Biological Control 51 (2009) 244–254

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Review

Aphidophagy by Coccinellidae: Application of biological control in agroecosystems

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ARTICLE INFO

Article history:
Received 28 January 2009
Accepted 25 May 2009
Available online 30 May 2009

Keywords:
Aphid predation
Arthropod predators
Biological control
Pest management
Aphid suppression
Conservation biological control

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.

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 Kirby and 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, 1973; Hagen and van den Bosch, 1968; van Emden 1972, 1988; 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

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doi:10.1016/j.biocontrol.2009.05.009

coccinellids without manipulating field populations (Harwood and Obrycki, 2005; Harwood and Greenstone, 2008; Weber and Lundgren, 2009), 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 *Hippodamia 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). 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