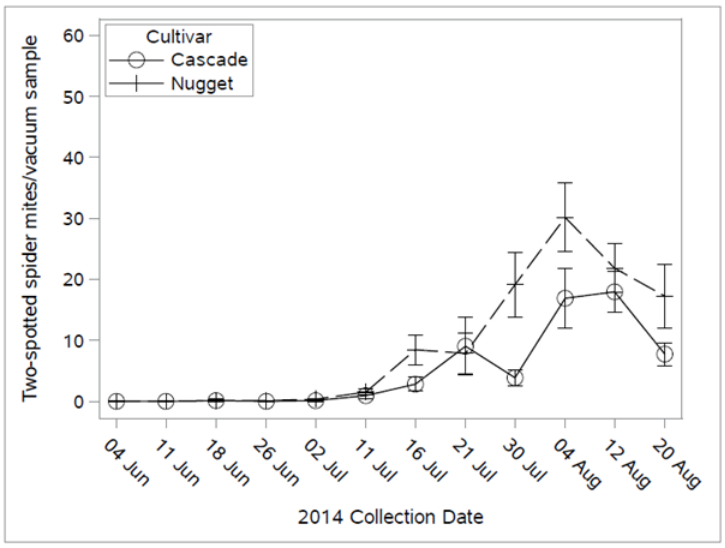

Figure A.3: Significant interaction between cultivar and date for TSSM/vacuum sample in 2014 (P = 0.0003). In 2014, TSSM remained higher on Nugget throughout the season.

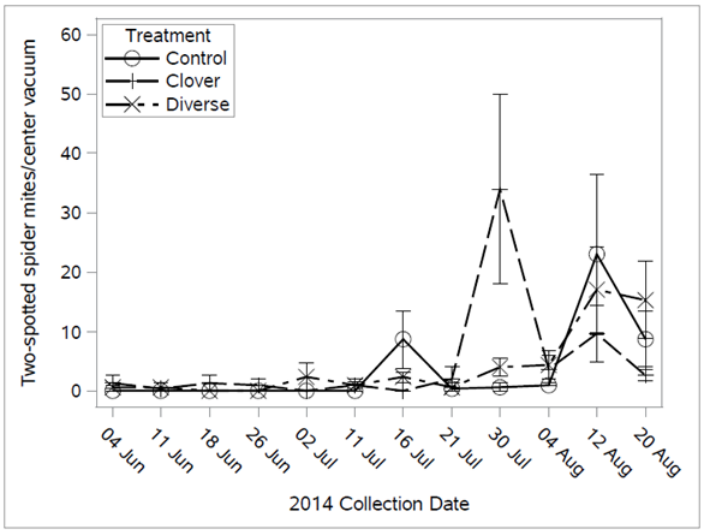

Figure A.4: Treatment and collection date for TSSM/vacuum sample in 2014 cover crop vegetation (P = 0.03). Clover vegetation had the highest TSSM peak which alternated with Control plots. TSSM abundance remained lowest in Diverse vegetation throughout the season.

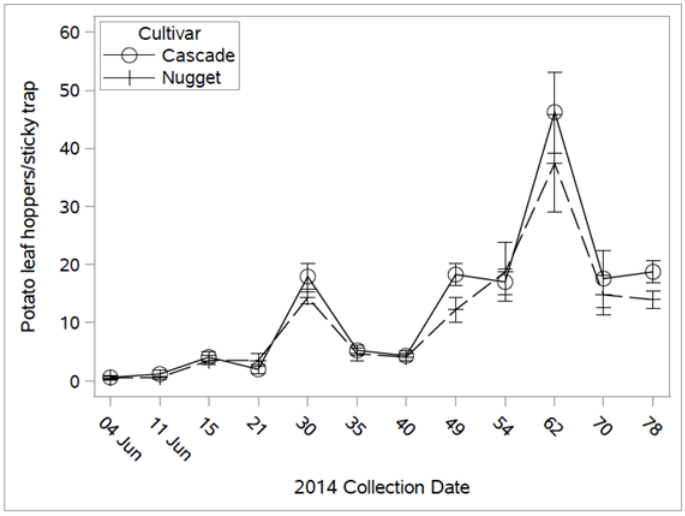

Figure A.5: Cultivar and date for PLH/sticky trap in 2014 (P = 0.04). There was higher PLH abundance on 'Cascade'.

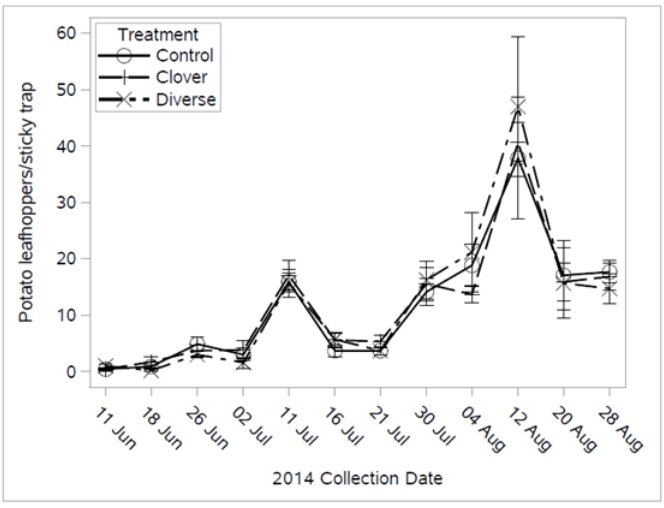

Figure A.6: Treatment and collection date for PLH/sticky trap in 2014. PLH was more abundant in Diverse plots likely due to Clover senescence. The late arrival of PLH in 2014 was uncharacteristic.

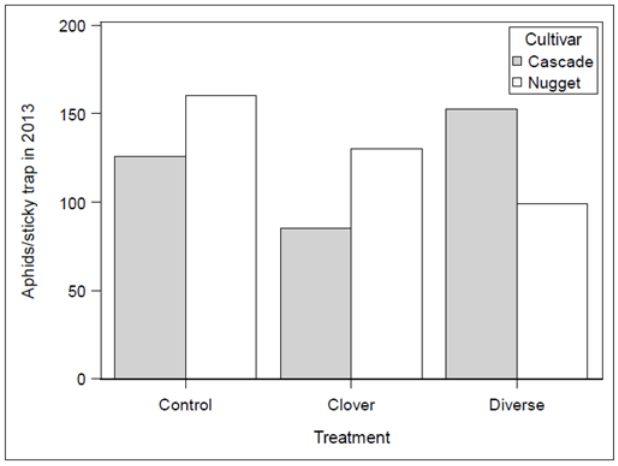

Figure A.7: Treatment and cultivar for HA in 2013 (P = 0.02).There was a significant interaction between treatment and cultivar in 2013. 'Nugget' Control and Clover plants had higher HA abundance yet more HA were observed on 'Cascade' plants in Diverse plots.

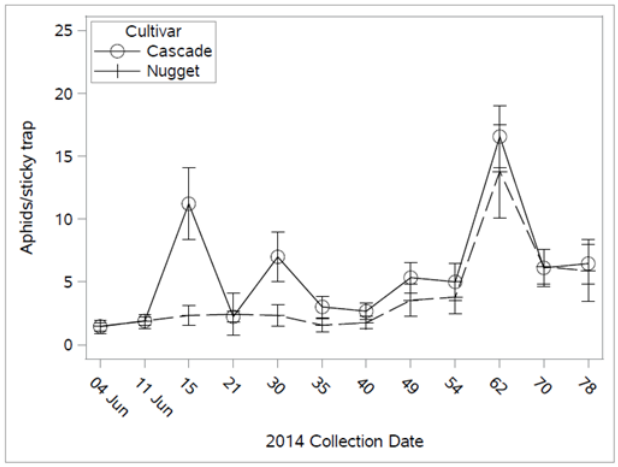

Figure A.8: Cultivar and date for HA/sticky trap in 2014 (P = 0.04). Abundance of HA spiked on 'Cascade' early in the season and remained highest on 'Cascade' through the late season spike.

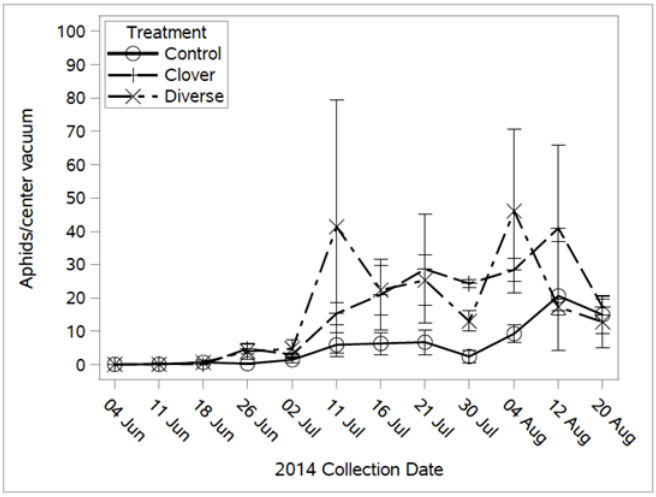

Figure A.9: Treatment and collection date for HA/sticky trap in 2014 cover crop vegetation (P = 0.04). Clover vegetation had the highest mean TSSM population while aphid populations in Diverse plots spiked twice. The Diverse population dropped earlier and remained lower than Control and Clover treatments.

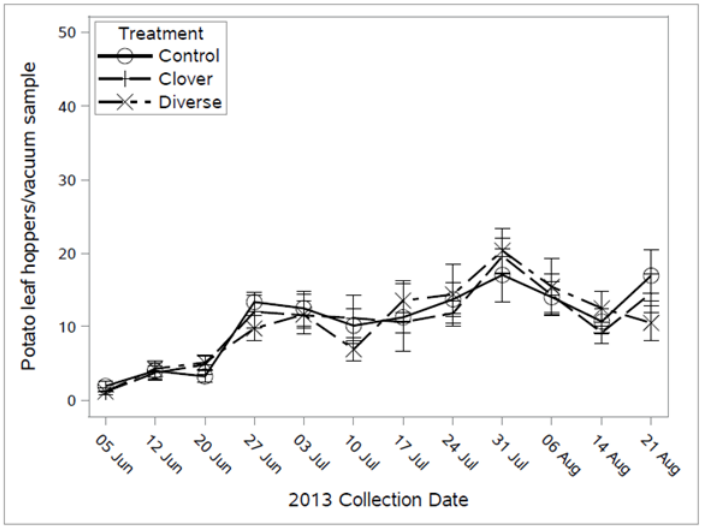

Figure A.10: Treatment and collection date for PLH/vacuum sample (P = 0.023) in 2013. Abundance of PLH on hop plants in Control plots remained lower than on plants in Clover and Diverse but overall had similar abundance.

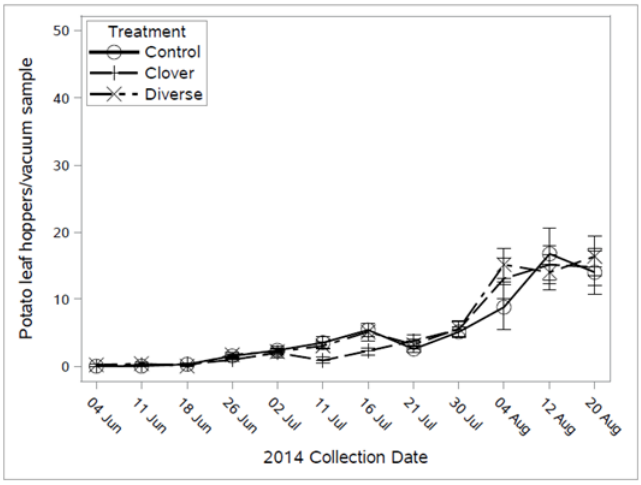

Figure A.11: Treatment and collection date for PLH/vacuum sample (P = 0.015) in 2014. Abundance of PLH on hop plants in Control plots spiked later and to a higher level than Clover and Diverse plots.

A.1.6 Pest Phenology Figures

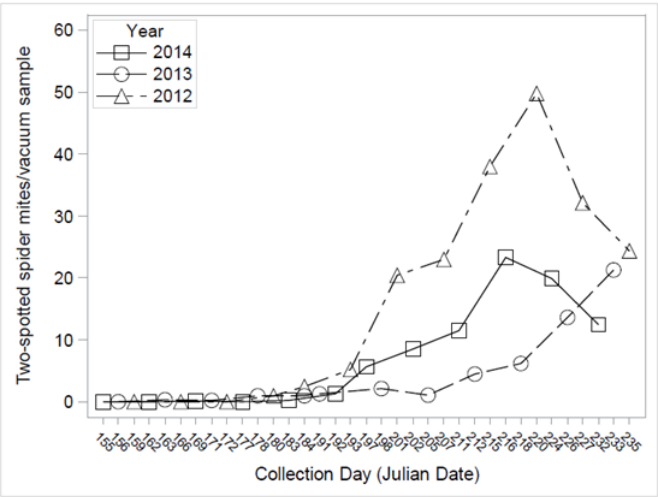

Figure A.12: Phenology of TSSM by year on hop plants from vacuum samples. Cultivars are combined. Collection date was significant with populations of TSSM peaking in early to mid-August.

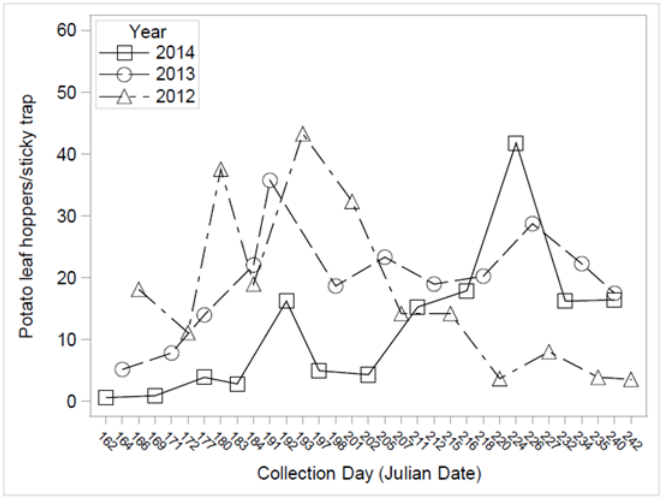

Figure A.13: PLH phenology by year on hop plants from sticky traps. Cultivars were combined and Julian date represents collection days. Collection date was significant in all years with populations of PLH peaking on 10 July in 2012 and 2013. In 2014, PLH peaked on 12 August.

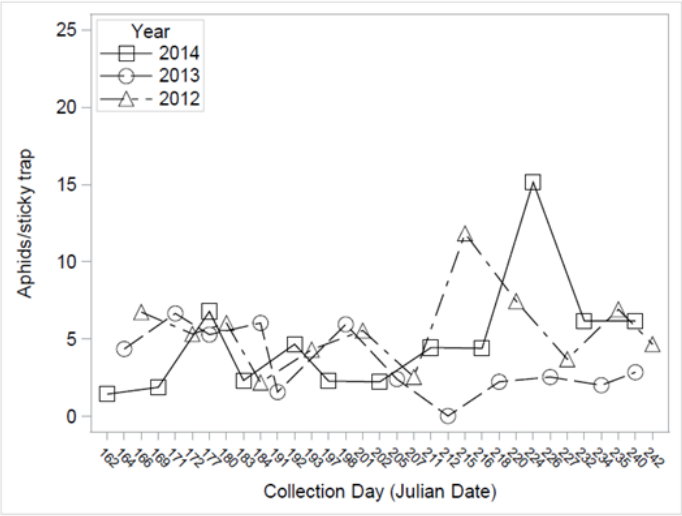

Figure A.14: HA phenology by year on hop plants from vacuum samples. Cultivars were combined and Julian date represents collection days. The effect of collection date was significant in all years with HA populations peaking in early to mid-August. In 2013 HA were less abundant with an earlier peak date in June.

A.1.7 Drive Row Nitrogen

One soil sample was taken from each drive row cover crop treatment after hop harvest. Five soil cores were taken per cover crop plot in a z-shaped pattern. Soil was mixed in a bucket and a subsample was taken. Soil was analyzed for plant available nitrogen (NO3-N mg/kg) at the University of Vermont Soil Testing Laboratory. Soil samples were taken on 6 September 2012, 23 August 2013, and 18 September 2014. Soil analyses indicate no significant difference between nitrate levels in cover crop drive row treatments over the course of the three collection years. Soil nitrates were evaluated using generalized mixed model analysis (PROC GLM, SAS Institute 2014). Fixed effects in this model included year, cover crop treatment, and year x treatment.

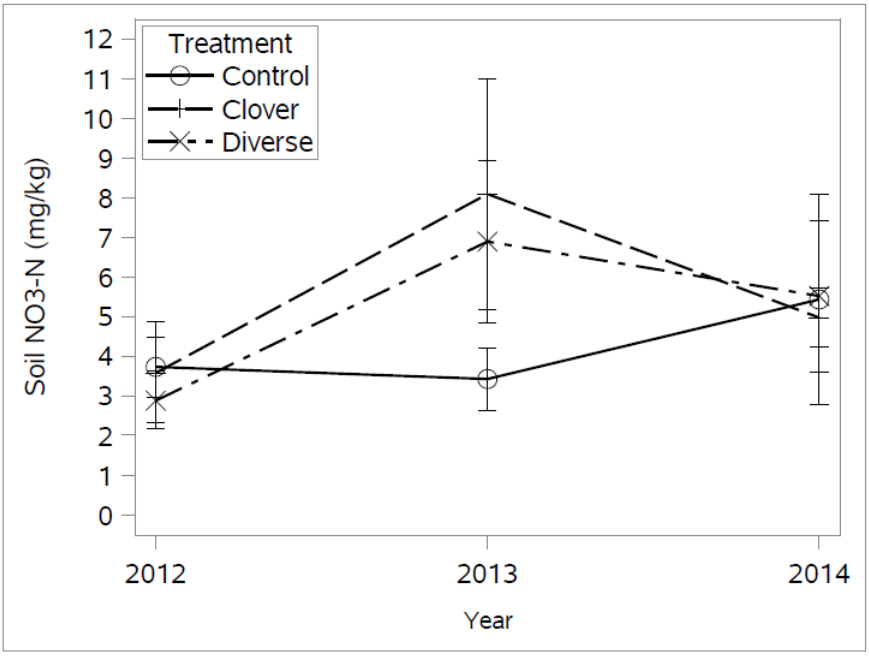

Figure A.15: Soil nitrate as part of total nitrogen (NO_3-N) did not vary significantly by cover crop treatment between 2012, 2013, and 2014.

A.2 Chapter 4

A.2.1 Stomatal Conductance Analyses

Due to the similarity of transpiration and stomatal conductance, this gas exchange measure is not reported in the text tables.

Table A.11: ANOVA summary statistics for stomatal conductance (mol H_2O $m^{-2}s^{-1}$) in the field after 3 d of exposure to potato leafhopper and 18 d of recovery from injury. F values and significance from linear mixed model are reported at 0.05 LOS.

Effects	Days After Exposure	Stomatal Conductance[a]	
Field		F (n, d)	Sig.
PLH Alive	3	2.1 (1, 56)	0.16
TSSM		0.0 (1, 56)	0.95
Baseline Measurement		0.1 (1, 56)	0.74
Treatment		37.6 (1, 56)	**< 0.0001**
Cultivar		4.0 (1, 56)	**0.001**
Cultivar x Treatment		3.9 (7, 56)	**0.001**
Day 3 Measurement	18	2419.4 (1, 47)	**< 0.0001**
Treatment		2.4 (1, 46.7)	0.13
Cultivar		2.0 (6, 43.7)	0.09
Cultivar x Treatment		1.6 (6, 43.7)	0.19

[a] Units are mol H_2O $m^{-2}s^{-1}$

'Horizon' is not included in 18 d summary statistics.

Table A.12: ANOVA summary statistics for stomatal conductance (mol H_2O $m^{-2}s^{-1}$) in the greenhouse after 3 d of exposure to potato leafhopper and 7 d of recovery from injury. F values and significance from linear mixed model are reported at 0.05 LOS.

Effects	Days After Exposure	Stomatal Conductance[a]	
Greenhouse		F (n, d)	Sig.
PLH Alive	3	0.4 (1, 54.7)	0.55
TSSM		2.4 (1, 57)	0.12
Baseline Measurement		16.5 (1, 56.7)	**0.0002**
Treatment		30.5 (1, 54.8)	< **0.0001**
Cultivar		1.1 (7, 53.7)	0.39
Cultivar x Treatment		1.2 (7, 53.2)	0.30
Day 3 Measurement	7	0.4 (1, 53)	0.56
Treatment		3.9 (1, 53)	**0.05**
Cultivar		1.4 (7, 53)	0.24
Cultivar x Treatment		0.8 (7, 53)	0.59

[a] Units are mol H_2O $m^{-2}s^{-1}$

Horizon' is not included in 18 d summary statistics.

A.2.2 Field Treatment Graphs with Cultivar Unpooled

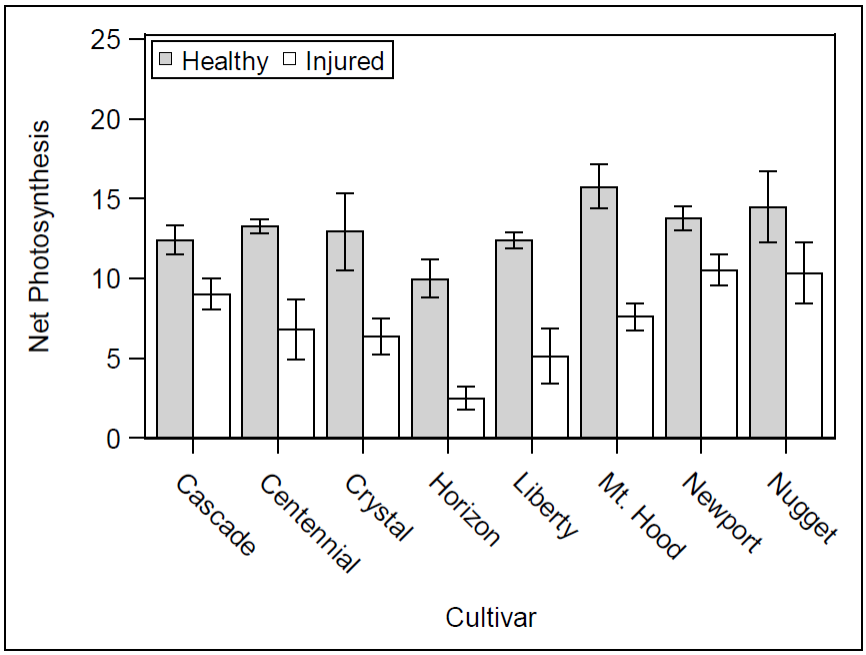

Figure A.16: Field net photosynthesis (µmol Co_2 $m^{-2}s^{-1}$) for eight hop cultivars after 3 d of individual leaf exposure to three adult potato leafhoppers.

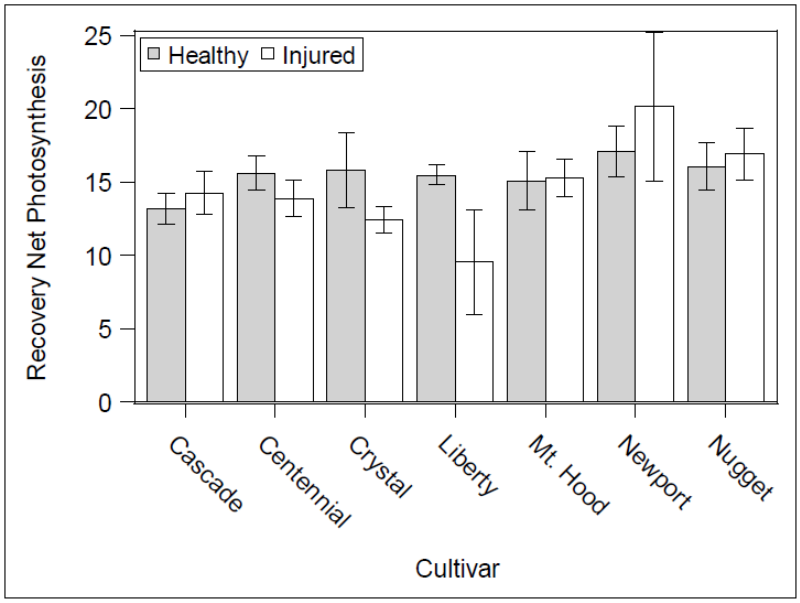

Figure A.17: Field net photosynthesis (µmol Co_2 $m^{-2}s^{-1}$) for seven hop cultivars 18 d after leafhopper removal. Cultivar 'Horizon' leaves did not survive to recovery measurements.

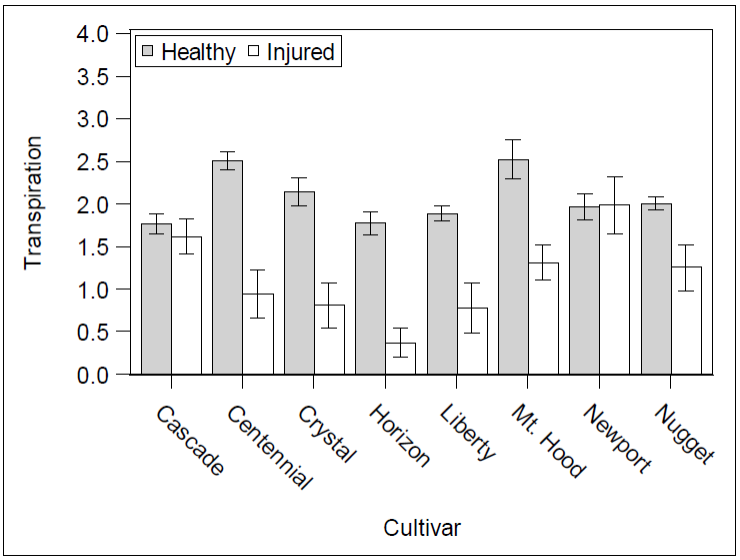

Figure A.18: Field transpiration (mmol H_2O $m^{-2}s^{-1}$) for eight hop cultivars after 3 d of individual leaf exposure to three adult potato leafhoppers.

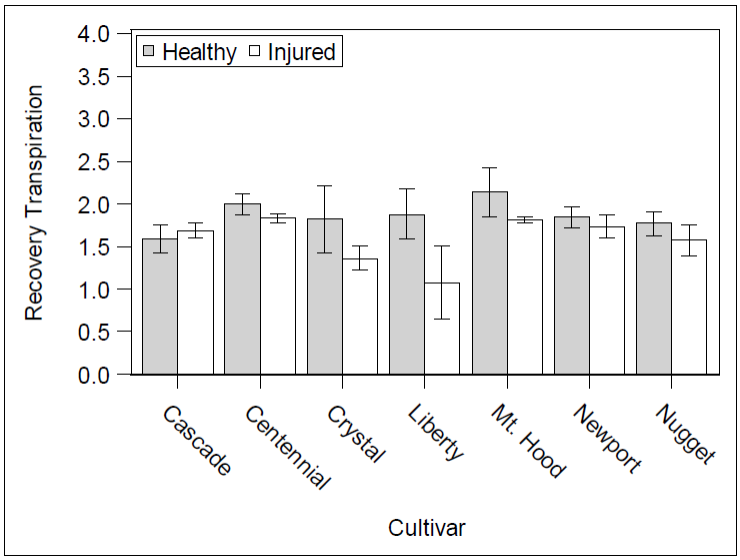

Figure A.19: Field transpiration (mmol H_2O $m^{-2}s^{-1}$) for seven hop cultivars 18 d after leafhopper removal. Cultivar 'Horizon' leaves did not survive to recovery measurements.

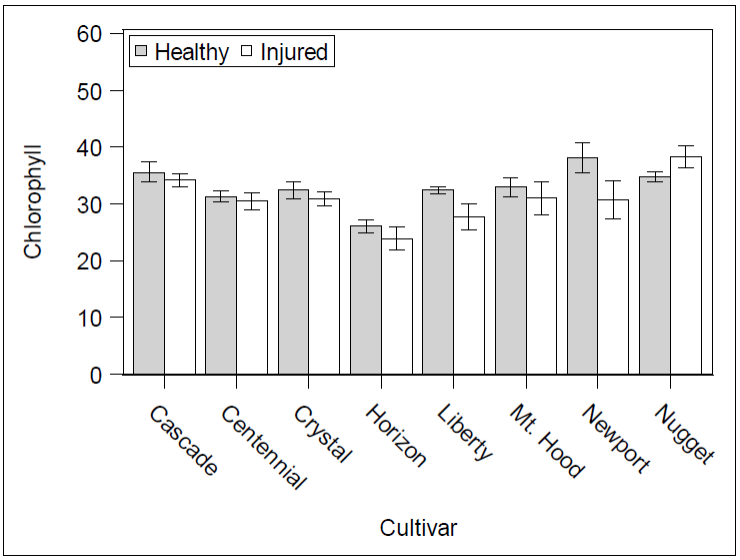

Figure A.20: Mean field leaf chlorophyll content for eight hop cultivars after 3 d of individual leaf exposure to three adult potato leafhoppers.

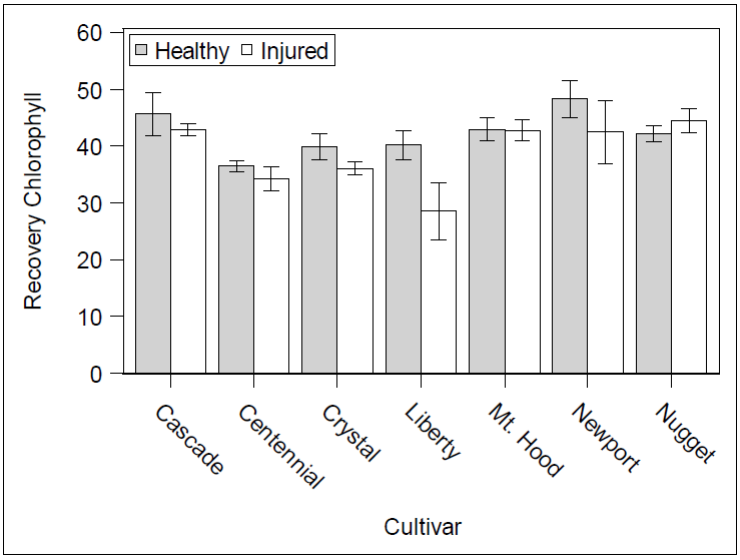

Figure A.21: Mean field leaf chlorophyll content for eight hop cultivars after 18 d of individual leaf exposure to three adult potato leafhoppers. Cultivar 'Horizon' leaves did not survive to recovery measurements.

A.2.3 Greenhouse Treatment Graphs with Cultivar Unpooled

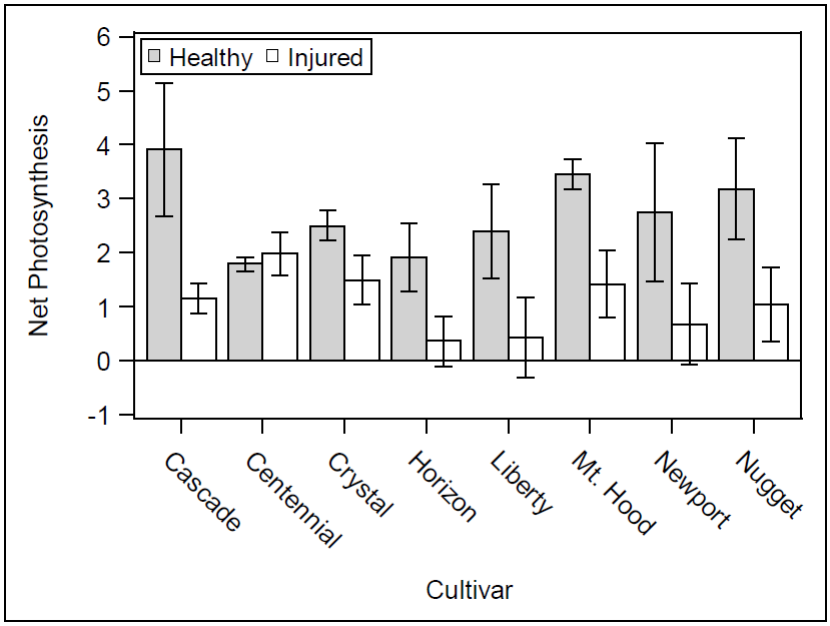

Figure A.22: Greenhouse net photosynthesis (µmol Co_2 $m^{-2}s^{-1}$) for eight hop cultivars after 3 d of exposure to three adult potato leafhoppers.

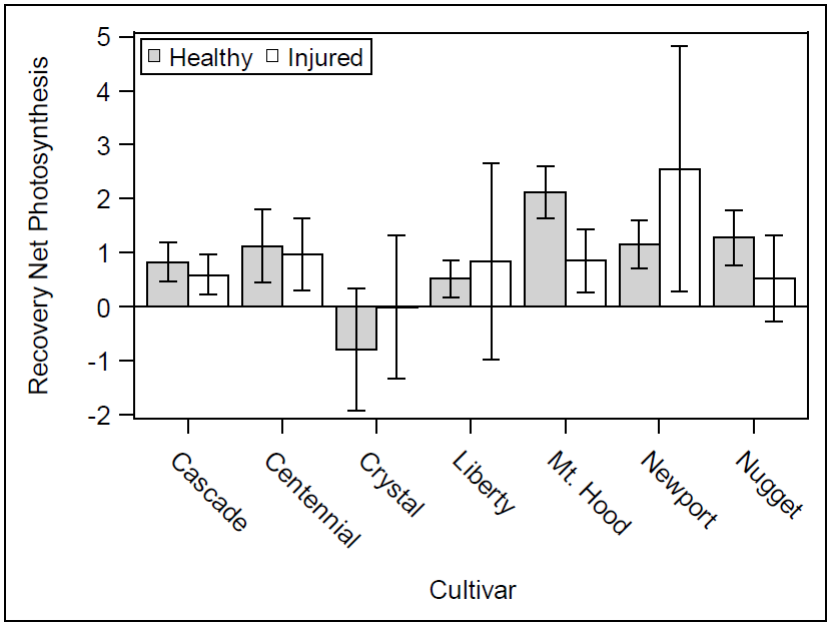

Figure A.23: Greenhouse net photosynthesis (µmol Co_2 $m^{-2}s^{-1}$) for eight hop cultivars 7 d after leafhopper removal.

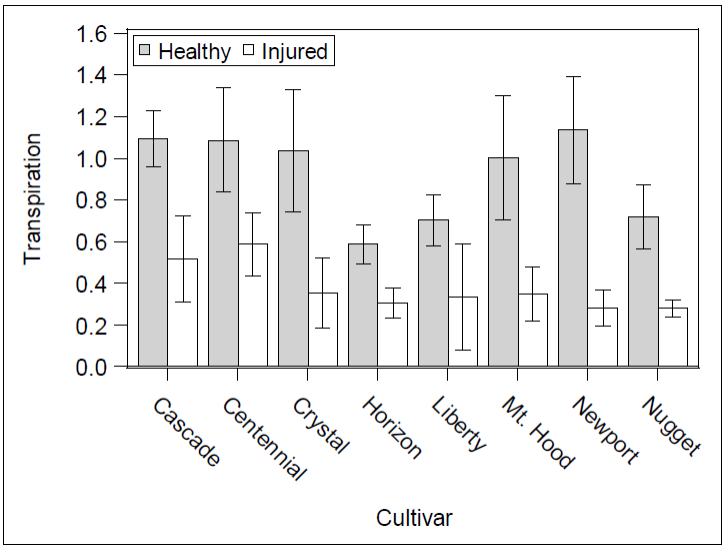

Figure A.24: Greenhouse transpiration (mmol H_2O $m^{-2}s^{-1}$) for eight hop cultivars after 3 d of individual leaf exposure to three adult potato leafhoppers.

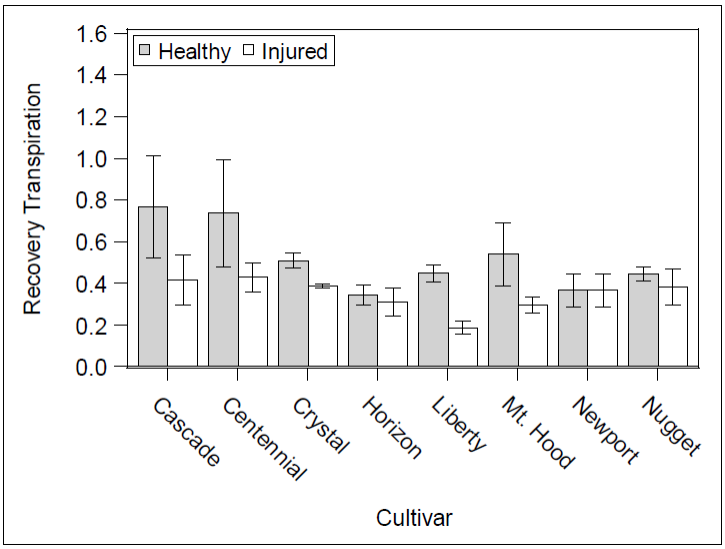

Figure A.25: Greenhouse transpiration (mmol H_2O $m^{-2}s^{-1}$) for eight hop cultivars 7 d after leafhopper removal.

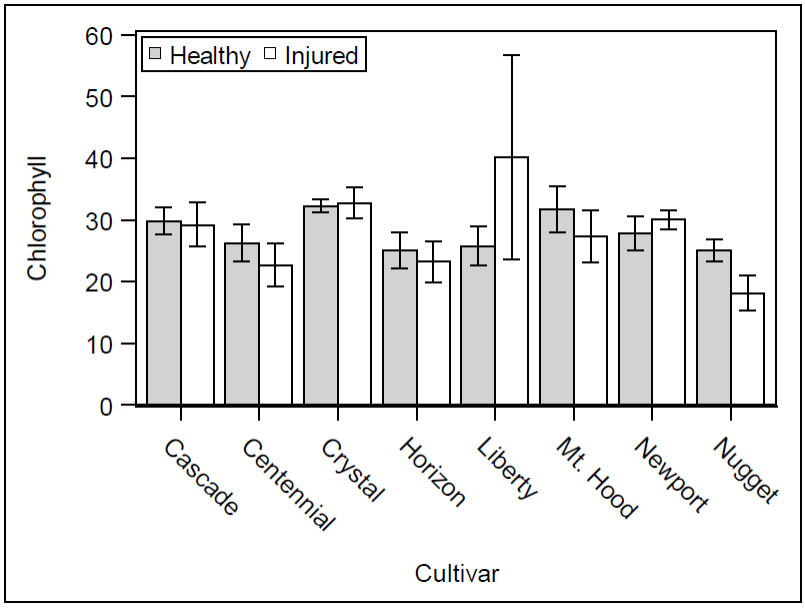

Figure A.26: Mean greenhouse leaf chlorophyll content for eight hop cultivars after 3 d of individual leaf exposure to three adult potato leafhoppers.

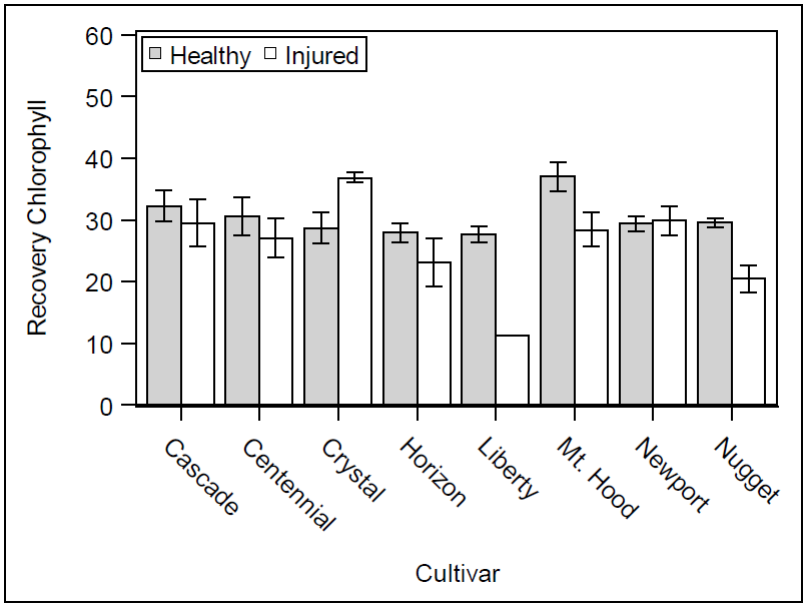

Figure A.27: Mean greenhouse leaf chlorophyll content for eight hop cultivars after 18 d of individual leaf exposure to three adult potato leafhoppers.

A.3 Preliminary Hop Cultivar Resistance Mechanisms

Hop Leaf Trichome Counts

A.3.0.1 Materials and Methods

After the Chapter 4 greenhouse experiment, first year hop plants were used for leaf peltate and boulbus trichome counts. Leaf trichomes were counted with a SZ-CTV Olympus dissecting microscope at 10x. Counts were made from a picture image displayed on a computer screen. Pictures were taken with a Leica DFC 320 camera attached to the microscope. The field of view was an area of 61.64 cm^2. One third leaf pair and one fifth leaf pair was randomly selected from each plant. Trichomes were counted at one leaf and one midrib location chosen at random per leaf.

Counts were square root transformed to fit a normal distribution. A linear mixed model with repeated measures (PROC MIXED, SAS Institute 2014) was used to evaluate trichome counts between third and fifth leaf pairs, leaf and midrib location on leaf, and the eight cultivars. The fixed effects included Cultivar, Leaf Pair, Cultivar x Leaf Pair, Location on Leaf, Cultivar x Location on Leaf, Leaf Pair x Location on Leaf. All statistics were run at the .05 LOS and generated using SAS software, Version 9.4 (Copyright 2014 by SAS Institute Inc., Cary, NC, USA).

A.3.0.2 Results and Discussion

Cultivars varied significantly in the number of both trichome types. Third leaf pairs had significantly higher mean density of peltate trichomes (lupulin glands) compared to bulbous trichomes. Leaf locations had significantly higher mean number of all trichomes than midribs. Leaf midribs exhibited very few trichomes. There were significant interactions between Cultivar x Location on Leaf and Leaf Pair x Location

on Leaf. Importantly, the hop cultivars that were observed to have a high number of potato leafhoppers/leaf in the field included 'Liberty', 'Crystal', 'Newport', Mt. Hood' (Figure 4.1). 'Liberty', 'Crystal', 'Mt. Hood', were observed to have an especially low number of lupulin glands (peltate trichomes) on the first year hop plants sampled (Figure 5.2).

Table A.13: ANOVA summary statistics for first year hop leaf trichome counts under a dissecting microscope field of view of 61.64 cm^2. F values and significance from linear mixed model are reported at 0.05 LOS.

Effects	# Peltate Trichomes (Lupulin Glands)		# Bulbous Trichomes	
1st yr Hop Leaves	F (n, d)	Sig.	F (n, d)	Sig.
Cultivar	5.8 (7, 246)	< **0.0001**	2.8 (7, 246)	**0.007**
Leaf Pair	15.3 (1, 246)	**0.0001**	1.5 (1, 246)	0.22
Cultivar x Leaf Pair	0.5 (7, 246)	0.86	0.3 (7, 246)	0.94
Location on Leaf	953.9 (1, 246)	< **0.0001**	134.2 (1, 246)	< **0.0001**
Cultivar x Location on Leaf	6.7 (7, 246)	< **0.0001**	1.3 (7, 246)	0.24
Leaf Pair x Location on Leaf	15.0 (1, 246)	**0.0001**	0.3 (1, 246)	0.62

*Indicates statistical significance at .05 LOS.

[a] The leaf area of counted was 61.64 cm^2

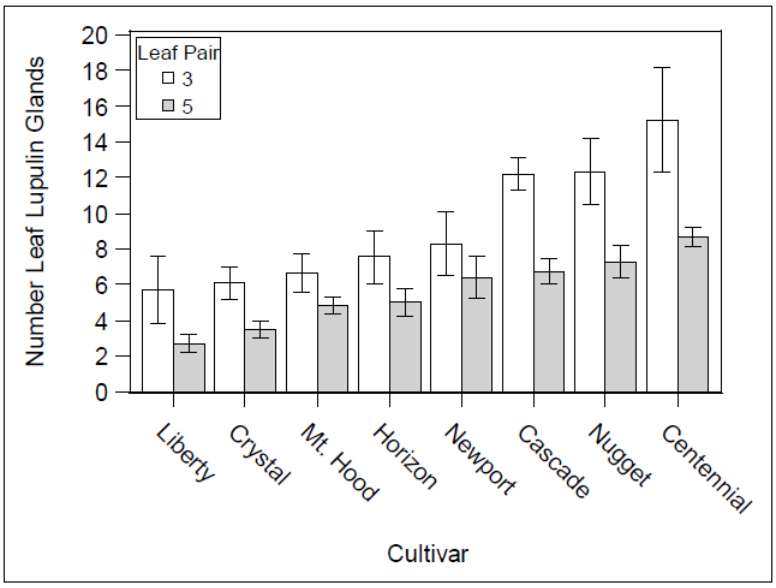

Figure A.28: Mean number of leaf lupulin glands (peltate type) on leaf tissue. Leaf pairs are significantly different. Pairwise comparisons were not made.

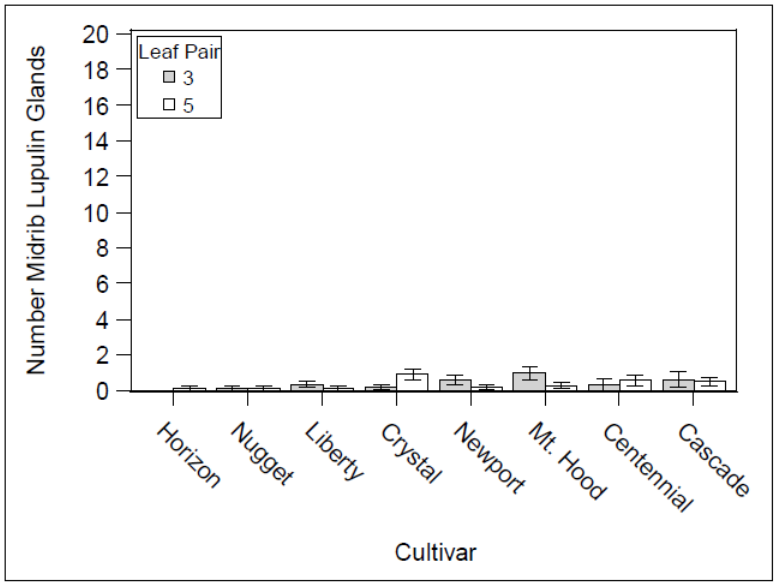

Figure A.29: Mean number of lupulin glands (peltate type) on leaf midrib. Leaf pairs are significantly different. Pairwise comparisons were not made.

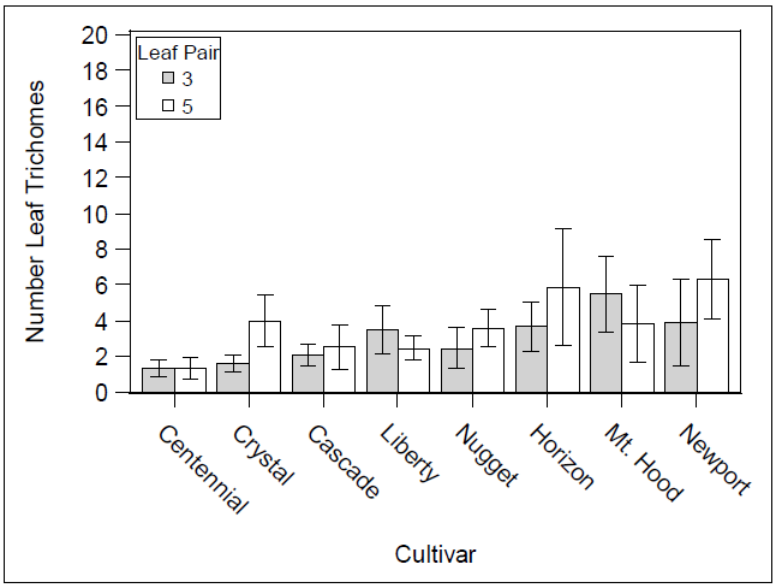

Figure A.30: Mean number of leaf trichomes (bulbous type) on leaf tissue. Leaf pairs are significantly different. Pairwise comparisons were not made.

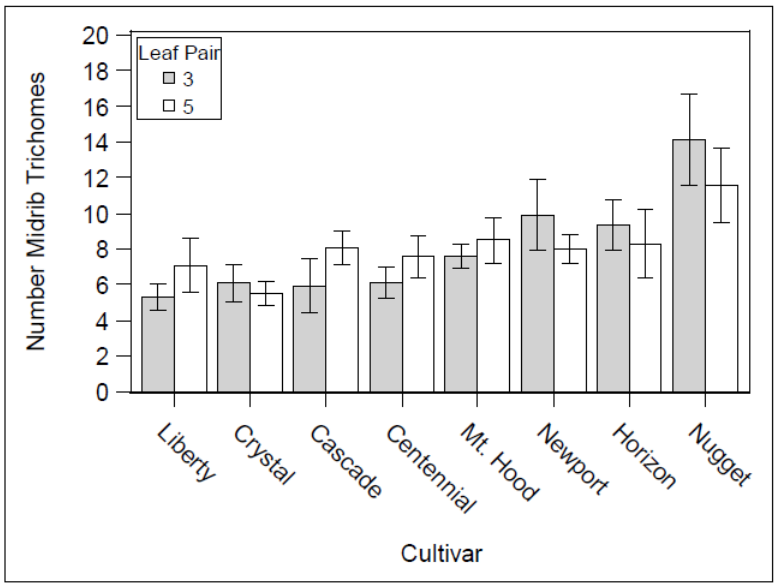

Figure A.31: Mean number of leaf trichomes (bulbous type) on leaf midrib. Leaf pairs are significantly different. Pairwise comparisons were not made.