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Mycophagy in Coccinellidae: Review and Synthesis

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Abstract. Mycophagy, though often overlooked, represents an interesting and unique ecological niche within the Coccinellidae. Facultative mycophagy has been reported from the aphidophagous Coccinellini and the polyphagous Tytthaspidini. Members of Halyziini, a cosmopolitan tribe of the Coccinellinae, are obligate mycophages specializing on the powdery mildew fungi of Erysiphales, a ubiquitous order infecting almost 10,000 angiosperm plants worldwide. Various researchers have recorded this mycophagous habit during the past 150 years, resulting in a large list of host-powdery mildew complexes around the world harboring these insects. Members of the Halyziini possess several attributes conducive to biological control, including host specificity (obligation), widespread native distribution, and strong aggregative response to host density. We compare historical attempts to quantify powdery mildew removal by Halyziini, and discuss the possible utility of mycophagous coccinellids for biological and integrated control, as well as mechanical transmission of powdery mildew inoculum through insect dispersal.

Keywords. *Psyllobora*, *Halyzia*, *Illeis*, *Macroilleis*, *Vibidia*, mycophagy, mechanical disease transmission, powdery mildew, Erysiphales, plant pathogen, biological control, integrated disease management

1. Introduction

Although the overwhelming majority are predators of other arthropods, the Coccinellidae are not all purely entomophagous insects (Weber and Lundgren, 2009, this issue; Giorgi et al., 2009, this issue; Lundgren, 2009b, this issue). Phytophagy within the Epilachninae and mycophagy (both facultative and obligative) within the Coccinellinae have evolved from a common coccidophagous ancestor (Giorgi et al., 2009, this issue) that, in turn, may have been derived from an ancient mycophagous group, the Cerylonid series, from which all coccinellids are descended (Sasaji, 1968; Leschen, 2000; Giorgi et al., 2009, this issue). Phytophagous ladybirds (Giorgi et al., 2009, this issue) are generally regarded as pests, but the beneficial or detrimental economic position of the mycophagous Coccinellinae is less clear. This review presents some of the important historical literature associated with mycophagous coccinellids, concentrating primarily on obligate mycophages. In addition, we will discuss the taxonomy, biology, ecology, and possible utility of this clade of ladybird beetles as biological control agents.

2. Origin of mycophagy in coccinellids

Coccinellids belong to the cerylonid series of Cucujoidea, and based on current phylogenetic data may be a sister taxon to Alexiidae or Endomychidae (Ślipiński and Pakaluk, 1991; Giorgi et al., 2009, this issue). Most members of this series are mycophagous. However, the vast majority of the Coccinellidae are predators on sternorrhynchan insects, and Giorgi et al. (2009, this issue) conclude that basal Coccinellidae were coccidophagous. Leschen (2000) and several others (Lawrence and Hlavac, 1979; Crowson, 1981; Thomas, 1993) suggest that honeydew production by the commonly sternorrhyncan prey of this family may have been the ecological opportunity for evolution of predatory habits. Honeydew, a digestive by-product composed of carbohydrates and proteins, often accumulates on plant substrates where hemipteran insects feed and supports the growth of a specific group of Ascomycete fungi commonly known as sooty molds. Leschen (2000) proposed a simple model whereby ancestral mycophagous beetles first accepted sooty molds as food items, then specialized as sooty mold consumers, and finally accepted the insects indirectly producing the mold as food items. This idea is strengthened by the fact that many predators of Hemiptera, including many coccinellids, also feed on honeydew and sooty mold to this day (Majerus, 1994; Lundgren, 2009a; Lundgren, 2009b, this issue).

3. Facultative and obligate mycophagy in coccinellids

Within the Coccinellidae, mycophagy can be viewed as a derived condition, and it has only been reported from the Coccinellinae (Giorgi et al., 2009, this issue). A molecular phylogenetic analysis by Giorgi et al. (2009, this issue) suggests that the Halyziini arose within the generally aphidophagous tribe Coccinellini. They conclude that, in spite of distinctive mandible shape, presumably related to mycophagy, both Halyziini and the poorly-known Tytthaspidini (see below) have distinctive features which provide further evidence for a derived condition.

3.1. Facultative mycophagy. Facultative mycophagy may be commonplace in the largely aphidophagous tribe Coccinellini Weise (Majerus, 1994). These predators are often polyphagous, feeding on pollen, nectar, honeydew, fungi, fruit and foliage, but specific animal foods (e.g. aphids) are necessary to complete development (Hodek, 1973; Lundgren, 2009b, this issue). This distinction between “essential” and “alternative” foods (Hodek, 1973) is important when discussing the polyphagy of the tribe. Additionally, at least some members of the tribe do not have a mandatory minimum level of predation: *Coleomegilla* Timberlake and its allies can complete development on pollen alone (Lundgren and Wiedenmann, 2004; Michaud and Grant, 2005; Majka and McCorquodale, 2006). Facultative mycophagy, or mixed feeding on pollen, mildews (Erysiphales) and aphids has been reported in *Rhyzobius litura* (F.) (Ricci, 1986) and *Propylea quatuordecimpunctata* (L.) (Turian, 1971; Hukusima and Itoh, 1976). Upon finding fungal spores in the gut of Coccinellini, many researchers have suggested incidental or accidental consumption of sooty mold fungi during honeydew grazing (Zoebelein, 1956; Putman, 1964; Carter and Dixon, 1984). However, Triltsch (1999) found *Alternaria* Nees conidia and *Puccinia* Persoon uredospores more frequently than aphids in the gut of *Coccinella septempunctata*. These fungi are plant pathogens, and since the spores were found in both the presence and absence of aphids, it is likely that they represent an important seasonal food for the aphid predator.

Also within the Coccinellinae there is a poorly-known group of polyphagous coccinellids that regularly include fungi in their diets along with pollen, arthropods and possibly some plants (Hodek and Honěk, 1996; Samways et al., 1997; Lundgren, 2009a). These interesting mycophilous polyphages, closely allied to the Coccinellini, have been deemed a separate tribe, the Tytthaspidini (Fursch, 1996; Kovar, 1996), containing two genera; *Tytthaspis* Crotch and *Bulaea* Mulsant. Some authors, while recognizing their polyphagous habit, place these genera within Coccinellini (Hodek and Honěk, 1996; Kuznetsov, 1997). Many times, however, they have escaped consideration during systematic treatment of the Coccinellidae, perhaps due to geographic obscurity or a dearth of specimens (Vandenberg, 2002). Ricci (1982) found fungal spores of *Alternaria* and *Cladosporium* Link ex Fries in the gut contents of *Tytthaspis* *sedecimpunctata* (L.) along with pollen, Acari and Thysanoptera remains. Mixed feeding in the same species on pollen, mildew and aphids was documented by Ricci et al. (1983). Turian (1969) also observed *Tytthaspis* feeding on Erysiphales and termed the behavior "micromycetophagy".

3.2. Obligate mycophagy. The cosmopolitan tribe Halyziini Mulsant (=Psylloborini, see Pakaluk et al., 1994) is comprised entirely of mycophages (Gordon, 1985), although some workers have reported aphidophagy (Schilder and Schilder, 1928; Borner and Heinze, 1957; Fulmek, 1957; Omkar and Pervez, 1999) or phytophagy (herbivory on higher plants) (Yurtsever, 2001). Davidson (1921) performed a series of simple no-choice feeding experiments with a variety of food items to establish *Psyllobora vigintimaculata* (Say) (Figure 1) as an obligate mycophage. Members of Halyziini feed on powdery mildew (PM) fungi (Ascomycotina: Erysiphales), a ubiquitous and diverse group of obligate plant parasites known to infect 9838 species of mostly dicotyledonous angiosperm plants worldwide in both natural and managed systems (Amano, 1986). Despite the wide host range of the order, individual species or biotypes within Erysiphales tend to be quite host-specific, often infecting only one species or genus of plant (Amano, 1986). Thus, the evolution of PM has closely followed the evolution of their hosts (Takamatsu, 2004). Similar environmental conditions are required for all PM to infect and develop, and unlike many other plant pathogenic fungi, spores can germinate and infect hosts under very low atmospheric humidity (Takamatsu, 2004). Positive osmotic potential is detrimental to the thin-membraned spores, and free water as overhead irrigation has even been proposed as a control measure (Sivapalan, 1993; Liu, 2001; Korner and Challa, 2003). Different PM fungi often infect many unrelated plants in an ecosystem simultaneously when conditions are favorable for PM germination and development. The ability of the Halyziini to feed on other fungi has not been reported in the literature. Other lower fungi including yeast (Saccharomycetales) and rust fungi (Uredinales) were refused in simple laboratory no-choice trials with *Psyllobora vigintimaculata* (Sutherland and Parrella, unpublished). We suspect that PM fungi are common and abundant enough worldwide for this group of beetles to maintain a relatively specialized diet in many different climates and ecosystems.

The specialized feeding exhibited by the Halyziini and Tytthaspidini is apparently facilitated by unique mandibular morphology. The typical bifed mandibular apex of all Coccinellinae is modified in the Halyziini such that the ventral tooth is further divided into a row of additional teeth (Samways et al., 1997). Furthermore, the inner mandibular cutting edge of Coccinellini is smooth, while in the fungal-feeding tribes it is covered in minute teeth, forming a comb. These structures are presumed to help the insects to rake fungal spores from conidial towers and spore-laden hyphae growing on leaf surfaces (Ricci, 1982; Lawrence, 1989; Samways et al., 1997). In the polyphagous Tytthaspidini these comb or rake-like structures may also serve as tools for removing individual pollen grains, and fungal spores may be an alternative or incidental food source. The specialized mycophages within Halyziini will be emphasized in the ecological and biological discussions of mycophagy in Coccinellidae below.

4. Brief taxonomic history of the Halyziini (= Psylloborini)

The obligate mycophages of the Coccinellidae are so similar morphologically to the other members of the Coccinellinae that they have often been overlooked as a distinct group. There are questions over whether the Halyziini is a distinct clade deserving of tribal status, since it is nested within the predatory Coccinellini (Giorgi et al., 2009, this issue). Mulsant (1850) studied the paraphyletic tribe Trimere, raised by Dejean (1837) and containing 22 coccinellid genera, and proposed the branch Halyziares which included the genera *Psyllobora* Dejean, *Halyzia* Mulsant, *Vibidia* Mulsant, *Thea* Mulsant (= *Psyllobora* Chevrolat in Dejean, 1837), *Illeis* Mulsant and *Propylaea* Mulsant. This represented the first attempt to taxonomically segregate mycophagy in the family. Chapuis (1876), however, considered *Psyllobora* to be a subgenus of *Halyzia* within the group Coccinellites, in turn nested within the Coccinellides Aphidophages. A major revision of the taxonomy of North American coccinellids, published in 1899 (Casey), organized the family into 16 tribes, one of which was Psylloborini. Korschefsky (1932), Sasaji (1968), Kovar (1996) and Kuznetsov (1997) have all retained the tribal name and nested it within the subfamily Coccinellinae. Twelve genera were identified by Kuznetsov (1997) within the tribe, including *Cleobora* (Mulsant), *Eothea* Iablokoff-Khnzorian, *Halyzia*, *Illeis*, *Macroilleis* Miyatake, *Metamyrrha* Capra, *Microneda* Crotch, *Neohalyzia* Crotch, *Oxytella* Weise, *Protothea* Weise, *Psyllobora* and *Vibidia*. The taxon Halyziini (from Halyziares Mulsant) was resurrected by Pakaluk et al. (1994) and recently adopted in Vandenberg's (2002) classification of the family along with Coccinellini under Coccinellinae. The division between Coccinellini and Halyziini is sometimes vague, as evident by Pope's (1988) consideration that *Illeis* resides within Coccinellini and by the recent movement of *Protothea* into Coccinellini (Poorani and Ślipiński, 2005).

5. Biology and ecology of Halyziini

Halyziini is a truly cosmopolitan taxon. It seems that any locale in which there are plant-parasitic PM fungi also contains mycophagous coccinellids to consume them. The most widespread genus, *Psyllobora* (= *Thea*), is found in Europe, the Americas, Asia and Africa. A second geographically extensive genus, *Illeis* (= *Leptothea*), is found in Asia, Australia and

Japan. Three other genera; *Halyzia*, *Vibidia* and *Macroilleis*, are Palearctic and Indomalayan in distribution. Given this wide tribal distribution, together with the obligation to feed on highly visible and important plant parasites, it is difficult to understand how these insects could remain understudied. The biology and ecology of this tribe were established by a series of historical observations, which are summarized in Table 1.

5.1. Biological observations. In 1874 the German taxonomist Kaltenbach noted that *Psyllobora vigintiduopunctata* (L.) was found on *Astragalus* L. leaves covered with the PM fungus *Erysiphe holosericea* (Wallroth) Link, yet he believed the beetles to be feeding on mites amongst the mildew, and so reported no mycophagy. Albert Koebele recorded mycophagy by *Illeis galbula* (Mulsant) while in Australia as early as 1893 (Timberlake, 1943). Prior to this, members of Halyziini had been regarded as aphidophagous (Chapuis, 1876). In Europe, Weise (1900), Martelli (1910; 1914) and Lichteinstein (1917) observed *Psyllobora vigintiduopunctata*, *Vibidia duodecimguttata* (Poda), and *Halyzia sedecimguttata* (L.), respectively, all to have mycophagous habits involving PM fungi. In the United States *Psyllobora vigintimaculata* was commonly associated with rose and apple PM, *Sphaerotheca pannosa* (Wallroth) Léveillé and *Podosphaera oxyacanthae* (de Candolle) de Bary, respectively, and was reared in the lab for biological observation and “essential” host determination (Davidson, 1921). Davidson (1921) predicted up to five generations a year in California’s Central Valley based on phenological observations and described a typical coccinellid life cycle; with elongate, oval eggs deposited on PM-infected plant parts, four stadia, a pupa, and a preovipositional period leading up to reproductive adulthood. Later life cycle studies with members of the Halyziini yielded results consistent with Davidson’s (Liu, 1951; Almeida and Milleo, 1998; Sutherland, 2005; Cividanes et al., 2007), but Dharpur et al. (1990) indicated that *Illeis cincta* (F.) had five stadia in India.

Perhaps most interesting were Davidson's laboratory feeding experiments. In a series of experiments, groups of newly hatched or PM-fed larvae were offered various arthropod prey, including aphids (*Chromaphis juglandicola* Kaltenbach, *Macrosiphum rosae* L., *Aphis gossypii* Glover, *Myzus persicae* Sulzer), spider mites (*Tetranychus* Dufour), coccids (*Saissetia oleae* (Olivier)), and diaspidids with "armor" removed (*Aspidiotus* Bouche). These offerings always resulted in dead, starved larvae while cohort larvae fed on rose PM developed and pupated. Adult beetles offered these prey items also refused them, and lived much longer than larvae, but also eventually succumbed to starvation. In Brazil, where the genus *Psyllobora* is represented by 17 species (Almeida, 1985), both *Psyllobora hybrida* Mulsant and *Psyllobora confluens* (F.) were recorded feeding on *Microsphaera caricae* (Maublanc) Hansford, a PM infecting castor bean, *Ricinus* L. (Lima, 1931). In China the food of *Halyzia hauseri* (Mader) , *Halyzia sanscrita* (Mulsant) and *Illeis cincta* was determined to be apple PM, *Podosphaera leucotricha* (Ellis & Everhart) E.S. Salmon, and PM consumption was quantified (Liu, 1951). Over the past 20 years, publications from around the world (Table 1) have provided data on halyziine biology as well as information regarding their biological control potential; Brazil (Almeida, 1985; Almeida and Milleo, 1998; Cividanes et al., 2007), China (Wu and Guo, 1987), India (Prasad and Rai, 1988; Dharpur et al., 1990; Krishnakumar and Maheswari, 2004), Cuba (Cruz et al., 1989), Italy (Ratti, 1996), Argentina (Bado and Rodriguez, 1998), Japan (Takeuchi et al., 2000), Turkey (Soylu and Yigit, 2002), Syria (Ahmad et al., 2003) and the United States (Sutherland, 2005; Sutherland and Parrella, 2006; Sutherland and Parrella, in press).

5.2. Host utilization and host range. Anderson (1982) tracked the seasonal habitat utilization of *Illeis galbula* near Sydney, Australia and found that the insect used one PM complex extensively (*Oidium* Saccardo on *Lonicera fragrantissima* Lindley & Paxton) during breeding, another (PM on *Senna pendula* [Willdenow] =*Cassia coluteodes*) sporadically, and an evergreen tree, *Ficus rubiginosa* Desfontaines ex Ventenat, as a protective overwintering site. Anderson (1982) found quantities of red *Ficus rubiginosa* trichomes in the insect's gut along with large air bubbles during winter. The author suggested that the trichomes could have been ingested accidentally along with latex, honeydew or water consumed at the overwintering site. The seasonal occurrence of the Japanese species *Illeis koebelei* Timberlake is thought to be synchronized with the abundance of essential fungi (Takeuchi et al., 2000), and the authors recorded the beetle's feeding on 11 PM species, documenting seasonal changes in host use and breeding complexes. A similar situation was observed in *Psyllobora vigintimaculata* in California (Sutherland 2005), with natural populations shifting to different PM-complexes throughout the year based on PM availability. When reviewing the literature on the relationships between halyziine species and PM, it appears that they are quite general in their acceptance of most PM fungi species as food (Table 2). Ahmad et al. (2003) in Syria and Turkey and Sutherland (2005) in California recorded 57 and 26 plant species, respectively, that served as hosts for PM fungi consumed by *Psyllobora*. However, there may be preferences or restrictions in host range for some species. For example, the PM genera *Uncinula* Léveillé and *Uncinuliella* Zheng & Chen (both now known as *Erysiphe* sect. *Uncinula*; Braun et al., 2002), and *Erysiphe* R. Hedwig ex DeCandolle were never associated with *Illeis koebelei* in field observations made by Takeuchi et al. (2000). However, larvae were later successfully reared on a diet of *Erysiphe kusanoi* (Sydow & P. Sydow) Braun & Takam (=*Uncinula kusanoi* Sydow & P. Sydow) in the laboratory. Sutherland (2005) found no *Psyllobora vigintimaculata* on severely PM-infected *Euonymus japonica* Thunberg and *Eschscholtzia californica* Chamisso throughout the year, and attributed this to differences in plant species rather than PM genera (*Oidium* and *Erysiphe*, respectively). Ratti (1996) reported *Psyllobora vigintiduopunctata* to feed and reproduce on *Oidium*-infected *Euonymus japonica* in Italy, but the same PM complex was conspicuously devoid of *Psyllobora* in California. Clearly the host ranges of these beetles are not completely known, and may specifically depend on the taxon, the geographic location, the host plant species, the PM species, and the other PM complexes available in local space and time.

5.3. Possibility for mechanical transmission. The asexual stage of a PM infection involves the abundant production of conidia borne on conidiophores, or spore towers (Glawe, 2008). Transmission in this stage from infected to uninfected plants is primarily mediated by wind, mechanical force (i.e. leaf fluttering) or ambient air movement (Glawe, 2008). After settling upon an appropriate host leaf substrate, and in the presence of specific environmental conditions, the conidia germinate and penetrate the host, initiating a new infection.

It is reasonable to consider that mycophagous coccinellids, foraging directly in these patches of asexual spores, may pick up conidial inoculum and serve as mechanical vectors of the pathogen. A microscopic examination of larvae and adults of *Psyllobora vigintimaculata* from a laboratory colony showed conidia and hyphal strands adhering to the insects' setae and their elytra (Sutherland, personal observation). Yet viable PM conidia are also present in large numbers in the air column, and need no vector insect to initiate new infection. In the Halyziini-PM system the fungal spores are thought to be the nutritive source for the beetles, and therefore most should not survive digestion. However, some spores could remain viable; more research is needed. For instance, Hed et al. (1999) found that a chaser diet of aphids versus apple for the coccinellid *Hippodamia convergens* Guérin-Méneville influenced the proportion carrying the fungal pathogen *Discula destructiva* Redlin (dogwood anthracnose) and excreting viable spores in their frass. Another system involves shore flies (Diptera: Ephydridae) and the transmission of

Thielaviopsis basicola (Berkeley & Broome) Ferraris, a soilborne, root-infecting pathogen. Here there is incidental ingestion of the fungus by flies after feeding on infected plants, passage through the digestive system, and viable, infective chlamydospores recovered in frass (Stanghellini et al., 1999).

We conducted a laboratory experiment to address the question of mechanical transmission. Groups of uninfected *Zinnia elegans* Jacquin "Peter Pan" plants, grown in divided growth chambers (each division ~ $1m^2$) with directional (vertical) airflow, were each exposed to conspecific plants uniformly infected with PM (*Erysiphe cichoracearum* Jaczewski) either in the presence or absence of adult *Psyllobora vigintimaculata*. Air movement in the chambers allowed for normal aerial transmission of PM. It was hypothesized that if *Psyllobora vigintimaculata* was a mechanical vector of PM, then uninfected plants exposed to both PM inoculum and beetles would show a higher and faster infection rate than uninfected plants exposed to inoculum alone. Software based on image analysis algorithms (Assess Image Analysis Software (AIAS) for Plant Disease Quantification, The American Phytopathological Society, 2002), coupled with digital photography, was used to quantify PM on *Zinnia* plants throughout the 4-wk study. Beginning with the introduction of inoculum, a digital camera was used to capture weekly images of each plant. The AIAS was used to separate visible PM from uninfected leaf tissue based on pixel saturation (Lamari, 2005), and then to express disease as the percentage of leaf area covered by visible PM colonies (%PM). Each chamber division was viewed statistically as one experimental unit, and each plant as a subsample within that unit. The results of this study showed no differences between the two treatments in terms of overall PM growth and %PM over time (Figure 2). This suggests that if mechanical transmission occurs in this small experimental system it is overshadowed by natural aerial transmission via airborne conidia. However, since this experiment only addressed very short-range transmission under specific conditions, more research is needed in this important area.

6. Biological control and the possibility for integrated disease management (IDM)

6.1. Biological control of PM. The PM pathogens (Erysiphales) are collectively considered one of the most important plant pathogens worldwide since many of their hosts are valued as agricultural and ornamental plants. Conventional management of PM employs regular applications of chemical fungicides. This approach can be costly and sometimes ineffective due to the development of resistance in the fungi (Gubler et al., 1996; del Pino et al., 1999; Heaney et al., 2000; McGrath, 2001). Biological control of PM may offer solutions to this resistance phenomenon and other fungicide-related issues such as residues in food crops, effects on nontarget organisms, impacts on farm worker health and safety, etc. Control of PM using commercially-available microbial controls, equivalent to that obtained through chemical fungicide applications, has been found with the spore-forming bacterium *Bacillus subtilis* (Ehrenberg) Cohn (Bacillales: Bacillaceae) and the pycnidial fungal hyperparasite *Ampelomyces quisqualis* Cesati (not currently assigned to order or family) (Chase, 2004; Falk et al., 1995). Interest in the development of *Pseudozyma flocculosa* (Traquair, Shaw & Jarvis) Boekhout & Traquair (Ustilaginales: Ustilaginaceae) as a biofungicide has been prompted by results against the PM *Sphaerotheca fuliginea* (Schlechtendal) Pollacci (Traquair et al., 1988; Paulitz and Belanger, 2001).

Little is known of the potential for arthropods to control or reduce PM through consumption. The biology of PM fungi is unique: fungal growth is exposed on the leaf surface as a hyphal mat and only the haustorium, a structure used for nutrient acquisition, is found to penetrate the host's cuticle in most species (Takamatsu, 2004). This may allow arthropod biological control to be a viable option. However, it is unknown whether PM colonies can recover from complete removal of the hyphal mat through growth from haustoria. Work by English-Loeb et al. (1999) in upstate New York demonstrated that the tydeid mite *Orthotydeus lambi* (Baker) (Acari: Tydeidae) reduced the incidence of PM in riparian grapevines, *Vitis riparia* Michx. Abundance of these mites is thought to be mediated by the host plant through acarodomatia (tufts of hair or invaginations on the abaxial leaf surfaces) which offer protection and a favorable microclimate for the mites (Norton et al., 2001). Larger arthropods able to consume greater amounts of PM, such as the coccinellid members of Halyziini, may offer superior PM removal and suppression. The Halyziini possess several characteristics deemed necessary by Solomon (1949) for successful biological control. The widespread distribution of the tribe ensures that most locations with PM problems already have a mycophagous species present, so that conserving and/or augmenting populations already in place may be all that is needed. Regular field observations (Sutherland and Parrella, in press) have revealed that adult *Psyllobora vigintimaculata* are able to locate isolated, low-density PM infections in a large and heterogeneous landscape. This suggests that beetles can detect and respond to cues resulting from PM infection. Also, *Psyllobora* species have an observed tendency to aggregate on plant parts most heavily infected with PM (Dharpur et al., 1990; Yurtsever, 2001; Sutherland and Parrella, in press) and consume as a group (Figure 3).

Biological control of a plant pathogen through consumption by an arthropod may be difficult. Many bacteria and fungi, including PM, have periods of intense asexual sporulation in which the infective population grows geometrically. Insects' generational time requirements may be several orders of magnitude longer than these microbes. Nevertheless, a handful of workers have gone beyond observation to speculate on the possible utility of these beetles for biological control of PM (Liu, 1951; Wu and Guo, 1987; Cruz et al., 1989; Dharpur et al., 1990; Soylu and Yigit, 2002; Krishnakumar and Maheswari, 2004; Sutherland and Parrella, 2006).

6.2. Quantification of PM consumption. The task of quantifying PM consumption is facilitated by the fact that PM-infected leaf areas, once fed upon by members of the Halyziini, are visibly discernable and easy to separate from those areas not fed upon (Figure 4). The first published attempt quantify mycophagy was made by Liu (1951), working with *Halyzia hauseri* feeding on the PM *Podosphaera leucotricha* infecting apple in China. Insect developmental periods, total feeding periods, and estimated daily feeding capacity (cm^2) were determined through daily observations. From this information, Liu (1951) estimated that the feeding capacity for *Halyzia hauseri* from egg eclosion until death was 99.72 cm^2. He also presented the comparative ratio 1:2:5:5:5 representing the relative total amounts of fungi consumed during each stage respectively, the 1st through 4th instars and adults, showing that the last two instars consumed a similar amount to the adults.

Soylu and Yigit (2002) stained okra leaves infected with PM *Erysiphe cichoracearum* with lactophenoltryphan blue and examined them using light microscopy, revealing that larvae and adults of *Psyllobora bisoctonotata* (Mulsant) fed upon mycelia as well as conidia and conidiophores on the leaf surface. Spore solutions were made from infected leaf areas exposed to larvae and compared with those unexposed to larvae via the counting of conidia with a haemocytometer. The authors reported a 92% reduction in conidial density in leaf sections fed upon by the beetles. Leaf area cleaned by *P. bisoctonotata* was quantified using excised leaf sections and a leaf surface scaler. Third and fourth instars were the most efficient consumers in terms of leaf area cleaned per unit time.

In India, Krishnakumar and Maheswari (2004) measured PM control provided by *Illeis cincta* and *Illeis bistigmosa* (Mulsant). They used potted mulberry plants, uniformly infected with the PM *Phyllactinia corylea* (Pers.) Karst., exposed to adult beetles, and sampled over time to determine percent infection, percent disease control (PDC) and the percent disease index (PDI) (Food and Agricultural Organisation, 1967). In addition, they compared the control offered by the beetles to the control provided by both the fungicide dinocap (0.2%) and neem oil emulsion (2%). A dramatic reduction in PDI (from 92.8 to 32.4) was recorded 10 d after five pairs of *Illeis cincta* were released per plant. No such reduction was observed when only two pairs of beetles were released. In the comparison with fungicides, the authors reported that the PDC was statistically similar 20 d after treatment in plants receiving beetles or an application of fungicide. Also, the PDI slowly increased over time in plants treated with fungicides, while PDI slowly decreased in plants receiving beetles.

A simple linear model was used by Sutherland and Parrella (2006) to quantify the total visible PM removed by *Psyllobora vigintimaculata* during its larval development. Neonate larvae were individually introduced into vented petri dishes containing an excised *Zinnia elegans* leaf disc infected with PM (*Erysiphe cichoracearum*). Disease severity, expressed as %PM (leaf area visibly-infected / total leaf area), was assessed using digital photography and image analysis methodology (see above) at regular intervals until pupation. PM-infected leaf discs that did not receive larvae (untreated) were monitored in parallel during this same period. In order to estimate the total amount of leaf area cleaned (LAC) by one *Psyllobora vigintimaculata* larva during development a model was constructed that included a measure of the normal PM growth (G) that should occur in the absence of feeding. The constructed model was as follows:

$$\mathrm{LAC}_{\mathrm{total}} = \mathrm{LAC} + \mathrm{G},$$

where LAC = mean (%$PM_{initial}$ - %PM_{final}) * leaf disc area ± standard error for all larva units, and G = mean (%PM_{final} - %$PM_{initial}$) * leaf disc area ± standard error for all untreated units. Based on the observed LAC measured in the laboratory, the model predicted that an average larva would clean 6.32 ± 3.3cm^2 of leaf area of PM spores and hyphae during development (Table 3). This figure is much lower than the 99.72 cm^2 reported by Liu (1951) for *Halyzia hauseri* feeding on apple PM. Possible explanations for this difference include the larger size of *Halyzia* (~6 mm adult diameter vs. ~3 mm for *Psyllobora*), the inclusion of adult feeding until death in Liu's study, and differences in PM spore density among plant host / powdery mildew combinations as discussed by Takamatsu (2004).

6.3. Integrated disease management. While biological control of PM using Halyziini alone may not be adequate for commercial applications, it may be possible to integrate PM consumption by these beetles with compatible fungicides and cultural approaches to control disease, as part of an integrated disease management (IDM) program. Such an integrated approach could include the augmentation and conservation of these native natural enemies as consumers and possibly as indicators of early or isolated PM infection.

For growers of wine grapes in California, PM is the most serious chronic disease problem (Delp, 1954; Pearson and Goheen, 1988). Sulfur, an elemental fungicide, insecticide and acaricide, and a staple PM prevention material, is the primary pest and disease management material used in winegrapes, with more than 20 million pounds of active ingredient applied in California during 2003 (CA. DPR, 2004). Sulfur has been shown to have direct and indirect negative effects on local beneficial arthropods (Coop and Croft, 1995; Kreiter et al., 1998; Martinson et al., 2001). Strobilurin fungicides, strong natural antibiotics that inhibit fungal respiration, are widely available as synthetic derivatives in commercial fungicide formulations.

Investigations have shown a decrease in adults and larvae of aphidophagous coccinellids after applications of strobilurins (Michaud, 2001) for disease control in orchards. Fungicide bioassays conducted in the laboratory have shown that topical applications of wettable sulfur and the strobilurin trifloxystrobin were toxic to adults and larvae of *Psyllobora vigintimaculata* (Sutherland, 2005). For instance, 100% mortality was recorded 2 hr after the direct application of wettable sulfur (label rate: 31.7 mL/L) to 2nd instars kept on filter paper in petri dishes (Sutherland, 2005). Preliminary data shows a similar trend in the field, with much lower *Psyllobora* densities found in vineyard plots treated with fungicides as compared to untreated plots, even when corrections are made for differences in PM densities. Since mycophagous coccinellids may be present feeding on PM within these agroecosystems, it is important to consider the effect of fungicide applications on their survival and utility as potential biological controls.

7. Conclusion

Mycophagous coccinellids are poorly understood, and despite a recent increase in research by the international community, this group is still understudied in comparison to its entomophagous brethren. There remains much to understand about this tribe in the areas of phylogenetics, biology, ecology and applied economic entomology (especially biological control). However, the possibility of mechanical transmission of PM conidia by these insects, and the relative potential for PM patches to regrow from haustoria after halyziine grazing, must be further explored before the true potential for biological control can be fully understood. Clearly mycophagous coccinellids are an important part of natural and agricultural systems around the world. Trying to determine how important they may be, especially in the quest for alternative management strategies for PM, is a challenge well worth undertaking.

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Figure 1. Adult *Psyllobora vigintimaculata*, a North American mycophagous coccinellid, grazing on a patch of powdery mildew fungi (photo by Jack Kelly Clark).

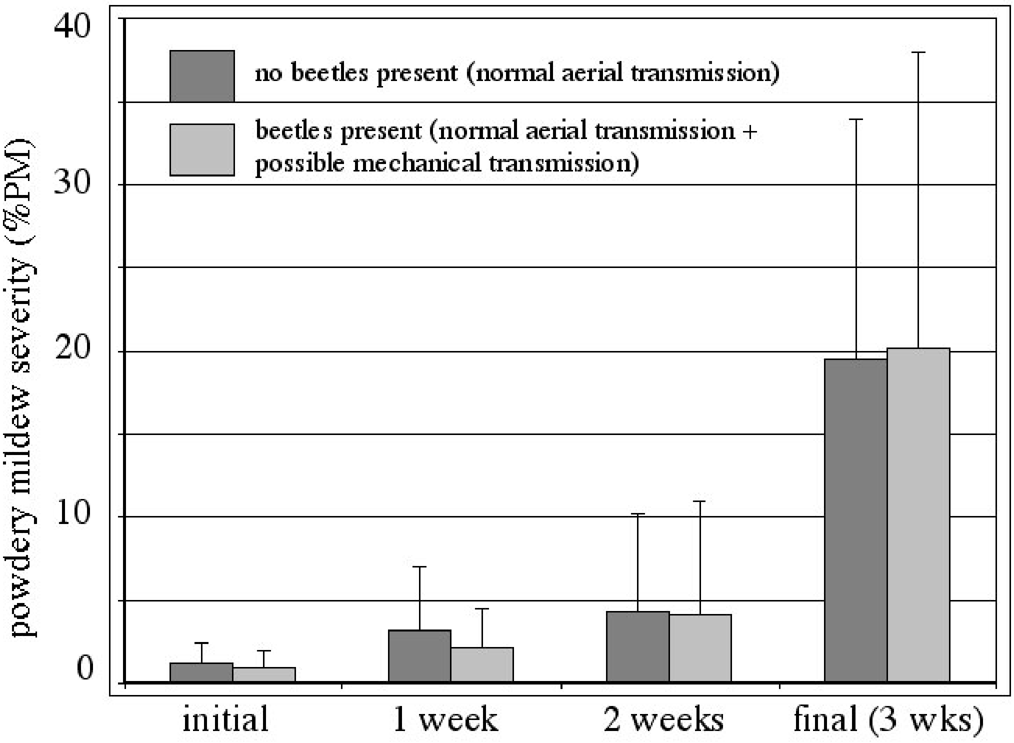

Figure 2. Transmission of powdery mildew (PM) in divided growth chambers, as expressed by severity (%PM) over time in groups of *Zinnia elegans* “Peter Pan” after the introduction of conspecific plants infected with the PM *Erysiphe chicoracearum* either in the presence or absence of adult mycophagous beetles, *Psyllobora vigintimaculata*. No significant treatment difference (F=0.79, p=0.38, df=1,94) detected through nested ANOVA (24 subsamples nested within each treatment) (Sutherland, unpublished data).

Figure 3. Aggregation of *Psyllobora vigintimaculata* larvae feeding together on a patch of the PM *Erysiphe chicoracearum* infecting *Zinnia elegans*.

Figure 4. An individual *Psyllobora vigintimaculata* larva feeding on the powdery mildew (PM) *Erysiphe chicoracearum* infecting *Zinnia elegans* "Peter Pan". Leaf area exposed to and fed upon by the larva is visibly discernable from unexposed PM-infected leaf area.

Table 1. A summarized chronological listing of biological and ecological observations and experimentation involving the mycophagous coccinellids of the tribe Halyziini and their food source, powdery mildew (PM) fungi.

Publication	**Species of Halyziini**	**Specific Topic**
Koebele, ~1893†	*Illeis galbula*	observation of mycophagy
Weise, 1900	*Psyllobora vigintiduopunctata*	observation of mycophagy
Martelli, 1910, 1914	*P. vigintidupunctata*, *Vibidia duodecimguttata*	observation of mycophagy, PM species determination
Lichteinstein, 1917	*V. duodecimguttata*, *Halyzia sedecimguttata*	observation of mycophagy, PM species determination
Davidson, 1921	*P. vigintimaculata*	biology, phenology and host range testing
Strouhal, 1926	*H. sedecimguttata*, *P. vigintiduopunctata*, *V. duodecimguttata*	biological observation, morphological description, and taxonomic key
Lima, 1931	*P. hybrida*, *P. confluens*	observation of mycophagy, PM species determination
Liu, 1951	*H. hauseri*, *H. sanscrita*, *I. cincta*	PM species determination, consumption quantification
Savoiskaya, 1961	*P. vigintiduopunctata*, *V. duodecimguttata*, *H. tschitscherini*	observation of mycophagy
Anderson, 1982	*I. galbula*	natural host range and utilization studies
Almeida, 1985	*Psyllobora* spp. (17)	biological descriptions
Wu and Guo, 1987	unknown	PM control efficacy
Prasad and Rai, 1988	*P. cincta*	biological observation
Cruz et al, 1989	*P. nana*	biological observation,

		suggestion of biocontrol
Dharpur et al, 1990	*P. cincta*	biological description
Ratti, 1996	*P. vigintiduopunctata*	biological observation
Bado and Rodriguez, 1998	*P. bicongregata*	biological and morphological descriptions
Almeida and Milleo, 1998	*P. gratiosa*	biological and morphological descriptions
Takeuchi, 2000	*I. koebeli*	Field phenology, natural host range and utilization
Soylu and Yigit, 2002	*P. bisoctonotata*, *P. vigintiduopunctata*	Biological observation, consumption quantification, host range observation
Ahmad et al, 2003	*P. bisoctonotata*	Natural phenology and host range observations
Krishnakumar and Maheswari, 2004	*I. cincta*, *I. bistigmosa*	PM control efficacy, release rate determination
Sutherland, 2005	*P. vigintimaculata*	Natural biology, phenology, host range determination, fungicide compatibility
Sutherland and Parrella, 2006	*P. vigintimaculata*	Consumption quantification, release rate determination
Cividanes et al, 2007	*P. confluens*	Biological observation and description
Sutherland and Parrella, in press	*P. vigintimaculata*	Natural biology, phenology, host range determination

† from Timberlake (1943)

Table 3. Observed consumption of the powdery mildew (PM) fungus *Erysiphe cichoracearum* by two age groups of the mycophagous coccinellid *Psyllobora vigintimaculata* during development from egg to pupa in terms of the leaf area cleaned (LAC) of visible PM and the naturally-occurring background growth (G) exhibited by PM in the absence of feeding. Based on the linear model: LAC_{total} = LAC + G; where LAC = mean ($\%PM_{initial}$ - $\%PM_{final}$) * leaf disc area ± standard error for all larva units, and G = mean ($\%PM_{final}$ - $\%PM_{initial}$) * leaf disc area ± standard error for all untreated units.

Age Group	**LAC**	**G**	**Amount Consumed**
eclosion to 3rd instar	-1.17 cm^2	4.38 cm^2	3.22 ± 1.8 cm^2
3rd instar to pupation	1.69 cm^2	1.41 cm^2	3.10 ± 1.5 cm^2
Total (egg to adult)	0.52 cm^2	5.79 cm^2	6.32 ± 3.3 cm^2

Table 2. Powdery mildews, and their plant hosts, on which Halyziini (Coccinellidae) beetles were observed to feed.

Plant family	Plant species	Powdery mildew genus	Location	Halyziine species (reference)
Aceraceae	*Acer macrophyllum*	*Sawadaea*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Adoxaceae	*Sambucus racemosa*	*Erysiphe (=Microsphaera)*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
Apiaceae	*Ainsworthia trachycarpa*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Ammi majus	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Torilis arvensis	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Torilis nodosa	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Asteraceae	*Calendula arvensis*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Centaurea calcitrapa	*Leveillula*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Erysiphe	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Chrysanthemum coronarium	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Cichorum intybus	*Podosphaera (=Sphaerotheca)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Cirsium arvense	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Conyza albida	*Podosphaera (=Sphaerotheca)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Cosmos bipinnatus	*Podosphaera (=Sphaerotheca)*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
		Erysiphe	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Dahlia coccinea	*Erysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Erigeron naudinii	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Gerbera jamesonii	*Erysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Guzotia abyssinica	*Podosphaera (=Sphaerotheca)*	India	*Psyllobora cincta* (Dharpur et al., 1990)
	Helianthus annuus	*Erysiphe*	Cuba	*Psyllobora nana* (Cruz et al., 1989)
		Podosphaera (=Sphaerotheca)	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
		Erysiphe	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Matricaria chamomilla	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Picris echioides	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Sonchus oleraceus	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Urospermum picroides	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Xanthium strumarium	*Podosphaera (=Sphaerotheca)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Zinnia elegans	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Erysiphe	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Balsaminaceae	*Impatiens balsamina*	*Podosphaera (=Sphaerotheca)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Bignoniaceae	*X Chitalpa tashkientsis*	*Erysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Brassicaceae	*Rapistrum rugosum*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)

	Sinapis arvensis	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Sisymbrium officinale	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Cannabaceae	*Celtis sinensis*	*Erysiphe (=Uncinula)*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
Caprifoliaceae	*Lonicera fragrantissima*	*Oidium*	Australia	*Illeis galbula* (Anderson, 1982)
Celastraceae	*Euonymus japonica*	*Oidium*	Italy	*Psyllobora vigintiduopunctata* (Ratti, 1996)
Chenopodiaceae	*Chenopodium opulifolium*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Convolvulaceae	*Calystegia sepium*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Convolvulus arvensis	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Cornaceae	*Benthamidia florida*	*Erysiphe (=Microsphaera)*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
Cucurbitaceae	*Cucumis sativa*	*Erysiphe*	Turkey	*Psyllobora bisoctonotata* (Soylu and Yigit, 2002)
		Erysiphe	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Cucurbita spp.	*Erysiphe*	Brazil	*Psyllobora lenta* (Almeida, 1985)
		Erysiphe	Argentina	*Psyllobora bicongregata* (Bado and Rodriguez, 1998)
		Erysiphe	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Podosphaera (=Sphaerotheca)	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Erysiphe	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Trichosanthes kilirowii	*Podosphaera (=Sphaerotheca)*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
Dipsacaceae	*Scabiosa columbaria*	*Erysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Euphorbiaceae	*Euphorbia heterophylla*	*Leveillula*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Erysiphe	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Ricinus spp.	*Ersiphe (=Microsphaera)*	Brazil	*Psyllobora hybrida* (Lima, 1931)
Fabaceae	*Ceratonia siliqua*	*Oidium*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Melilotus indica	*Erysiphe (=Microsphaera)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Onobrychis caput-galli	*Erysiphe (=Microsphaera)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Onobrychis christa-galli	*Erysiphe (=Microsphaera)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Senna pendula	Unidentified	Australia	*Illeis galbula* (Anderson, 1982)
	Trigonella hamosa	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Fagaceae	*Quercus agrifolia*	*Ersiphe (=Microsphaera)*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Quercus lobata	*Ersiphe (=Microsphaera)*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Fumariaceae	*Fumaria judaica*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Fumaria officinalis	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Geraniaceae	*Erodium malacoides*	*Podosphaera (=Sphaerotheca)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Erodium moschatus	*Podosphaera (=Sphaerotheca)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Hydrangeaceae	*Hydrangea hortensis*	*Oidium*	Brazil	*Psyllobora gratiosa* (Almeida and Milleo, 1998)
Lamiaceae	*Clerodendrum trichotomum*	*Podosphaera (=Sphaerotheca)*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)

	Mentha spicata	*Erysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Monarda punctata	*Neoerysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Salvia spathacea	*Oidium*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Linaceae	*Linum usitatissimum*	*Oidium*	India	*Psyllobora cincta* (Prasad and Rai, 1988)
Lythraceae	*Lagerstroemia indica*	*Erysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Malvaceae	*Abelmoschus esculentus*	*Erysiphe*	Turkey	*Psyllobora bisoctonotata* (Soylu and Yigit, 2002)
		Erysiphe	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Podosphaera (=Sphaerotheca)	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Erysiphe	Brazil	*Psyllobora confluens* (Cividanes et al., 2007)
	Alcea rosea	*Leveillula*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Malva neglecta	*Leveillula*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Moraceae	*Morus* spp.	*Phyllactinia*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
		Phyllactinia	Turkey	*Psyllobora bisoctonotata* (Soylu and Yigit, 2002)
		Leveillula	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Phyllactinia	India	*Illeis bistigmosa* (Krishnakumar and Maheswari, 2004)
		Phyllactinia	India	*Illeis cincta* (Krishnakumar and Maheswari, 2004)
Oleaceae	*Syringa vulgaris*	*Ersiphe (=Microsphaera)*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Papaveraceae	*Papaver rhoeas*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Plantaginaceae	*Plantago lanceolata*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Erysiphe	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Veronica persica	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Platanaceae	*Platanus X acerifolia*	*Sawadaea*	Turkey	*Psyllobora bisoctonotata* (Soylu and Yigit, 2002)
		Sawadaea	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
Poaceae	*Avena sterilis*	*Blumeria*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Phalaris paradoxa	*Blumeria*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Polygonaceae	*Polygonum aviculare*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Rumex conglomeratus	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Ranunculaceae	*Ranunculus scandicinus*	*Erysiphe*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Rosaceae	*Malus* spp.	*Podosphaera*	USA	*Psyllobora vigintimaculata* (Davidson, 1921)
		Podosphaera	China	*Halyzia hauseri* (Liu, 1951)
		Podosphaera	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Prunus spp.	*Podosphaera*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
		Podosphaera	Turkey	*Psyllobora bisoctonotata* (Soylu and Yigit, 2002)
		Podosphaera (=Sphaerotheca)	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Podosphaera	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)

	Pyracantha coccinea	*Oidium*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
	Rosa spp.	*Podosphaera (=Sphaerotheca)*	USA	*Psyllobora vigintimaculata* (Davidson, 1921)
		Podosphaera (=Sphaerotheca)	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
		Podosphaera (=Sphaerotheca)	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Podosphaera (=Sphaerotheca)	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Spiraea douglasii	*Ersiphe (=Microsphaera)*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Stephanandra incisa	*Podosphaera (=Sphaerotheca)*	Japan	*Illeis koebelei* (Takeuchi et al., 2000)
Solanaceae	*Capsicum annuum*	*Leveillula*	Turkey	*Psyllobora bisoctonotata* (Soylu and Yigit, 2002)
		Leveillula	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
	Solanum lycopersicum	*Erysiphe*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
		Leveillula	Turkey	*Psyllobora bisoctonotata* (Soylu and Yigit, 2002)
	Solanum melongena	*Leveillula*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Verbenaceae	*Verbena officinalis*	*Podosphaera (=Sphaerotheca)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
Vitaceae	*Vitis californica*	*Erysiphe (=Uncinula)*	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)
	Vitis vinifera	*Erysiphe (=Uncinula)*	Syria	*Psyllobora bisoctonotata* (Ahmad et al., 2003)
		Erysiphe (=Uncinula)	USA	*Psyllobora vigintimaculata* (Sutherland & Parrella, in press)