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Aphidophagy by Coccinellidae: Application of biological control in agroecosystems

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Abstract

Coccinellids and aphids interact in a wide range of agricultural and forest habitats and the value of coccinellid predation for aphid suppression in these systems varies from a minor role to significant reductions leading to within-season control. Although aphid-feeding coccinellids rarely play a role in the long-term regulation of population dynamics of aphid species within agroecosystems, they are effective predators reducing within-season densities of selected species of aphid pests. For example, conserving Coccinellidae through the presence of non-target aphid prey has resulted in reliable suppression of target aphid pests in cereal grain crops. Methods to manipulate within field-distributions of Coccinellidae have been developed (e.g., semiochemically based lures, artificial food sprays) and associations with flowering plants and extrafloral nectaries have been documented, but these components have yet to be integrated into biological control systems based on experimental assessments of the numerical, reproductive, and functional responses of these predators. A comparative discussion of the management of the cotton aphid (*Aphis gossypii* Glover) and the soybean aphid (*Aphis glycines* Matsumura) highlights the importance of documenting levels of pest mortality by coccinellids. Recently, the planting of transgenic cotton varieties has reduced insecticide use in cotton, thereby allowing predaceous Coccinellidae to be incorporated into IPM treatment decisions for *A. gossypii*. Detailed long-term field research was required to include coccinellid predation into economic thresholds for management of the cotton aphid. In contrast, the relatively recent pest status of the soybean aphid in North America has resulted in a series of studies showing the variation in the role of predation by Coccinellidae and other natural enemies across the aphid's North American range. Our understanding of coccinellid predation in aphid suppression will ultimately be enhanced through comprehensive behavioral studies that include manipulative laboratory experimentation, field studies and molecular techniques to analyze coccinellid feeding behavior and enhance our understanding of intercrop movement and their dispersal among crop and non-crop habitats.

KEY WORDS: aphid predation, arthropod predators, biological control, pest management, aphid suppression, conservation biological control

1. Role of Coccinellidae in aphid suppression

The association between the predatory behaviors of Coccinellidae and aphids was recognized centuries ago. In the early 1800s, the English entomologists William Kirby and William Spence (1846) described growers who conserved coccinellids as predators of hop aphids (*Phorodon humuli* (Schrank) (Hemiptera: Aphididae)) by protecting them from bird predation; additionally, Kirby and Spence summarized the concept of augmentative releases in greenhouses (see DeBach and Rosen, 1991). From this historical appreciation, numerous studies have described predator-prey interactions involving coccinellids and quantified levels of biological control resulting from predation of aphids by these natural enemies (reviewed by Hagen, 1962; Hodek, 1967; Hagen and van den Bosch, 1968; van Emden 1972, 1988; Hodek, 1973; Frazier, 1988; Hodek and Honek, 1996; Obrycki and Kring, 1998; Hagen et al., 1999; Powell and Pell 2007; Volkl et al., 2007).

A plethora of laboratory, greenhouse and field studies (including many conducted in enclosures) have documented the contributions of coccinellids to the decreased population growth rates of aphids and reductions in peak aphid densities (reviewed in Hodek et al., 1972; Frazier, 1988; Hodek and Honek, 1996). For example, in a two-year field cage study, releases of larval *Coleomegilla maculata* (DeGeer) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) reduced peak densities of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) (green peach aphids) on potatoes by an average of 85% compared to control cages with no coccinellid larvae (Obrycki et al., 1998). Models of the interactions between coccinellids and aphid pests predict reductions of aphid densities based on predation rates and numbers of Coccinellidae, and these predictions are supported by empirical field studies (e.g., Tamaki et al., 1974; Frazier and Gilbert, 1976; Tamaki and Long, 1978; Mack and Smilowitz, 1982). More recently, serological and molecular techniques have provided new insights into aphid predation by coccinellids without manipulating field populations (Harwood and Obrycki, 2005; Harwood and Greenstone, 2008; Weber and Lundgren, 2009, this issue), building on previous data collected by gut dissections (e.g., Forbes, 1883; Putman, 1964; Sunderland and Vickerman, 1980; Anderson, 1982; Triltsch, 1999; Lundgren et al., 2004, 2005) and fecal analysis (Conrad, 1959; Honek, 1986) that relied on the visual identification of indigestible food remains.

2. Biological Control of Aphids by Coccinellidae

The importance of coccinellid predation of aphids in multiple cropping systems has recently been reviewed in a comprehensive text by van Emden and Harrington (2007), which includes case studies of aphid pest management systems (e.g., cotton (Deguine et al., 2007) and grain sorghum (Michels and Burd, 2007) and several chapters that review the biology and role of Coccinellidae as aphid predators (i.e., Kindlmann et al., 2007; Pickett and Glinwood, 2007; Powell and Pell, 2007; Volkl et al., 2007). Here, we discuss the role of conservation biological control techniques (Jonsson et al., 2008) in promoting Coccinellidae for aphid pest suppression, their role in management of selected aphid pests, and examine strategies to improve levels of aphid suppression by coccinellids. Finally, we highlight two recent examples of the role of coccinellids in the biological control of aphids: (1) the incorporation of mortality caused by coccinellids into management decisions for suppression of the cotton aphid (*Aphis gossypii* Glover) (Hemiptera: Aphididae) and (2) the role of coccinellid predation in the reduction of the soybean aphid (*Aphis glycines* Matsumura (Hemiptera: Aphididae)), a newly introduced aphid pest in North America. We selected these two examples to contrast our current level of understanding of Coccinellidae in aphid suppression in these two systems. The soybean aphid has recently become a major pest of soybeans in the upper Midwestern USA and Canada (Ragsdale et al., 2004, Venette and Ragsdale, 2004; Mignault et al., 2006) triggering insecticide applications in many regions (Rodas and O'Neil, 2006). The value of coccinellids as a component of "biological services" has been described in soybeans (Costamagna and Landis, 2007; Costamagna et al., 2008; Landis et al., 2008). However, as these authors describe these ecological services, this value changes annually based on overall soybean aphid densities and their annual population dynamics. The current knowledge base is not sufficient to incorporate aphid mortality due to coccinellid predation (or "biological services") for treatment decisions on a field-by-field basis. Our discussion presents an overview of quantification of soybean aphid predation levels by Coccinellidae in the context of a developing pest management program. In contrast, the cotton aphid has been the focus of numerous studies of natural and biological control for decades. The use of parasitoids, predators and pathogens are a major component in management of cotton aphids (Abney et al., 2008). Furthermore, the ability of predators and parasitoids to reduce and maintain cotton aphid populations below the level of economic importance has been documented in the southern United States (e.g., Kerns and Gaylor 1993; Rosenheim et al., 1997). Thus, knowledge of predation of the cotton aphid by Coccinellidae is much more developed (Deguine et al., 2007) than that of the soybean aphid and provides a sufficient basis for incorporating mortality caused by Coccinellidae into management decisions for cotton aphid suppression in Arkansas (Conway et al., 2006).

2.1. Coccinellid predation of exotic aphids

Comprehensive investigations of Coccinellidae - aphid pest interactions, which started in the early 1950s (reviewed by Hagen and van den Bosch, 1968; van Emden, 1972), include studies of several exotic aphid species that established in North America. For example, following an accidental introduction into California in the 1950s (Clausen, 1978), the spotted alfalfa aphid, *Therioaphis trifolii* (Monell) (Hemiptera: Aphididae), was attacked by several naturally occurring *Hippodamia* species, but predominately *H. convergens* (Guerin) (Coleoptera: Coccinellidae) (Hagen, 1974). Although predation alone was unable to sufficiently suppress aphids, subsequent studies documented the importance of predation when complemented by the use of selective insecticides for the suppression of *T. trifolii* (Stern and van den Bosch, 1959). Thus, coccinellid predation of *T. trifolii* provided the basis for the integrated control concept (Stern et al., 1959).

Starting in the 1960s, the role of coccinellid predation in cereal crops was examined for the suppression of greenbugs (*Schizaphis graminum* (Rondani)) (Hemiptera: Aphididae) and later for Russian wheat aphids (*Diuraphis noxia* (Kurdj.)) (Hemiptera: Aphididae) (reviewed by Brewer and Elliot, 2004). Predation by Coccinellidae was the basis for the biological control of these two invasive aphid species in North American cereal production systems (Rice and Wilde, 1988; Michels et al., 2001). Further studies documented how early-season populations of non-pest cereal aphid species allowed coccinellid densities to increase, which then suppress greenbug densities in grain sorghum and wheat (Kring et al., 1985, Michels and Matis, 2008). The importance of early-season predation, which reduces prey populations at low densities, has been demonstrated many times in several predator-prey systems (e.g., Chiverton, 1986; Sunderland et al., 1987; Landis and van der Werf, 1997; Harwood et al., 2004; Brosius et al., 2007).

2.2 Early-season aphid predation

Landis and van der Werf (1997) examined predation of early-season populations of *M. persicae*, which subsequently reduces the spread of beet yellows virus in sugar beet, *Beta vulgaris* L., (Caryophyllales: Chenopodiceae), fields in Europe. Although results were not replicated across all fields, some evidence suggested that virus spread was impacted and was primarily due to the early-season pressure on aphid populations by generalist predators. Sunderland et al., (1987) reported a high percentage of Cantharidae testing positive for aphid proteins in winter wheat fields in the United Kingdom, but foliar and pitfall trapping indicated that *C. septempunctata* and *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) were important predators in these agroecosystems.

Within complex agroecosystems where predator and prey biodiversity is promoted through conservation biological control, it is the range of natural enemies, each of which exhibit some degree of niche partitioning, which improves impact on herbivore populations (Sunderland et al., 1997; Cardinale et al. 2003; Aquilino et al. 2005; Snyder et al., 2006, 2009, this issue). Furthermore, coccinellids represent major predators of pest aphids (Volkl et al., 2007) and are integral to the community of predators that regulate herbivore population dynamics early in the season. However, development of suitable management tactics is necessary to enable early-season subsistence on alternative prey or non-prey foods (see Lundgren 2009a,b) with subsequent immigration and suppression of pests at low densities.

2.3. Perspectives on the Effectiveness of Coccinellidae in Biological Control

Predation by Coccinellidae contributes to the suppression of aphids in several agricultural systems (e.g., potatoes, sugar beets, alfalfa, cotton, and wheat) (e.g., Tamaki and Long, 1978; van Emden, 1972; Frazier et al., 1981; Frazier and Gilbert, 1976; Coderre, 1999; Lee et al., 2005; Deguine et al., 2007; Michels and Burd, 2007; Powell and Pell 2007; Michels and Matis, 2008). Reductions of pest populations may occur at specific times during an aphid infestation; for example, predation by coccinellids may slow the growth of an aphid population early in the season or reduce aphid densities during a critical phase of a crop's development (Powell and Pell, 2007). However, because they are generalist predators, coccinellids have been implicated as potentially disruptive intraguild predators in several agricultural systems, including soybeans and cotton (Chacón et al., 2008; Simelane et al., 2008). Further, it has been documented that predation by coccinellids does not provide season-long regulation of aphid populations in very stable habitats (e.g., trees) or in highly disturbed annual cropping systems (Dixon, 2000; Kindlmann et al., 2007; Volkl et al., 2007). Several life history characteristics of aphidophagous Coccinellidae and their aphid prey contribute to this lack of regulatory capacity. For example, under most environmental conditions coccinellids have lower population growth rates than their aphid prey, which allows these aphids to escape population regulation (Dixon, 2000; Mills, 1982a,b; Hemptinne and Dixon, 1997; Kindlmann and Dixon, 2001). Additionally, the relatively large ratio of the generation time of coccinellid predators to their aphid prey, further exacerbates this lack of reliable regulatory ability (Kindlmann et al., 2007). One aspect of the biology of aphidophagous coccinellids that may balance their comparatively low population growth rates is their mobility and ability to aggregate rapidly to aphid populations. Coccidophagous species are particularly well known for their ability to provide long-term biological control within perennial systems, and comparisons between aphidophagous and coccidophagous coccinellids provide insights into why aphids may be more difficult to suppress with predation than are coccids (Hagen, 1974; Dixon et al., 1997; Dixon, 2000; Hirose, 2006). Aphidophagous coccinellid predators may have little or no effect on the long-term population dynamics of aphids, but these predators reduce aphid densities during a portion of a crop production season, contributing to within-season management of aphid pest populations (see review by Kindlmann et al., 2007).

For over four decades, divergent viewpoints regarding the effectiveness of coccinellids as predators of aphids have been discussed (van Emden 1966, Frazier 1988, Dixon 2000). Conclusions pertaining to the “effectiveness” of these predators were based on how this term was defined and what was considered sufficient data to support these conclusions (Frazier 1988). Data supporting effectiveness include statistical correlations and relationships between numbers of coccinellids and aphids, prey consumption rates, and searching behaviors. Frazier (1988) defined “effective” to mean a pattern of abundance in time or a density of an aphid population that would be different in the absence of coccinellid predation. A key element of this definition is that effectiveness is not related to the ability of a predator to reduce pest densities below an economically defined level. From a multi-year field study, Frazier et al. (1981) reported that *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae) (pea aphid) densities would increase faster and to a greater level in the absence of coccinellids, but in only one of four years did aphid numbers decrease rapidly due to coccinellid predation. Frazier (1988) concludes by stating "Coccinellids exploit aphid populations in a manner that is optimal with respect to the population dynamics of the coccinellids, but we cannot expect coccinellids to keep aphid numbers very low, or to do so for very long, without human intervention.” Later we illustrate this point using a case study explaining the role of coccinellid predation in the management of cotton aphid densities early in the Arkansas growing season (Conway et al., 2006).

3. Approaches to improve aphid suppression

Once the levels of pest reduction by natural enemies have been documented and some assessment of their effectiveness has been made, additional research is required to identify those measures (importation, conservation, and/or augmentation) that can be taken to enhance levels of biological control (Frazier, 1988). The importation of Coccinellidae for the biological control of aphids has been reviewed numerous times (e.g., Hagen, 1974; Obrycki and Kring, 1998; Dixon, 2000; Hirose, 2006; Powell and Pell, 2007). In North America, the importation of aphid feeding Coccinellidae has not been a prudent use of these predators (Obrycki and Kring, 1998), relatively few species have been carefully and deliberately released and established (Gordon, 1985). Few data have been collected that document improved levels of biological control of aphid pests, and potential effects on indigenous natural enemy communities and non-target species have been reported (reviewed by Obrycki et al., 2000).

3.1. Augmentative releases

Based on the assumption that increased numbers of predators will enhance levels of aphid suppression, pest managers have undertaken efforts to artificially augment coccinellid predators within a given habitat. Augmentative releases of aphid-feeding Coccinellidae have reduced aphid densities in field and glasshouse environments, but considerable variability in results have been observed (Powell and Pell, 2007). Overwintering field-collected adult *Hippodamia convergens* are commercially available for augmentative releases in North America (Obrycki and Kring, 1998), but due to the non-reproductive, overwintering physiological state of these adults, high rates of dispersal from release sites typically occur within 24 hours. However, transient reductions of aphid densities have been documented (Raupp et al., 1994; Flint and Driestadt, 2005; Powell and Pell, 2007). Releases of *H. convergens* may contribute to aphid suppression in enclosed environments, e.g., glasshouses or conservatories (Powell and Pell, 2007), but precautions should be taken to eliminate parasitoids and pathogens from these field-collected adults prior to release (O'Neil et al., 1998, Bjornson, 2008). Additionally, the geographic variation in populations of *H. convergens* should be considered when making augmentative releases of adults collected from overwintering sites in California into other regions of North America (Obrycki et al., 2001b; Flint and Driestadt 2005). Recently, encouraging results have been documented following releases of flightless morphs of adults of two species of aphid feeding coccinellids (*Adalia bipunctata* L. and *Harmonia axyridis* Pallas) (Coleoptera: Coccinellidae) that suppress *Aphis gossypii* and *Myzus persicae* better than winged adults (Lommen et al., 2008; Seko et al., 2008). Thus while augmentative releases do not provide levels of suppression for an entire season, they can provide some reductions in aphid densities for a short period in selected environments.

3.2. Supplemental food sprays

Several techniques have been used in conservation biological control to manipulate the distribution of natural enemies naturally occurring within an environment (Barbosa, 1998; Pickett and Bugg, 1998; Letourneau and Altieri, 1999; Landis et al., 2000; Jonsson et al., 2008). Most notable of these methods include the application of artificial food sprays of carbohydrates and proteins to retain coccinellids in the environment and enhance their reproductive capacity (Hagen et al., 1971; Hagen and Hale, 1974; Hagen and Bishop, 1979). Wade et al. (2008) discuss the need to examine the ecological, nutritional, and behavioral mechanisms by which food sprays alter the behavior of Coccinellidae to better understand how their positive responses can be integrated into conservation biological control programs. Questions remain, including how these carbohydrate and protein substances alter the behavior of adults, what quantity of these materials are consumed by adults, what numerical and functional responses result, and finally, whether responses by predators result in reduced densities of the target aphid pest (Wade et al., 2008). In the following section we summarize the field studies that have used food sprays to manipulate Coccinellidae in corn, alfalfa, cotton, and potato fields to formulate a series of conclusions regarding their use in biological control.

In North America, four *Hippodamia* spp., three *Coccinella* spp., *Coleomegilla maculata* (DeGeer) and *Scymnus postpinctus* Casey (Coleoptera: Coccinellidae) respond to field-applied sprays of proteins and sugars. Protein and sugar sprays arrested the movement of adults, retained individuals, and induced oviposition (in the presence of *T. trifolli* and *Acyrthosiphon pisum* in alfalfa fields) by *Hippodamia convergens* and *Hippodamia quinquesignata* (Kirby) (Hagen et al., 1971). Adults were not attracted directly to the protein and sugar food sprays, but their movements were arrested by the materials, which were then consumed. Twenty-four hours after spraying an alfalfa field with protein and sucrose solutions, the numbers of adult *H. convergens*, *H. quinquesignata*, and *Coccinella novemnotata* Herbst were up to five times higher compared to control areas, although no statistical tests were provided by Hagen et al. (1971). Similarly, in a 2-yr study in Utah, individual caged potato plants were sprayed with combinations of honey, molasses, and proteins. Six species of Coccinellidae responded to these treatments (*H. convergens*, *H. quinquesignata*, *Hippodamia sinuata* (Mulsant), *Hippodamia tredecimpunctata* L., *Coccinella transversoguttata* Faldermann, and *S. postpinctus*) (Ben Saad and Bishop, 1976a), and the application of proteins and sugars to these potato fields increased numbers of adult *C. transversoguttata*, *H. quinquesignata*, *H. sinuata*, and *H. convergens* (Ben Saad and Bishop, 1976b). Protein and sugar solutions applied to corn and cotton plots in Mississippi increased the number of adult *Coleomegilla maculata* (Nichols and Neel, 1977), highlighting the widespread applicability of using food sprays to enhance coccinellid densities. However, these results contrast with protein-only applications in potato plots in Maine, where no effects on numbers of adult *Coccinella transversoguttata* and *C. septempunctata* were observed (Shands et al., 1972).

Not surprisingly, coccinellid species differ in their response to food sprays. This is further highlighted by Schiefelbein and Chiang (1966) who reported that weekly sprays of a 5% sucrose solution to corn plots resulted in increased numbers of adult *H. convergens*, a slight increase in total number of *H. tredecimpunctata* , but no effect on *C. maculata*. The number of coccinellid eggs tended to be higher in the control plots compared to the sucrose treated plots, but corn leaf aphid infestations were lower in the plots receiving sucrose applications (Schiefelbein and Chaing 1966), demonstrating the complexity of interactions among predators, aphids and supplemental food sprays. Similarly, five coccinellid species (*Coccinella transversoguttata*, *C. septempunctata*, *H. convergens*, *H. quinquesignata*, and *H. tredecimpunctata*) responded to sucrose sprays applied to alfalfa fields in Utah (Evans and Swallow, 1993; Evans and Richards, 1997) but in contrast, a 2-yr field study using two concentrations of sucrose and molasses applications failed to document a significant increase in numbers of coccinellids (*H. convergens*, *H. tredecimpunctata*, and *C. maculata*) in treated corn plots in Minnesota (Carlson and Chiang, 1973).

The lack of general consensus on the role of food sprays to enhance coccinellid numbers is likely due to a range of factors that influence predator behavior. High densities of aphids in field studies appear to interfere with the responses of Coccinellidae to sucrose sprays and species-specific responses to sucrose sprays were reported (Schiefelbein and Chiang, 1966; Carlson and Chiang, 1973; Evans and Richards, 1997; Lundgren, 2009b). For example, a higher proportion of *C. transversoguttata* adults were collected from alfalfa plots treated with sucrose compared to the *C. septempuctata* collected (Evans and Richards, 1997). The use of these artificial food sprays is, therefore, dependent on the physiological state and availability of Coccinellidae in the environment; habitat management is required to ensure that these predators are in these agroecosystems at the time of application (Hagen et al., 1971; Mensah, 2002; Wade et al., 2008; Lundgren, 2009b).

3.3. Response to semiochemicals

The application of food sprays is based on an understanding of how these compounds (sugars and proteins) influence the dispersal and predatory behaviors of Coccinellidae (Hagen, 1987) and intersects with the chemical ecology of these predators. Thus, while the use of food sprays (Wade et al., 2008, Lundgren, 2009b) and the responses of coccinellids to semiochemicals (Khan et al., 2008) are discussed as separate components of conservation biological control, they arise from the same suite of behaviors that predators use to locate their prey and other food (Hagen and Bishop, 1979).

Several plant and pest volatiles influence the behaviors of adult and larval Coccinellidae (reviewed by Pickett and Glinwood, 2007; Hatano et al., 2008; Khan et al., 2008; Pettersson et al., 2008) and the effects of these semiochemicals provides the basis for understanding behaviors of Coccinellidae (Ninkovic et al., 2001; Girling and Hassall, 2008). However, enhanced effectiveness in biological control of aphids arising from the use of these compounds has not been documented. Adults of selected species of Coccinellidae clearly respond to plant volatiles, e.g., *Coleomegilla maculata* to 2- phenylethanol and α-terpineol (Zhu et al., 1999), *Anatis ocellata* (L.) (Coleoptera: Coccinellidae) to pine needle volatiles (Kesten, 1969), and *Adalia bipunctata* and *Harmonia axyridis* to the aphid alarm pheromone, E-β- farnesene (Francis et al., 2004; Verheggen et al., 2007). *Coccinella septempunctata* responds to plant volatiles (Girling and Hassall, 2008), E-β- farnesene, (Al Abassi et al., 2000), volatiles from *Toxoptera aurantii* (Fonscolombe) (Hemiptera: Aphididae) (tea aphid) (Han and Chen, 2002), herbivore-induced plant volatiles (Pettersson et al., 2008) and specifically to methyl salicylate released from aphid-infested soybean plants (Zhu and Park, 2005). Several plant-derived volatiles and aphid-induced plant volatiles attract significantly higher numbers of adult Coccinellidae to lures placed in the field (Zhu et al., 1999; Zhu and Park 2005; Yu et al., 2008). The plant volatile 2-phenylethanol was the attractant used in a commercially developed lure (Benallure) for Coccinellidae and Chrysopidae (Zhu et al., 1999). Recent behavioral bioassays also indicate that *H. axyridis* uses olfactory cues to locate soybean aphids in buckthorn hedgerows, their primary overwintering habitat (Bahlai et al., 2008).

3.4. Habitat management to enhance Cocccinellidae

Similar to the application of food supplements, the use of semiochemicals to enhance conservation biological control is influenced by many factors, including the diversity and abundance of natural enemies in the surrounding environment. The effectiveness of plant and pest-induced plant volatiles might be enhanced by diverse environments, which may serve as reservoirs of natural enemies (Colunga-Garcia et al., 1997; Khan et al., 2008; Gardiner et al., 2009). The retention and manipulation of Coccinellidae in crops can be further improved by providing nutritional resources (e.g. pollen sources, nectar producing plants (Pemberton and Vandenberg, 1993) or artificial food supplements (Lundgren, 2009a. this issue). Recently, plants have been genetically modified to produce higher levels of herbivore-induced plant volatiles that are attractive to predatory mites and parasitoids (Kappers et al., 2005; Schnee et al., 2006), potentially increasing densities and improving biological control.

Conservation of diverse habitats (e.g., beetle banks, cover crops, landscape diversity or intercropping) and the associated enhancement of predator biodiversity have been demonstrated to promote aphid suppression in a number of agroecosystems (Gurr et al., 1998; Landis et al., 2000; Alhmedi et al., 2007; Gardiner et al., 2009; Lundgren, 2009b). It is the complex relationship between the planned biodiversity in crop habitats and the associated biodiversity of surrounding environments that ultimately contributes to ecosystem services and function (Colunga-Garcia et al., 1997; Altieri and Nicholls, 1999). Additionally, a range of tactics (e.g., use of selective insecticides and within-crop management) can further enhance the role of natural enemies in biological control.

Beetle banks (Sotherton, 1995) are primarily used as a means for providing suitable overwintering sites for predatory arthropods within crop habitats thereby promoting overwintering predator populations (Thomas et al., 1991, 1992; MacLeod, 2004; Collins et al., 2003). However, very few studies have examined their effect at promoting aphid suppression in agricultural crops (e.g., Collins et al., 2002). These features undoubtedly enhance predator density and diversity, but their subsequent role in biological control is poorly understood. In winter wheat fields in the United Kingdom, Collins et al. (2002) created beetle banks consisting of *Dactylis glomerata* L. (Poales: Poaceae) and *Holcus lanatus* L. (Poales: Poaceae) grasses and examined the role of predator communities in aphid control the following year. They reported that levels of aphid suppression decreased with distance from the bank and improved biological control was primarily attributed to carabids, staphylinids and spiders (lycosids and linyphiids): coccinellid numbers were not reported. However, it is interesting to note that within beetle banks, coccinellid numbers can be high (Thomas et al., 2001) yet no studies have reported their role in promoting aphid control following the establishment of beetle banks, despite the fact that many species overwinter as adults (Hodek and Honek, 1996) and such within-crop refugia could significantly increase early-season predation by Coccinellidae.

Pollen and nectar (from floral and extrafloral sources) are used by adult Coccinellidae within agricultural environments (Pemberton and Vandenberg, 1993; Nentwig, 1998; Harmon et al., 2000; Bertolaccini et al., 2008; Lundgren, 2009a, this issue). These plant resources may be especially important for early season suppression of low densities of aphids, which prevent or reduce outbreak levels later in the growing season. Due to the high mobility of coccinellids and their tendency to occur in crops later in a growing season, the use of habitat manipulation to enhance aphid suppression by Coccinellidae has been documented in relatively few systems (Frechette et al., 2008). For example, cover crops in pecan orchards increase densities of Coccinellidae, but enhanced levels of biological control of pecan aphids has been difficult to quantify and is influenced by a range of biotic and abiotic factors (Bugg et al., 1991; Dutcher, 1998). In a 2-yr field study in two pecan orchards in Georgia, three species of Coccinellidae (*Hippodamia convergens, Olla v-nigrum* (Mulsant), and *C. septempunctata*) were more abundant in cool-season cover crops compared to existing vegetation in the orchard understory (Bugg et al., 1991). However, only *H. convergens* numbers were higher on pecan trees above the cool-season cover crops and aphid numbers were similar in both systems. Bugg et al. (1991) speculate that immigration of Coccinellidae from adjacent small grain fields may have masked the effects of the cover crops on predator abundance in the pecan trees, documenting the importance of associated biodiversity of highly mobile predators in surrounding environments that readily immigrate into and emigrate from crop habitats. Similarly, augmentative releases of *H. convergens* into pecan orchards with a ground cover of perennial and annual plants did not result in enhanced predator/aphid prey ratios in pecan orchards in New Mexico (LaRock and Ellington, 1996). Due to the relatively high mobility of adult Coccinellidae, techniques are needed to assess movement between crops and habitats (Lavandero et al., 2004), e.g., stable isotope analysis and immunological techniques based on protein marking have been used to assess movements of *H. convergens* (Prasifka et al., 2004; Hagler and Naranjo, 2004).

3.5. Reduction of insecticide use

The widespread deployment of transgenic (especially those expressing *Bacillus thuringiensis* (Bt) endotoxins) cultivars in many agricultural production systems provides new challenges and opportunities for natural enemies (Obrycki et al., 2001a, 2004), particularly among the aphidophagous coccinellids. Although coccinellids ingest Bt toxins in the field (Harwood et al., 2005; 2007a), several studies have documented no significant direct impacts of Bt crops on coccinellid populations (Naranjo, 2005; Pilcher et al., 2005; Torres and Ruberson, 2005, Whitehouse et al., 2005; Hoheisel and Fleischer, 2007). There are also some reported negative effects (e.g., increased mortality, reduced weight gain, delay in development) on non-target organisms, including predators (Hilbeck et al., 1998; Schmidt et al., 2009) and parasitoids (Ramirez-Romero et al., 2007) feeding on Bt-intoxicated arthropods. However, it should be noted that most studies do not document effects on non-target coccinellids from commercialized transgenic crops (e.g., Al-Deeb et al., 2001; Lundgren and Wiedenmann, 2002, 2004, 2005;

Pilcher et al., 2005; Shelton et al., 2009; but see Birch et al. 1999; Lovei et al., 2009). Aphidophagous coccinellids that suppress aphid populations may also rely on species targeted by the Bt crop (e.g., lepidopteran eggs or larvae; Evans, 2009, this issue), or prey that contain large amounts of Bt toxin (e.g., mites Dutton et al., 2002; Biddinger et al., 2009, this issue), or altered crop-based non-prey foods including pollen (Lundgren, 2009a,b). A meta-analysis of the effects of Bt cotton on predator guilds revealed a slight decrease in densities of Coccinellidae in Bt cotton compared to non-Bt cotton (Wolfenbarger et al., 2008). In contrast to the situation in cotton, the same meta-analysis revealed higher numbers of predators in Bt potatoes compared to non-Bt potatoes, and variable effects of Bt corn on coccinellid species; increased densities of *C. maculata*, but no quantifiable effects on *Hippodamia* species (Wolfenbarger et al., 2008). Thus, although no direct deleterious interactions among Bt crops and coccinellids have been identified, tri-trophic interactions in Bt transgenic crops are complex and warrant further study.

In some cropping systems including cotton, Bt-containing cultivars reduce broad spectrum insecticide use and may facilitate the integration of biological control into IPM programs for pests not targeted by the Bt toxin. For example, there were no consistent effects of transgenic and isoline varieties of sweet corn (Cry1Ab), potatoes (Cry3A) and squash (viral coat proteins) in a diversified vegetable system on densities of *Harmonia axyridis*, *Coleomegilla maculata*, and *Coccinella septempunctata* (Hoheisel and Fleischer, 2007). This study demonstrated the importance of transgenic sweet corn in this vegetable production system; transgenic varieties reduced the need for insecticides by 25 % and provided pollen and aphid prey for the Coccinellidae (Hoheisel and Fleischer, 2007).

3.6. Biological control by Coccinellidae in aphid IPM

Adjusting insecticide applications can enhance biological control of aphids where naturally-occurring coccinellids are predictably efficacious during a portion of the pests' population dynamics. The contributions of coccinellids to the suppression of target aphids, an important component of IPM systems, are based on an understanding of their role in affecting seasonal aphid population densities. For example, treatment decision thresholds for aphids in row crops typically are established based on an estimation of overall seasonal aphid abundance, estimating the length of time aphids have been in residence on the crop through the calculation of cumulative aphid days (the area under a population curve) (Andrews and Kitten, 1989; Hanafi et al., 1989; Kieckhefer et al., 1995; Ragsdale et al., 2007; Rhainds et al., 2007). In other cases, decisions based on individual aphid density estimates may be modified based on previous density estimates (i.e., densities in decline but nearing the threshold may not be treated) and may or may not include an estimate of the proportion of infested plants in the field (Conley, 2008; Ragsdale et al., 2007). Generally, pest management sampling protocols do not incorporate natural enemy abundance, although in some systems the presence of Coccinellidae at a sampling location is suggested as an indication to look more closely for aphids (Rice and O’Neal, 2007). However, the contributions of natural enemies to pest suppression can help to reduce insecticide applications if they are enumerated during sampling procedures.

Although commonly considered important for aphid management in crop systems at certain times of the production season (e.g., Kring et al., 1985, Michels and Matis, 2008), coccinellids are rarely formally considered in aphid management programs in the United States. Even in agricultural systems where their impact has been well-documented (Obrycki and Kring, 1998), implementation of thresholds that incorporate coccinellid densities is often stymied by numerous challenges, including: (1) difficult or time-consuming sampling procedures, (2) diversity of the natural enemy fauna (other predators, parasitoids and pathogens), (3) between-year variability in efficacy (reliability), and (4) interference caused by insecticides applied for other pests. Accordingly, the systems most amenable to the incorporation of coccinellids in the decision-making process are those where multiple pest species do not coexist temporally and where the coccinellids are the most abundant aphid predators, which are easily sampled and annually predictable. In many crops coccinellid populations are easily sampled and identified. The cotton aphid example described below demonstrates the indirect benefit for managing a pest through explicit reliance on coccinellids, and was made possible through widespread use of transgenic (Bt) cotton resulting in a reduction in insecticides for the target pest (e.g., bollworm and budworm in cotton) during a portion of the production season (early-season).

4. Two recent case studies: Role in aphid suppression

One example illustrates an approach to conserve naturally occurring predators of the cotton aphid by including coccinellids in cotton aphid management decisions. Our second example, examines the current state of knowledge of coccinellid predation of the soybean aphid, in which our understanding is still insufficient to reliably depend on coccinellid predation for predictable aphid suppression on a field-by-field basis.

4.1. *Aphis gossypii:* Cotton aphid

The successful conclusion of the boll weevil eradication program and an increased use of Bt cottons in the southeastern United States resulted in significant reductions of early-season insecticide use (Long et al., 2003). Thus an opportunity arose to adjust cotton aphid treatment decisions to account for the presence of aphidophagous coccinellids that were previously eliminated from the crop by early-season insecticide applications.

Previous research recommended the incorporation of beneficial insects, particularly coccinellids, into the decision-making process for insecticide applications targeting *A. gossypii* in cotton (Conway et al., 2006). A simple threshold that requires estimates of the percentage plants infested by aphids, status of the aphid population (growing or declining), and coccinellid densities was created to amend insecticide treatment decisions. The coccinellids in the Arkansas cotton system vary in relative abundance within and among seasons, and typically include *Hippodamia convergens*, *Coleomegilla maculata*, *Harmonia. axyridis*, *Coccinella septempunctata*, and various Scymninae. The impact of other predators and parasitoids of cotton aphid can be significant in some years (Kerns and Gaylor, 1993), but the threshold developed only requires enumeration of coccinellid adults and larvae. This threshold is one of the first developed for an annual row crop system that explicitly incorporates insect predation in the decision-making process (Studebaker, 2009). Chappell (2007) demonstrated the effectiveness of this new cotton aphid treatment threshold in comparison to the previous Arkansas threshold that only used gross estimates of aphid densities for making treatment decisions. Paired, large-scale comparisons of the thresholds were made at seven locations during the 2004 and 2005 growing seasons in commercial cotton fields (each plot was more than 4 ha). Locations selected were representative of the varied Arkansas cotton production region between Missouri and Louisiana in the Mississippi River delta region.

Application of the new threshold resulted in elimination of aphid insecticide treatments at six of seven locations (Chappell, 2007). Aphid densities after 7 d declined by 81.5 and 85.5% in fields treated with conventionally administered and coccinellid-incorporated thresholds, respectively. The plots using the conventional threshold in these fields required an insecticide application (imidacloprid, 0.062 kg ai/ha) to achieve a comparable aphid density to that of plots using the new threshold, which relied solely on the natural enemies in the field for aphid suppression. At one location the new threshold called for an initial application of insecticide coincident with a second application recommended by the conventional threshold. Aphid densities were thus similar in this field using the conventional threshold receiving two insecticide applications and the area receiving only one application as recommended by the new threshold (Chappell 2007). The need for a second application on the conventional plot at this location was most likely a result of the disruption of the natural enemy complex by the initial insecticide application (Leclant and Deguine, 1994). Further, when aphid treatments were triggered using the new threshold (as in this final example), the application of the insecticide was delayed and could be coupled to treatments for other insect pests of cotton (e.g., plant bugs). Combining insecticide treatments reduces insecticide usage and conserves additional beneficial insects in the cotton agroecosystem, provided that less selective insecticides are not used in the combined applications. In all demonstrations to date, the use of the new threshold allowed cotton producers to eliminate or reduce (by half) insecticide applications targeting *A. gossypii*, while not reducing yield. The reduction in aphicide use saves an average of ca. US$9.00 per acre (Chappell, 2007). While one may argue that the conventional threshold was merely too conservative, incorporation of the number of coccinellids in the treatment decision on a field basis improves threshold reliability by accounting for annual variability in the dynamics of the aphid pest and natural enemy populations.

4.2. *Aphis glycines*: Soybean aphid

In 2000, the soybean aphid (*Aphis glycines*) was discovered in Wisconsin, and within 5 yr this species had become the key insect pest of soybeans throughout the upper Midwestern and Northeastern USA and Canada (Costamagna and Landis, 2007; Costamagna et al., 2007, 2008; Donaldson et al., 2007). The potential yield losses and infestation levels contributed to significant insecticide applications in many areas of the upper Midwestern USA, often the first such applications within this region (Rodas and O'Neil, 2006). Importation biological control has received considerable emphasis (Heimpel et al., 2004; Hoelmer and Kirk, 2005) because of the high levels of mortality induced by parasitoids (Liu et al., 2004; Miao et al., 2007) and predators (van den Berg et al., 1997; Miao et al., 2007) of *A. glycines* in its native range. However, recent studies have indicated that a group of predatory species in North America exert significant pressure on soybean aphid populations, including coccinellids (Fox et al., 2005; Costamagna and Landis, 2007; Costamagna et al., 2007, 2008; Landis et al. 2008) and *Orius insidiosus* Say (Hemiptera: Anthocoridae) (Desneux et al., 2006; Desneux and O'Neil, 2008; Harwood et al., 2007b, 2009).

The importance of coccinellid predation of *A. glycines* varies within seasons and geographically in the upper Midwestern United States, which complicates the incorporation of this biotic mortality into pest management decisions. For example, Costamagna and Landis (2007) documented a relatively minor role for predation by *O. insidiosus* in Michigan, in contrast to its major role in soybean aphid predation in Indiana (Rutledge and O'Neil, 2005; Desneux et al., 2006). Molecular techniques developed to assess predation of *A. glycines* by *O. insidiosus* (Harwood et al., 2007b, 2009) can be used to examine this variation in coccinellid predation. Evaluations of studies across four states illustrated that pest suppression by natural enemies ("biological services") in soybeans left untreated for soybean aphids was sufficient to prevent economic damage when aphid population densities were low, but not when aphid densities were high (Landis et al., 2008). The authors appropriately note that annual population fluctuations strongly influence the realized value of pest suppression by natural enemies. Recommendations based on coccinellid (and/or other natural enemies) density estimates at the field level may provide a way to account for this year-to-year variability.

5. Future reliance on coccinellids in agroecosystems

Aphid predation by Coccinellidae, which may be a major source of within-season mortality of these pests in selected agricultural crops, has not been shown to provide long-term regulation of the population dynamics of aphids. Documenting their role in slowing aphid population growth or reducing peak population densities within a growing season will continue to rely on well-designed field experiments. Data from manipulative field experiments and assessments of predator and prey population densities can now be enhanced through the use of molecular techniques to determine the proportions of predators feeding on target aphid prey and alternate foods within an agroecosystem. Historically, molecular techniques have been used in cotton agroecosystems to analyze the role of natural enemies in reducing *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) (Hagler and Naranjo, 2005; Zhang et al., 2007), heliothine eggs (Ruberson and Greenstone, 1998; Sansone and Smith, 2001) and *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae) (Hagler and Naranjo, 1996). While these studies have clearly demonstrated the ability of natural enemies (including coccinellids) as viable biological control agents of pest species, little information pertaining to *A. gossypii* has been forthcoming.

Su et al. (2000) used a polyclonal antibody, coupled with a double-antibody sandwich enzyme linked immunosorbent assay approach, to document predation rates of *A. gossypii* by *Chrysopa phyllochroma* Wesmael (Neuroptera: Chrysopidae), but more recently a stable isotope approach has been utilized to examine the foraging behavior of *Hippodamia convergens* on *A. gossypii* in cotton agroecosystems in Texas (Prasifka et al., 2004). The use of stable isotope techniques in food web ecology has a long history (Hood-Nowotny and Knols, 2007; Weber and Lundgren, 2009, this issue) and carbon signatures of field collected *H. convergens* revealed that when cotton aphids were present, these coccinellids were important natural enemies. However, during periods of prey scarcity, non-aphid resources were rarely utilized as an alternative food item suggesting levels of food limitation in the field. Although stable isotope data are not capable of deciphering subtle and specific trophic connections for arthropod predators within some agroecosystems (Daugherty and Briggs, 2007; Weber and Lundgren, 2009, this issue), the application of post-mortem gut content analyses clearly complements empirical field studies and aids in our understanding of mechanisms of biological control by aphidophagous coccinellids in the field. Sometimes such results can be contrasting: field studies of Costamagna and Landis (2007), for example, indicated predation of soybean aphid by *O. insidiosus* occurred, but these natural enemies were considered to be ineffective regulators of these pests; Harwood et al. (2007b), however, revealed significant levels of early season predation, when aphid densities were low, and suggested valuable levels of aphid suppression at certain times during the growth of aphid populations.

As we have discussed in this paper, many invasive species of aphids in North America are attacked by naturally occurring species of Coccinellidae. The role of this predation in the suppression of aphid pests will vary and may require several years of detailed experimentation before morality due to coccinellid predation can be included into management decisions. Due to the mobility of Coccinellidae and their broad feeding habits, combining detailed laboratory and field studies with molecular and/or serological approaches to analyze gut contents and movement of field-collected individuals will provide a more comprehensive understanding of their relationships to aphid prey and enhance our ability to use this knowledge in aphid pest management.

Aphidophagy by Coccinellidae is a significant mortality factor of aphid pests in a number of agricultural systems. The role of aphidophagy by Coccinellidae will likely expand in crop systems using transgenic crops that have supported a significant reduction in insecticide use (e.g., cotton and sweet corn). However, in crops that previously received relatively few insecticide applications for above-ground pests (e.g., field corn) there may be little additional benefit of conservation programs for Coccinellidae. Coccinellid adults are attracted to plant volatiles, herbivore-induced plant volatiles and components of aphid alarm pheromones and are arrested by artificial food sprays containing sugar and proteins. However, carefully designed field experimentation is required to document increased levels of biological control of target aphid species resulting from the manipulation of within- and between- field distributions of Coccinellidae, and between fields and non-crop habitats. Multiple habitat management techniques have yet to produce consistent positive effects on Coccinellidae, which may be related to their relatively high rates of movement through agroecosystems. However, additional manipulative studies are needed to fairly assess these management techniques on a landscape scale. Additional work needs to focus on the combined use of habitat management to conserve Coccinellidae in the environment with semiochemicals and food supplements to manipulate densities within fields to ultimately enhance levels of biological control. Some of the best examples of biological control of aphid pests by Coccinellidae are based on their use of early season non-target aphid species providing resources for the build-up of Coccinellidae, resulting in within-season suppression of target aphid pests (e.g., corn leaf aphids and greenbugs on grain sorghum and wheat). Ultimately, combining the use of non-pest aphid prey or plant resources (nectar and pollen) within agroecosystems with current technologies that reduce insecticide use (e.g., Bt transgenic crops) provides the basis for a significant advancement in the utilization of Coccinellidae for aphid suppression in diverse agricultural systems.

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