CHAPTER 1 LITERATURE REVIEW

1.1 A small introduction to some herbivorous acari

Mites and ticks belong to a subclass of small arachnids known as the Acari, an incredibly diverse group of arthropods. Despite their ubiquity, mites and invertebrates in general remain understudied relative to other animal fauna (Grodsky et al. 2015, Rosenthal et al. 2017, Titley et al. 2017). Hoy (2011) speculates that our understanding of mite diversity and abundance may be around 50-100 years behind the taxonomy of the Insecta: The small size and cryptic habits of mites make them easy to overlook, and difficult to observe. In addition, their disputed placement in the Arachnida (Giribet 2018) presents a real challenge for taxonomists (Giangrande 2003). Lastly, many mite species have been misclassified, and cryptic species make taxonomic certainty elusive (Bickford et al. 2007). In spite of these impediments, technological improvements, such as Low-Temperature Scanning Electron Microscopy (Achor et al. 2001, Wergin et al. 2006), Confocal Laser Scanning Microscopy (Chetverikov 2012, Chetverikov et al. 2012), X-ray computed tomography (Dunlop et al. 2011, Facchini et al. 2019), and advances in molecular biology-including high-throughput sequencing-(Dasch et al. 2019), have helped to alleviate the pains of mite identification. The combination of these techniques allows for greater taxonomic certainty (Chetverikov et al. 2012). The most well known species of mites have gained scientific recognition primarily due to their pest status (Savory 1964, Jeppson et al. 1975, Hoy 2011): many acari are parasites of plants and animals, causing disease and economic injury (Jeppson et al. 1975, Hoy 2011, Walter and Proctor 2013). Even so, the majority of mite species are of no economic importance, and are harmless, or even beneficial: many show promise as biological control agents for weeds and arthropod pests (Gerson et al. 2003, Carrillo et al. 2015). Although the majority of arachnids are predatory, mites are unique in that there are species which feed on plants (Savory 1964). Phytophagy arose at least seven times in

the Trombidiformes: Parasitengonae, Tetranychoidea, Raphignathoidea, Heterostigmata, Eupodoidea, Tydeoidea and Eriophyoidea all have species which feed on plants (Lindquist 1999). Phytophagy is thought to be a facultative development for the majority of mite taxa outside of the Tetranychoidea and Eriophyoidea; few species of Eupodoidea and Raphignathoidea are obligate herbivores—only *Halotydeus*, *Penthaleus* (Raphignathoidea: Penthaleidae) and Eustigmaeus (Raphignathoidea: Stigmaeidae (Gerson 1971))—and the other mite groups have few morphological adaptations associated with plant feeding (Krantz and Lindquist 1979, Lindquist 1999). An important development in the evolution of a carine phytophagy is the reduction of the chelicerae into sharp stylets used for piercing plant tissues (Lillo et al. 2018). These styliform mouthparts are thought to reduce damage to the plant in order to avoid some of the toxic chemistry plants use to defend themselves from arthropod feeding (Brattsten and Ahmad 1986). Herbivorous mite damage is dependent on the specific mite-plant interactions for a given plant spp. or cultivar (Petanović and Kielkiewicz 2010a). Mites generally feed on plant epidermal and mesophyll cells (McCoy and Albrigo 1996, Rancic et al. 2006). High mite populations can reduce the amount of chlorophyll available to the plant (Khederi et al. 2018b), primarily causing bronzing/russetting/silvering by direct feeding, but this damage often spreads to the surrounding tissues as the plant's immune system responds (Bensoussan et al. 2016). Mite salivary secretions can also cause a condition known as toxemia, which causes plant tissues to become chlorotic or discolor (Oldfield 1996a). Feeding on young tissues often forms distortions and delays plant growth, and some mites—many eriophyoidea and two spp. of Tenuipalpidae-form galls on their host plants (Jeppson et al. 1975, Westphal and Manson 1996, Oldfield 2005). The majority of herbivorous mites do not transmit pathogens (Oldfield and Proeseler 1996), but those which do act as vectors of plant viruses principally from two families from the Prostigmata: Eriophyidae and Tenuipalpidae (Slykhuis 1965). Members of these mite superfamilies are obligate herbivores considered to be some of the more ancient lineages of phytophagous mites (Lindquist 1999). There have

been singular reports of spider mites—tetranychidae—associated with viruses (Slykhuis 1965, Robertson and Carroll 1988), but other studies have failed to reproduce similar results (Granillo and Smith 1974). Plant mites are generally considered secondary pests, but often cause significant losses when conditions are optimal, due to the fast reproductive rate of many pest species (Gerson and Cohen 1989, Dutcher 2007).

1.1.1 Co-evolved plant specialists: the eriophyoidea

The eriophyoidea are the second most economically-important group of herbivorous mites, right behind Tetranychidae. Where eriophyoids lose out in damage output, they pull ahead in diversity: It is estimated that the 2,838 species reported in the "Catalog of the Eriophyoidea of the World" represent only about 10% of the total number of species which exist (Amrine and Stasny 1994). Publications of new species descriptions of eriophyids averaged about 70 per year from 1996 to 2007, and have greatly increased since the publication of Eriophyoid Mites - their Biology, Natural Enemies and Control (Lindquist et al. 1996), a landmark publication for the field of eriophyoid studies. Eriophyids range in size from 80-500 µm long (Nuzzaci and Lillo 1996), and seem to have evolved specifically for plant feeding (Krantz and Lindquist 1979, Oldfield and Proeseler 1996, Lindquist 1999, Skoracka and Dabert 2010, Lillo et al. 2018): they have styliform chelicera covered with a protective sheath (Lindquist 1999, Bolton et al. 2018), elongate vermiform bodies, and adult mites have a reduced number of legs from the typical eight to four (Lindquist 1996). The stylets of eriophyids are short, $\leq 20 \, \mu \text{m}$ (Oldfield and Proeseler 1996), which primarily limits their feeding to epidermal cells, with young/tender meristematic tissues being preferred (Petanović and Kielkiewicz 2010a, 2010b). Feeding is thought to rely on enzymes in their saliva to break down plant cells contents and feed on the resulting soup (Hoy 2011). Eriophyoid mites also have an abbreviated lifecycle, progressing from egg, to larva, followed by nymph, then adult (Manson and Oldfield 1996). Many eriophyoid mites have summer forms (protogynes) which readily proliferate and winter forms (deutogynes), which are able to survive harsher conditions until they can disperse when environmental

conditions are moderate (Kassar and Amrine Jr 1990). Eriophyids are not able to disperse very far by walking (Calvet et al. 2020), but are known to disperse aerially (Kuczyński et al. 2020) and passively (Galvão et al. 2012), rarely by phoresy on other animals (Li et al. 2018). Eriophyid lifestyles are generally sorted into leaf vagrants/rust mites and galling/bud forms, with rust mites being fusiform and living on the plant surfaces, while bud and gall mites tend to have more cryptic lifestyles, as suggested by their names (Hoy 2011). The majority of eriophyids studied to date are considered host specific, limited to feeding on a single genus, or one host plant. (Oldfield and Proeseler 1996, Lillo et al. 2018). The few mite species which appear to have a broader host range may be misidentified cryptic species (Navia et al. 2012, Skoracka et al. 2013), a hypothesis strengthened by their limited ability to disperse and close associations with their host plants (Magalhaes et al. 2007). These lifestyles and feeding habits of the Eriophyoidea are thought to have shaped both their relationships with their host plants and their ability to transmit pathogens (Mauck et al. 2012, Biere and Bennett 2013): Eriophyid mites represent the majority of mites involved in virus transmission to plants Lillo et al. (2018). In the absence of an infectious agent, most damage from the feeding of vagrant forms of eriophyids is superficial and causes minimal damage to their host plant (Krantz and Lindquist 1979, Oldfield and Proeseler 1996). To date, eriophyids have only been associated with plant viruses (Lillo et al. 2018), which may be explained by the small size of eriophyoid mouths and foreguts, which preclude the acquisition and circulation of large pathogens (Oldfield and Proeseler 1996). Although these developments can be considered an evolutionary advantage for the Eriophyoidea, it puts the lifestyles of these minute arachnids in direct conflict with the interests of modern agriculture, and motivates the need for management of mite populations.

1.1.2 *Phyllocoptes fructiphilus*: the vector of Rose Rosette Virus, the causal agent of Rose Rosette Disease

Phyllocoptes fructiphilus Keifer, (Acari: Trombidiformes: Prostigmata: Eriophyoidea: Eriophyidae) is an eriophyoid mite from the Prostigmata group. Like many other eriophyoids, the relationships P. fructiphilus has with its host and virus are very specific, and create problems for growers (Krantz and Lindquist 1979, Oldfield and Proeseler 1996): P. fructiphilus only feeds on plants in the genus Rosa (roses), but it doesn't create noticeable damage by feeding. Instead, the increased interest in P. fructiphilus stems from its relationship with a virus known as Rose Rosette Virus (RRV) Emaraviridae (Allington et al. 1968, Tzanetakis et al. 2006, Lanev et al. 2011). P. fructiphilus transmits RRV while feeding on the rose epidermis (Allington et al. 1968). A single mite is enough to transmit RRV, and can inoculate a rose in less than an hour (Di Bello et al. 2017). Infection creates the following symptoms: clusters of deformed flowers known as rosettes/witches' brooms, increased thorniness, elongated shoots, reddened leaves and stems, and increased cane die-back which ultimately kills the rose host (Epstein and Hill 1995). This disease is known as Rose Rosette Disease (RRD) and is the most serious disease of roses, creating millions of dollars of losses for growers (Babu et al. 2014) and threatening the ornamental rose industry Rwahnih et al. (2019). RRD was first described in North America in 1941 from an outbreak in Manitoba, Canada (Conners 1941). P. fructiphilus later became recognized as the vector for RRV (Allington et al. 1968, Doudrick et al. 1986, Jesse et al. 2006) and RRV was eventually confirmed to be the casual agent for the RRD (Doudrick et al. 1987, Tzanetakis et al. 2006, Laney et al. 2011, Bello et al. 2015, Dobhal et al. 2016, Di Bello et al. 2017). The mite and virus were generally associated with invasive multiflora rose, Rosa multiflora (Thunb) Amrine Jr (2002) and spread along with the rose throughout the central US (Crowe 1983), and the east (Hindal et al. 1988). Initially the relationship between R. multiflora and the pathogen was considered as a type of natural biological control (Epstein and Hill 1999), and some studies even considered artificially

spreading viruliferous P. fructiphilus to eradicate these pestilent roses (Tipping and Sindermann 2000). The relationship between, R. multiflora, mite and virus also has a positive influence on P. fructiphilus fecundity: Epstein and Hill (1999) reported a 17-fold increase in the mite population of diseased roses compared to uninfected plants. Like many other species of plant-feeding mites, P. fructiphilus reproduce via arrhenotokous parthenogenesis (Oliver 1971), meaning that unfertilized eggs become male, while fertilized eggs become female (Oldfield and Michalska 1996). P. fructiphilus grows from egg to adult in 11 days (Kassar and Amrine Jr 1990), which allows a single female to quickly found a new colony without being fertilized a priori to dispersion (Helle and Wysoki 1996). Together, these factors likely contribute to P. fructiphilus's dispersal ability. RRD and P. fructiphilus can spread through the landscape in various ways: RRV can be spread by grafting (Doudrick et al. 1987) and the mites can crawl from plant to plant or be blown by the wind over long distances (Zhao and Amrine 1997, Zhao and James 1997, Michalska et al. 2009). Unfortunately, P. fructiphilus and RRD have the ability to infest commercial rose cultivars as well (Epstein and Hill 1995, Byrne et al. 2018), and can be spread by humans moving infested plants (Navia et al. 2009). A survey for P. fructiphilus and RRD in the southeastern US (Solo 2018) found both mite and virus to be present in southern Georgia, and P. fructiphilus was recently detected in northern Florida (Fife et al. 2020). The presence of P. fructiphilus and RRD in the southeast emphasizes the need to monitor for and manage RRD to prevent its establishment in these rose growing regions.



Figure 1: Typical symptoms of Rose Rosette Disease (RRD), caused by Rose Rosette Virus: clusters of deformed flowers known as rosettes/witches' brooms, increased thorniness, elongated shoots, reddened leaves and stems. RRD ultimately kills the rose host.

1.2 Integrated pest management: best practices for modern agriculture

Integrated Pest Management (IPM) is a philosophy of pest control based on integrating as many different types of control to keep pest populations underneath their economic injury level (EIL) (Stern et al. 1959, Flint and Bosch 1981). The EIL is a breaking point, where the cost of controlling the damage from pests exceeds the costs of crop production (Stern et al. 1959). This EIL is informed by an economic threshold, a point where a specific pest density has been exceeded, and interventions are required to prevent the crop from reaching the EIL (Stern et al. 1959). A useful framework for controlling plant pathogens has been developed in the concept of the disease triangle. For a long time, plant pathologists have recognized the importance of pathogen, environment and host on disease proliferation (Gäumann 1950), and all of these factors must be present in sufficient quantity and quality for disease to occur (McNew 1960, N 1960, Agrios 2004). Extensions of the basic disease triangle have been considered, including adding extra dimensions to

account for more variables (Francl 2001), or applying it to different systems (Scholthof 2006), but the basic concept is that removing of one of these main factors of disease gives a point of attack for control efforts: Management may focus on removing a suitable host by crop rotation, or by using cultivars resistant/tolerant to pests and/or pathogens. Pathogens can be excluded from the crop via sanitation measures such as insect screens, tissue culture, seed certification programs, cleaning harvesting equipment, or by growing crops in a greenhouse. Environment can also be manipulated by growing crops in areas where the pest/pathogen isn't present or can't survive under normal conditions. The IPM paradigm encourages the combination of as many of these methods as possible for improved pest control. Although there is some overlap in the technologies and terminologies used, pest management traditionally divides pest interventions into four main categories: chemical, mechanical, cultural (environmental), and biological control methods (Bradley and Moore 2018). Chemical controls are an effective way to quickly control pest outbreaks, but pesticides have many drawbacks as well: they pose a risk to the applicator, harm beneficial insects/pollinators, leave residues on crops meant for consumption, and can harm the environment through runoff/drift, polluting surface and groundwater (Driesche et al. 2007, Marquina et al. 2010). Pesticides also can create secondary pest outbreaks (Gerson and Cohen 1989) and pest resurgence by killing natural predators in the environment (Driesche et al. 2007), while encouraging pesticide resistance in surviving pest populations (Dutcher 2007, Ciancio and Mukerji 2007). Even so, chemical controls remain useful when used judiciously in an IPM program (Dent 2000, Driesche et al. 2007). Mechanical control is the physical manipulation of plants to prevent pests and pathogens. Mechanical controls include pruning, raking, tilling, removing pests and infected plants (roguing) by hand, creating physical barriers such as raised beds, insect screens, organic or plastic/reflective mulch, solarizing/heating the soil, sticky traps/barriers, and etc. (Ciancio and Mukerji 2007, Bradley and Moore 2018). Cultural control has some overlap with mechanical control methods, but cultural controls tend to refer to controlling the

environment of your crops to exclude pests. Some examples include: selecting resistant cultivars, cultivating and planting in healthy soil, managing weeds, interplanting/trap cropping, aerating the soil, choosing appropriate planting dates, rotating crops, letting the field lie fallow, and etc. (Ciancio and Mukerji 2007, Bradley and Moore 2018). Biological control in the classical sense relies on reintroducing the various biological entities which keep pest populations in check in their natural/native environments (Heimpel and Mills 2017, Hajek and Eilenberg 2019). This concept is based off of the enemy release hypotheses from invasion ecology, which hypothesizes that introduced pest populations flourish because they have no natural enemies present to control their growth (Liu and Stiling 2006, Heger and Jeschke 2014). The corollary being that biological control agents such as parasitoids, predators, herbivores and pathogens can injure pest populations sufficiently to provide control (Heimpel and Mills 2017, Hajek and Eilenberg 2019). One of the primary benefits of biological control is that these natural enemies can become established in the environment, creating long term control while adapting to fluctuations in pest populations over time (Hajek and Eilenberg 2019). Biological control has found success in a variety of natural and agricultural environments, protecting crops against insect pests and combating invasive weed species (Driesche et al. 2010).

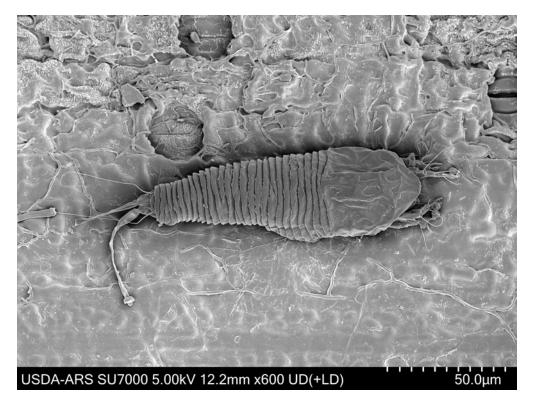


Figure 2: Cryo-SEM image of Eriophyid mite infected with unidentified fungus, collected from *Liriope muscari*. Photo Credit: Dr. Gary R. Bauchan, USDA-ARS, 2020 Current Management of RRD is not effective

1.2.1

Nursery managers have been recommended to manage RRD by removing sick plants and spraying acaracides (Hong et al. 2012, Olson et al. 2017, "Control - rose rosette" 2018). Although eriophyid mites are often controlled via chemical means (Messing and Croft 1996, Leeuwen et al. 2009), a handful of eriophyoid species have developed resistance to some acaricides, including Phyllocoptruta oleivora (Ashmead) and Acalitus vaccinii (Keifer) becoming resistant to dicofol (Omoto et al. 1994, 1995) while Aculus cornutus (Banks) and Aculops lycopersici (Tryon) have developed resistance to various organophosphates (Baker 1979, Abou-Awad and El-Banhawy 1985). In addition, to date there is limited information regarding the toxicity and effectiveness of acaricides used to combat P. fructiphilus. Pesticide applications are further complicated by the biology of the mite: P. fructiphilus are a refuge seeking species of eriophyoids which prefer to feed on the small plant hairs on the sepals, underneath the petals (Amrine and Stasny 1994,

Jesse et al. 2006, Lillo et al. 2018, Otero-Colina et al. 2018). The petals help shield the mites from conventional pesticide treatments. Furthermore, a single mite is potentially enough to transmit the virus (Di Bello et al. 2017), which can infect a rose in less than an hour, yet plants can remain sick and symptomless for months to years (Amrine Jr 1996, Di Bello et al. 2017). This slow onset of disease symptoms creates an additional challenge for management (Di Bello et al. 2017), because by the time the disease is noticed, the mites may have already spread to the whole garden. Disease detection is also difficult: Symptoms can appear similar to natural plant growth or herbicide damage, making it hard to diagnose in the field (Hong et al. 2012). Molecular methods for testing RRV are becoming readily available Di Bello et al. (2017), and newer technologies, such as Raman spectroscopy (Farber et al. 2019) are being developed to test for RRV, but it remains to be seen if these methods are capable of identifying asymptomatic infections or if these tests are suitable for disease monitoring on larger scales. Host plant resistance is not a viable option for controlling RRD: currently, all roses are known to host P. fructiphilus, and few roses show signs of resistance to RRV (Di Bello et al. 2017, Byrne et al. 2018). Mechanical control via pruning and sanitation have not proven to be effective (Olson et al. 2017). The use of windbreaks has been suggested to reduce the number of mites landing on roses (Windham et al. 2014), The lack of management options for mites, as well as the increased cost of rose production due to RRV make it difficult for growers to compete with an increasingly competitive international market. Rose growers need better methods to combat *P. fructiphilus* and RRV.

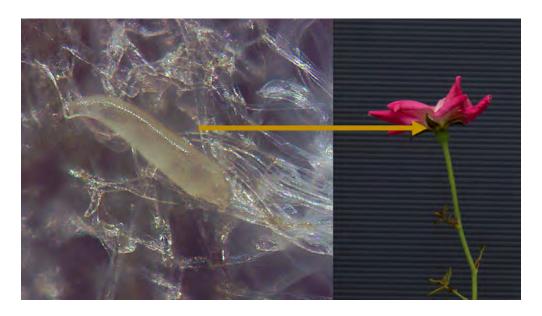


Figure 3: Illustration of the typical location of *Phyllocoptes fructiphilus* on roses. *P. fructiphilus* are difficult to manage with pesticides due to the protection offered by the sepals.

1.2.2 Phytoseiids mites: good options for biological control of mites?

Many mites species have potential as a biological control (Gerson et al. 2003, Carrillo et al. 2015). Their efficiency as predators of pest species has been recognized for many years: One of the earliest recorded attempts at biological control was of a mite Tyroglyphus phylloxerae (Riley & Planchon), which was imported to France from the USA in an attempt to control the grape phylloxera, Daktulosphaira vitifoliae (Fitch 1855) (Riley 1874, Dent 2000, Kirchmair et al. 2009). Although this early attempt was unsuccessful, several mite species have been successful in controlling pest species (Bellows Jr et al. 1996, Driesche et al. 2010). The most well-studied family of predatory mites used for biological control are the Phytoseiidae (Gerson et al. 2003, Farragut et al. 2010, Carrillo et al. 2015). The lifestyles of Phytoseiid mites are generally split into four categories based on feeding guilds as described in McMurtry and Croft (1997): Type I mites belong to the genus Phytoseiulus, the only group considered to be specialists on spider mites from the genus Tetranychus. These mites reproduce faster than other phytoseiid groups, but only thrive on spider mite prey. They also respond to kairomones emitted by Tetranychus

feeding (McMurtry and Croft 1997, Farragut et al. 2010). Type II phytoseiids are also heavily associated with *Tetranychus*, including representatives from the genera *Neoseiulus*, Galendromus, and Typhlodromus, but Type II mites also can feed on other mite groups, such as eriophyid, tydeid, and tarsonemid mites. They also can feed on pollen or plant exudates if necessary (McMurtry and Croft 1997, Farragut et al. 2010). Both Type I and Type II mites often live in the web colonies of their Tetranychid hosts, and have longer dorsal setae to avoid entanglement (McMurtry and Croft 1997, Farragut et al. 2010). Type III phytoseiids are considered to be generalists, and can grow and reproduce on a variety of different mite groups, including Eriophyoid, Tetranychoid, Tarsonemid and Acarid mites. They also feed on plant pollen, nectar, and insects such as whiteflies and thrips (McMurtry and Croft 1997, Farragut et al. 2010). The breadth of their feeding guild has encouraged their use in biological control programs (Farragut et al. 2010). Type III mites are more likely to feed on other mites of the same species, and require more prey for development than the specialist phytoseiid groups (McMurtry and Croft 1997, Farragut et al. 2010). Type III live on plants rather than in spider mite colonies, and accordingly have shorter dorsal setae. Type III mites will still feed opportunistically on *Panonychus*, a groups of Tetranychid mites which produce less dense webbing (McMurtry and Croft 1997, Farragut et al. 2010). Lastly, Type IV mites belong to the genus Euseius, which are polyphagous mites which primarily feed on pollen, although they will feed on other mites and small insects as well. They have short dorsal setae (McMurtry and Croft 1997, Farragut et al. 2010). Phytoseiid mites of all four types have been integrated successfully into various pest management programs. Many phytoseiids have been tested with various combinations of other biocontrol agents, such as predatory bugs and Beauveria bassiana (Chow et al. 2010, Midthassel et al. 2016, Bouagga et al. 2018, Freitas et al. 2021), as well as certain pesticides (Trumble and Morse 1993, Nicetic et al. 2001, Fernández et al. 2017). Phytoseiid reproduction has been studied to develop methods for mass-rearing and releasing as biological control agents for thrips, whiteflies, spider mites (Tetranychidae),

flat mites (Tenuipalpidae), scale insects and other pests (Gerson et al. 2003, Chen et al. 2006, Carrillo et al. 2011a, Carrillo and Peña 2011, Sarwar 2017, Knapp et al. 2018, Argolo et al. 2020). One of the more popular species of commercially-available predatory mite is Amblyseius swirskii Athias-Henriot (Calvo et al. 2014). A. swirskii is a Type III mite species (Farragut et al. 2010), which has been used successfully in agriculture for pest control of crop pests such as whiteflies (Bolckmans et al. 2005), spider mites (McMurtry et al. 1970), rust mites (Park et al. 2010, Onzo et al. 2012), broad mites (Tarsonemidae) (Lopez et al. 2016), and thrips (Wimmer et al. 2008). A. swirskii tolerate shipping well (Lopez and Smith 2016) and are often sold packaged in vermiculite or in sachets with wheat bran which allows the mites to slowly release into the environment (Buitenhuis et al. 2014, Calvo et al. 2014). A. swirskii can be reared on artificial diets (Nguyen et al. 2013), natural and supplemental pollen (Loughner et al. 2011, Park et al. 2011, Delisle et al. 2015) and/or other arthropods present in the environment even when the pest of concern is absent (Janssen and Sabelis 2015, Kumar et al. 2015). This allows A. swirskii to be released periodically as a preventative measure instead of reacting to an outbreak (Kutuk and Yigit 2011). Volunteer and banker plants near cropping systems can also provide shelter for phytoseiids to live in (Smith and Papacek 1991, Coli et al. 1994, Xiao et al. 2012, Nunes et al. 2020). Type III phytoseiid mites are generally associated with plants (Farragut et al. 2010), and do not survive well without them (Jung and Croft 2000). Plant structures affect many aspects of a phytoseiid's life (Cortesero et al. 2000, Schmidt 2013), influencing dispersal (Buitenhuis et al. 2013, Lopez et al. 2016), as well as performance as predators (Cédola et al. 2001, Seelmann et al. 2007, Buitenhuis et al. 2013). For example, Type III phytoseiids prefer to live on 'hairy' plants with dense trichomes, and will leave glabrous leaf surfaces (Loughner et al. 2010a, 2010b), often laying their eggs in the densest patches of plant hair, or the thick tufts of trichomes along axillary veins known as 'domatia' on the underside of leaves (O'Dowd and Willson 1991, Walter 1992, 1996, Grostal and O'Dowd 1994, Agrawal and Karban 1997), possibly to

avoid predation (Faraji et al. 2002). Predator-plant mutualisms also extend into the realm of chemical communications: many types of phytoseiids learn to associate their prey with Volatile Organic Compounds (VOCs) released when plants are injured by pests or infected with pathogens (Sabelis et al. 1999, Maeda and Takabayashi 2001, Boom et al. 2002, Boer and Dicke 2004a, 2004b, 2005). VOCs can repel (Moraes et al. 2001) attract (Nomikou et al. 2005, Gadino et al. 2012), encourage predation (Kessler and Baldwin 2001, Halitschke et al. 2007), or poison arthropods (Vancanneyt et al. 2001). Plant responses to herbivory differ between plant and predator species (Maeda and Liu 2006, Qualley and Dudareva 2008), underlining the importance of studying the specific interactions for each crop (Boom et al. 2004).



Figure 4: *Phytoseiulus persimilis* are type I phytoseiid mites: specialists of spider mites from the genus *Tetranychus* (McMurtry and Croft 1997, Farragut et al. 2010).

1.3 Induced plant defenses for biological control

Plants are primarily sessile organisms which aren't able to run or hide, therefore undefended plants struggle to grow in the face of the constant threat of herbivory (Kessler et al. 2004). In order to combat being eaten, plants rely heavily on their ability to

protect themselves *in-situ*, via a myriad of different physical and chemical defenses (Walling 2000). These defenses are categorized as either constitutive defenses or induced defenses (Farmer 2016). Constitutive defenses are always 'on,' being produced by the plant constantly, such as tannins and latex, while inducible defenses rely on some sort of signal before the plant will produce them. Physical defenses of herbivory includes spines, prickles, thorns, glandular trichomes, latex, sclereids, epicuticular wax, bark, thick cell walls, and compensatory growth to prevent tissue damage while increasing wear on herbivore mouthparts (Farmer 2016). In addition to these physical barriers to herbivory, plants are also efficient chemical factories which produce a bevy of secondary plant metabolites, including inhibitory proteins, enzymes, and toxins which reduce palatability of plant tissues, prevent uptake of essential amino acids, or kill the herbivore outright (Farmer 2016). It is hypothesized that inducible defenses must have evolved in response to threats that were sporadic in nature, but strong enough to necessitate a response (Edelstein-Keshet and Rausher 1989, Tollrain and Harvell 1999). The idea is that inducible defenses allow plants a type of cost-saving for their limited resources (Optimal Defense Theory, Steppuhn and Baldwin (2008); Adler and Karban (1994)), or to avoid damaging themselves with the compounds used (Steppuhn and Baldwin 2008). Otherwise, the evolution of constitutive defenses would seem to be a better option for plant defense (Karban and Myers 1989, Järemo et al. 1999). A corollary of the optimal defense theory is that inducible defenses should have cues that trigger dependably, accurately and be an effective deterrent once activated, so as to avoid opportunity costs (Berenbaum and Zangerl 1999, Järemo et al. 1999). Induced chemical defenses are thought to have an added benefit of being faster and less costly for plants to produce than other types of defense, such as developing spines or thicker cell walls (Berenbaum and Zangerl 1999, Järemo et al. 1999). Even so, chemical defenses still have drawbacks in allocation costs: plants investing energy into defenses are not using those resources for growth or reproduction (Berenbaum and Zangerl 1999). There are also probably genetic tradeoffs to

keep inducible costs active rather than other essential plant functions, and there may be ecological compromises as well: adaptation to one form of defense may preclude the use of another (Berenbaum and Zangerl 1999). Another confounding factor with induced defenses occurs in the presence of specialist herbivores, many of which are especially adapted to overcoming a particular plant defense (Ehrlich and Raven 1964, Schoonhoven et al. 2005, Farmer 2016).

1.3.1 Can systemic acquired resistance be used to reduce mite herbivory?

Järemo et al. (1999) considered the development of systemic responses to be more probable if plant defenses required larger doses for deterrence, and posited that localized responses to herbivory are benefit the plant when small amounts of initial damage are a reliable cues of larger damage to come. This framework readily considers the feeding activities of stylet feeders like mites, whose initial damages are minimal, but quickly accelerate due to mites' fast population growth rates. Accordingly, plants need to be responsive and accurate when identifying a threat before a defense can be mounted. Plants rely on pattern recognition receptors (PRRs) (Couto and Zipfel 2016), to detect pathogenassociated molecular patterns (PAMPS) (Boller and Felix 2009), and herbivore-associated molecular patterns (HAMPS) (Mithöfer and Boland 2008), molecules released from attacking pathogens and herbivores, respectively. These PRRs are part of innate plant immunity: PAMP-triggered immunity and effector-triggered immunity (ETI) (Chisholm et al. 2006, Jones and Dangl 2006). Plant cell-surface receptors detect common pathogen molecules, such as flagellar proteins, chitin and ergosterol. If activated PTI typically stops further invasion, by depositing callose at the site of infection, releasing reactive oxygen species (ROS), mitogen-activated protein kinases (MAPK, Howe and Jander (2008)), and inducing pathogen-responsive genes. If this first line of defense is surpassed, ETI has evolved to identify the proteins used to overcome PTI, by detecting pathogen effectors with the R proteins encoded by the corresponding R-genes in the plant (Boller and Felix 2009). One of the most well known effects of activating ETI is the hypersensitive response

(HR), rapid localized cell death/necrosis at sites of infection. The HR also activates pathogensis-related (PR) genes and upregulates intercellular Salicylic Acid (SA), which converts to the VOC, Methyl Salicylate (MeSA), a signal which propagates resistance throughout the plant. The increased expression of PR genes primes the plant for long term resistance to future attack, via a process known as systemic acquired resistance (SAR) (Boller and Felix 2009, Vlot et al. 2009, Zhang et al. 2010). HAMPs work in a similar way to PAMPs, but instead of detecting molecular patterns associated with pathogens, they detect molecules associated with herbivores, such as arthropod oral secretions, eggs, pheromones, or other chemicals conserved across a wide range of arthropods (Mithöfer and Boland 2008). Plants respond to triggered HAMPS in similar ways: they also trigger ROS, MAPKs, and Ca^{2+} influx at the site of injury (Vincent et al. 2017). Another important plant defense is the Jasmonic Acid (JA)-Ethylene (ET) signalling pathways. The JA/ET pathways are activated when JA upregulates in response to wounding and/or arthropod damage, and provides protection from herbivory as well as pathogen damage (Thaler et al. 2001, Farmer et al. 2003, Guo and Ecker 2004, Glazebrook 2005, Howe and Jander 2008). Plants can be primed directly through application of SA, MeSA or even synthetic chemical analogues, such as acibenzolar-S-methyl (ASM) to activate SAR (Conrath et al. 2006, Vlot et al. 2009, Zhang et al. 2010). SAR-induction increases levels of β-1,3-glucanase and chitinases (Bronner et al. 1991a, Ward et al. 1991), which prevent fungal disease development (Goy et al. 1992, Xue et al. 1998, Narusaka et al. 1999, Suo and Leung 2001). These proteins have potential for the biological control of pest mites: Bronner et al. (1991b); Bronner et al. (1991a) observed that feeding by the gall mite Aceria cladophthirus (Nalepa) triggered the hypersensitive response on Solanum dulcamara, producing chitinase and β-1,3-glucanase activity, which suggested that these may have a role in plant defenses against herbivores. Subsequent experiments by Westphal et al. (1991) also found that S. dulcamara's SAR response to A. cladophthirus produced long lasting protection from subsequent colonization by more A. cladophthirus or another

eriophyid, Thamnacus solani Boczek and Michalska, a rust mite. Unfortunately, later research by Westphal et al. (1992) demonstrated that these induced responses were not enough not protect the plant from Tetranychus urticae Koch, but instead increased their fecundity. This type of interplay between induced defenses is common, and varies by plant species (Boom et al. 2004). The induction of SA and JA are known to exhibit negative cross-talk in some plant systems (Baldwin et al. 1997, Belliure et al. 2010, Thaler et al. 2012): Warabieda et al. (2020) observed that JA helped increase plant resistance to T. urticae, but applying JA and ASM together was less effective than applying JA alone, due to SA interference with JA pathways. Other studies have found opposite effects: Favaro et al. (2019) reported reduced numbers of T. urticae on strawberries post SA induction, and Khederi et al. (2018a) found that SA and JA induction was sufficient to control erineum forming Colomerus vitis (Pagenstecher). This type of inconsistency is best explained by the results of Kant et al. (2007), which found examples of interspecific variation of T. urticae's ability to induce—and resist—JA defenses. Furthermore, there have been a number of cases where mites have been known to avoid or prevent upregulation of plant defenses entirely: Both T. urticae and Aculops lycopersici Massee, have been reported to suppress the JA pathways without relying on antagonistic cross-talk between the responses (Sarmento et al. 2011, Alba et al. 2014), instead by suppressing downstream accumulation of JA (Alba et al. 2014, Glas et al. 2014). Glas et al. (2014) observed that A. lycopersici would still induces SA defenses, while an inducer species (Kant et al. 2007) of T. urticae feeding on tomato (Solanum lycopersicum) induces both JA and SA pathways, but when both mites were introduced to the same plant, the JA response plummeted and SA doubled (Glas et al. 2014). This caused A. lycopersici populations to suffer while the T. urticae populations benefited from A. lycopersici's reduction of JA (Glas et al. 2014). Vectors of plant pathogens create a similar struggle for their host plants by manipulating and suppressing the SA and JA/ET pathways for their mutual benefits (Agrawal and Karban 1999, Belliure et al. 2010). An example can be seen in

the interactions of *B. yothersi*, the vector of *Citrus leprosis virus C* (CiLV-C): infection of *Arabidopsis thaliana* and *Citrus* spp. with CiLV-C induces SA and suppresses JA/ET pathways through crosstalk (Arena et al. 2016). A follow-up study of *B. yothersi* feeding on *A. thaliana* was similar in result: mite feeding triggered both SA and JA/ET pathways, but *B. yothersi* reared on mutant *A. thaliana* with no SA response had lower fecundity (Arena et al. 2018), suggesting that *B. yothersi* rely on inducing SA to antagonize JA production. Inducing plant defenses can have negative consequences for the predators as well as the herbivores (Pappas et al. 2017): Ataide et al. (2016) observed that inducing a plant JA pathway reduced *T. urticae* and *T. evansi* mite performance, but also negatively affected ovophagy by *Phytoseiulus longipes*, which ate fewer eggs from mites living on induced plants (Ataide et al. 2016), slowing their reproductive rate. It is also possible that the differences feeding methods between mite species is creating different defense responses, as has been seen in other arthropod groups (Zarate et al. 2006, Zhang et al. 2009, Arimura et al. 2011).

1.4 A second mite-plant-pathogen system: Brevipalpus californicus and Orchid fleck virus

The most important superfamily of herbivorous mites is the Tetranychoidea. The Tetranychoidea are comprised of 2,000 species divided into 5 families (Krantz 2009), two of which have economic significance, Tetranychidae—the spider mites—and Tenuipalpidae. Tenuipalpidae are known colloquially as the false spider mites, or flat mites due to their flattened character and superficial similarity to the Tetranychidae. In contrast to tetranychids, tenuipalpids do not spin webs and are considered to be a pest of reduced severity: Krantz (2009) places them as the 'third most important family of phytophagous mites.' Flat mites are considered to be a tropical to subtropical group of mites (Gerson 2008), the majority of which are not of economic significance (Hoy 2011). Consequently, tenuipalpids have been studied much less than the Tetranychidae (Jeppson et al. 1975, Childers et al. 2003a, Gerson 2008), but flat mites from the genus *Brevipalpus* have been

gaining importance in recent years as vectors of plant viruses (Chagas et al. 2003, Childers et al. 2003c, Childers and Derrick 2003, Kitajima et al. 2003, Rodrigues et al. 2003, Kitajima et al. 2008, 2010, Childers and Rodrigues 2011, Melzer et al. 2013, Rodrigues and Childers 2013, Ramos-González et al. 2017, Chabi-Jesus et al. 2018, Dietzgen et al. 2018a). Another major pest of modern concern is Raoiella indica (Hirst), a pest of palms (Arecaceae), ginger (Zingiberaceae), bananas (Musaceae), and bird of paradise plants (Strelitziaceae) (Jeppson et al. 1975, Etienne and Flechtmann 2006, Hoy 2011, Beard et al. 2012), which has been invading the Neotropics since their introduction to the Caribbean (Etienne and Flechtmann 2006, Rodrigues et al. 2007, Roda et al. 2008, Vásquez et al. 2008, Carrillo et al. 2011b, Dowling et al. 2011, Kane et al. 2012, Peña et al. 2012, Alcívar et al. 2020, Escobar-Garcia and Andrade 2020, Ramírez et al. 2020, Rodrigues et al. 2020, Amaro et al. 2021). Flat mites are typically small (200 to 300 µm) red or green, and move slowly (Jeppson et al. 1975, Hoy 2011). Tenuipalpids feeding is typically restricted to a few hosts, and mites can usually be found on the underside of leaves, often along leaf veins or the midrib (Jeppson et al. 1975, Hoy 2011). Some species feed on grass, bark, flower heads, leaf sheaths, or form galls (Jeppson et al. 1975, Hoy 2011). Flat mites have egg, larva, protonymph, deutonymph and adult forms over an average of 3-4 weeks (Hoy 2011). A few species have only six legs as adults. Tenuipalpid mites can be difficult to classify correctly with light microscopy, due to distortions during mounting of characters used in species identification (Welbourn et al. 2003). Furthermore, flat mites are thelytokous parthenogenic: Males are seldom encountered, due to infections with the feminizing bacteria Candidatus Cardinium (Cytophaga-Flavobacterium-Bacteroides phylum) Chigira and Miura (2005). This has caused some concern that some Brevipalpus species are actually isofemale lines specialized on their specific hosts (Groot et al. 2005), an idea which is further complicated by the occurrence of cryptic species in these groups (Navia et al. 2013, Skoracka et al. 2015). Few methods of pest management have been reported from past reviews of tenuipalpids (Jeppson et

al. 1975, Gerson 2008, Hoy 2011): a number of different mite predators have been tested for their efficacy, as well as the pathogenic fungi *Hirsutella thompsonii* and *Metarhizium anisopliae* (Rossi-Zalaf and Alves 2006, Gerson 2008). Zheng et al. (2012) tested the ability of water and phytoseiids to reduce populations of *B. obovatus. Beauveria bassiana* has been tested to control *R. indica*, and is potentially compatible with the previously-tested phytoseiid species *Amblyseius largoensis* and *Typhlodromus ornatus* (Carrillo and Peña 2011, Freitas et al. 2021). Chemical applications are typically used to control tenuipalpids (Childers 1994), but some species have begun to develop chemical resistance to the more common applications (Campos and Omoto 2002, Rocha et al. 2021).

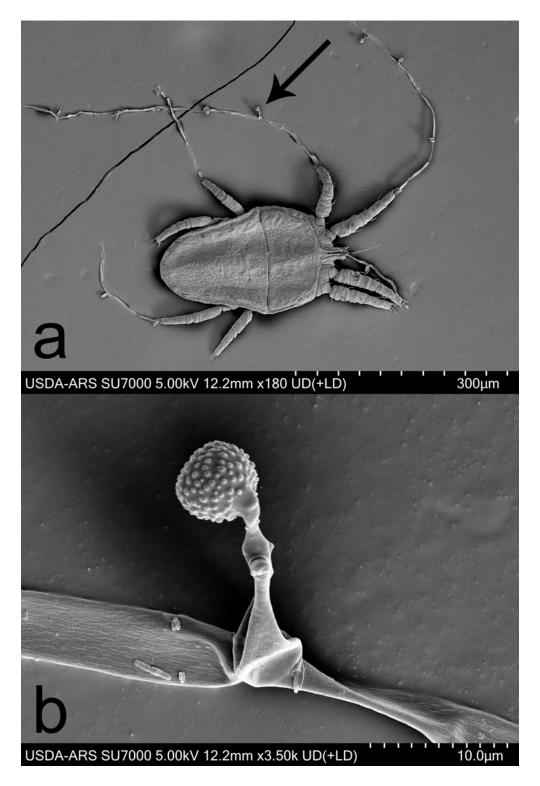


Figure 5: a) Cryo-SEM image of Tenuipalpid mite infected with unidentified fungus, collected from *Liriope muscari* b) detail of sporangia. Photo Credit: Dr. Gary R. Bauchan, USDA-ARS, 2020

One of the more cosmopolitan species of tenuipalpid is Brevipalpus californicus (Banks). B. californicus is a common pest with a large host range of agricultural and ornamental crops, including tea, orchids, citrus, cotton and tobacco (Jeppson et al. 1975, Hoy 2011). B. californicus acts as the primary vector for Orchid fleck dichorhavirus (OFV), the type member for the genus *Dichorhavirus*, family *Rhabdoviridae*; a bacilliform, nuclear rhabdoviruses composed of two segments of single-stranded, negative-sense RNA which infects plants (Dietzgen et al. 2014, Walker et al. 2018, Amarasinghe et al. 2019). Dichorhaviruses are only known to be transmitted by mites in the genus Brevipalpus (Dietzgen et al. 2014). Other members of this genus are: Citrus chlorotic spot virus, Citrus leprosis virus N, Clerodendrum chlorotic spot virus and Coffee ringspot virus (Dietzgen et al. 2018a). Many orchid genera are able to become infected with OFV (Kondo et al. 2006, 2006), as well as some Asparagaceae (Nolinoidaea) (Dietzgen et al. 2018a), and Citrus plants (Rutaceae), where it causes leprosis-like symptoms (Bastianel et al. 2010, Roy et al. 2013, García-Escamilla et al. 2018). Mechanical transmission of OFV is possible under lab conditions to various Chenopodiaceae, Aizoaceae, Fabaceae, and Solanaceae (Chang et al. 1976, Kondo et al. 2003, Peng et al. 2013). B. californicus has been collected from OFV-infected Nolinoidaea plants in Australia (Mei et al. 2016, Dietzgen et al. 2018b). B. californicus was historically associated with cases of citrus leprosis disease of Florida and Texas prior to 1925, when the disease mysteriously disappeared from the US sometime during the 1960s (Knorr et al. 1968, Childers et al. 2003b). Later studies of herbarium specimens from this time period revealed this disease to be caused by a Dichorhavirus, distantly related to modern OFV strains (Kitajima et al. 2011, Hartung et al. 2015). Maeda (1998) found evidence that B. californicus can transmit OFV in a persistent propagative manner, which means that the virus may replicate inside of its mite vector. OFV was first described infecting Cymbidium orchids in Japan (Doi et al. 1977). Many countries have reported OFV and OFV-like rhabdoviruses infecting orchids worldwide (Kondo et al. 2003), including Asia: [China (Peng et al. 2017), Korea (Peng et al. 2013)],

Africa: [South Africa (Blanchfield et al. 2001, Cook et al. 2019), North America: [The US (Blanchfield et al. 2001), (Bratsch et al. 2015)], South America: [Brazil Kitajima et al. (2001), Colombia (Kubo et al. 2009b), Costa Rica (Freitas-Astúa et al. 2002), Paraguay (Ramos-González et al. 2015), Europe: (Begtrup 1972), Germany (Petzold 1971, Lesemann and Doraiswamy 1975)] and Oceania: (Australia Lesemann and Begtrup 1971, Lesemann and Doraiswamy 1975, Gibbs 2000), Fiji (Pearson et al. 1993), Vanuatu (Pearson et al. 1993)]. The prevalence of OFV and its mite vector is thought to be associated with the importation of infected orchids (Dietzgen et al. 2018a). Orchids infected with OFV develop chlorotic/necrotic flecks on leaves and reduces plant vigor (Peng et al. 2013). Citrus infected with OFV develop chlorotic/necrotic bullseye lesions on leaves, fruits and bark (Roy et al. 2015, Ramos-González et al. 2017). Citrus-infecting strains of OFV have been encountered in Mexico (Roy et al. 2015) and recently in Hawaii (Ocenar 2020, Olmedo-Velarde et al. 2021), introduction of this virus is considered a threat to the billion dollar citriculture industries of the US.



Figure 6: Oncidium orchid infected with Orchid fleck virus

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