COCCINELLIDS IN BIOLOGICAL CONTROL

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11.1 INTRODUCTION

Historically, the term biological control has had various meanings (DeBach 1964). **In the ecological sense**, it refers to the 'top-down' action of predators, parasites or pathogens on organisms occupying a lower trophic level, action that maintains their populations at lower levels than would occur in the absence of these natural enemies, i.e. a **natural process** that does not depend on any human intervention. **In the applied sense**, it refers to the **specific use or manipulation** of populations of organisms to achieve reduction or improved regulation of pest populations. In practice, this distinction is not always clear as modern integrated pest management programs usually rest on a foundation of 'background' natural control which occurs without intervention. However, cultural activities may be implemented or modified to facilitate natural biological control, or simply to spare beneficial species from adverse human impacts, including application of pesticides. The diverse approaches to achieving this end are now collectively termed **conservation biological control** (Barbosa 1998). In contrast, **classical biological control** involves importing and releasing exotic species with the goal of establishing a self-perpetuating population in a novel geographic region that exerts permanent suppression of a specific pest. Alternatively, **augmentation** has the goal of immediate, if temporary, reduction of a pest population through occasional or periodic releases of a natural enemy. Such releases may be **inundative** (large numbers released for immediate effect) or **inoculative** (fewer individuals released with some reproduction expected). Predatory coccinellids have been deployed and studied extensively in all these contexts. Furthermore, certain species, either through intentional or accidental introductions, have garnered attention as **invasive species** with significant impacts on biodiversity and human economies beyond their contributions to biological control.

11.2 THE ROLES OF COCCINELLIDAE IN BIOLOGICAL CONTROL

Dixon (2000) emphasized three attributes of successful biological control agents: specificity, voracity and a high rate of population increase. Whereas these attributes are certainly desirable for **rapid impact** when the target is increasing in abundance and approaching economic injury levels, many pest populations tend to be transient or seasonally cyclical. These same attributes may therefore become **handicaps for survival** of the agent when the pest is rare or absent. For example, the availability of alternative prey can be critical to coccinellid impact in biological control. This effect is illustrated by the case of *Cleobora mellyi*, which was introduced into New Zealand in 1977 for control of the eucalyptus tortoise beetle, *Paropsis charybdis*. Both larvae and adults of *C. mellyi* feed readily on tortoise beetle eggs and larvae, but rely heavily on psyllids to maintain their populations year-round in plantations of *Eucalyptus* and *Acacia* trees. Although establishment of the species on the North Island was initially successful, populations remained small and limited in distribution for about 25 years until the invasion of another tortoise beetle and several additional pysllid species led to a dramatic increase in the range and abundance of this 'forgotten ladybird' and its emergence as a significant biological control agent of this guild of arboreal defoliatiors (Withers & Berndt 2010).

11.2.1 Prey specificity

Prey specificity is desirable from the perspective of concentrating mortality on the pest and minimizing non-target impacts, but it can also be an impediment for predator survival when the preferred prey is at low density (Chang & Kareiva 1999). Likewise, **voracity** is not invariably an asset. Although high voracity is advantageous for maximizing the rate of conversion of prey biomass into predator biomass, it implies a greater food demand for successful development and reproduction of the predator. Thus coccinellids with lower voracity require a smaller critical intake of prey to complete development or remain actively foraging, making their populations more resilient to local extinctions when prey become scarce, and better able to track prey populations at low densities. Coccinellids exhibit a range of prey specificity (5.2), but species that dominate their communities tend to be **relative generalists**, though they often exhibit preferences for particular habitats (e.g. Colunga-Garcia et al. 1997). This is especially true of species that display good numerical responses to outbreaks of aphids, a prey that no natural enemies save fungal pathogens can

match in reproductive rate. Adults of such species often survive for extended periods on **alternative prey** or **supplementary food** sources, even if these resources are inadequate to sustain their reproduction. Thus most ecologically dominant aphidophagous species tend to be opportunistic generalists with high voracity, traits adaptive for exploiting prey that are periodically abundant, but highly ephemeral and widely distributed. Although a few species do specialize on aphids associated with particular plants, most dietary specialists tend to exploit non-aphid prey that are more diffusely distributed, but more continuously available, in well-defined habitats, (e.g. coccids on trees).

Small ladybeetles of the genus *Stethorus* are specialized predators of phytophagous mites that can be important in biological control of tetranychid pests on a wide range of fruit crops (Biddinger et al. 2009). For example, Ullah (2000) found that *Stethorus vegans* was effective in locating and reproducing on *Tetranychus urticae* even at low densities, supplementing its diet with alternative prey as necessary. However, not all coccinellid species that specialize on one kind of prey are necessarily a cornerstone of its biological control. For example, ladybeetles of the genus *Nephaspis* are relatively specific to aleyrodid prey and *Clitostethus oculatus* is credited with reducing large infestations of spiralling whitefly, *Aleurodicus dispersus* in Hawaii (Waterhouse & Norris 1989) and India (Ramani et al. 2002). Nevertheless, this species does not provide adequate biological control of *A. dispersus* without the assistance of *Encarsia* spp. parasitoids that are better able to maintain the pest at low densities and are now considered to be solely responsible for the biological control of *A. dispersus* through much of Africa (Legg et al. 2003). Roy et al. (2005) concluded that predation by *Stethorus pusillus (= punctillum)* was complementary to that by *Amblyseius fallacis* in controlling *Tetranychus mcdanieli* in Quebec raspberry fields due to different patterns of seasonal activity. Another *Stethorus* sp. was observed to provide effective control of *Panonychus citri* in citrus when acting in concert with the predatory mite *Agistemus longisetus* (Jamieson et al. 2005). Similarly, Snyder et al. (2008) used field experiments to demonstrate that *C. septempunctata* and *Hip. convergens* provided more effective control of *Brevicoryne brassicae* and *Myzus persicae* on broccoli in combination with other natural enemies than when these were absent.

11.2.2   Generalist coccinellids

After multiplying their numbers on aphid outbreaks within particular habitats, many generalist coccinellids switch to feed on alternative prey species, a fact that warrants recognition in assessing their overall value as residents of agroecosystems. Many primarily aphidophagous species also contribute to biological control of pest species that serve only as supplementary food or non-essential prey. Through consumption of eggs and small larvae, *Col. maculata* may contribute to the control of *Ostrinia nubilalis* in corn (Musser & Shelton 2003), *Helicoverpa zea* in soybean and sweet corn (Pfannenstiel & Yeargan 2002), and *Leptinotarsa decemlineata* in potatoes (Groden et al. 1990). *Har. axyridis* may consume psyllids (Michaud 2004, Pluke et al. 2005), tetranychid mites (Lucas et al. 2002, Villanueva et al. 2004) and root weevil eggs (Stuart et al. 2002). Similarly, *C. septempunctata* prey on larvae of *Hypera postica* in alfalfa when aphids are scarce (Kalaskar & Evans 2001, Evans et al. 2004). By virtue of their ecology, such species tend to provide diffuse pest mortality in their favoured habitats, rather than being solely responsible for continuous suppression of a single pest. This is true in systems as diverse as the alfalfa fields of California (Neuenschwander et al. 1975) and the citrus groves of Puerto Rico (Michaud & Browning 1999).

11.2.3   Intraguild predation

Although large coccinellid species can supplement the effects of parasitoids in biological control (Bilu & Coll 2007) they may also be important agents of intraguild predation (Ferguson & Stiling 1996, Kaneko 2004, Michaud 2004; Chapter 7). Consequently, their role in suppressing a particular pest must be considered within the larger context of the entire guild of natural enemies that contribute to pest mortality. Because their interactions within and between trophic levels are complex, their net impacts in novel ecosystems are unpredictable. Thus, most conspicuous aphidophagous species are unsuited for foreign introduction even though they may be important agents of biological control in their native ecosystems. Once established, they may simply replace aphid mortality provided by local species, cause non-target impacts on other herbivores, or even displace autochthonous species from

Figure 11.1 An assassin bug (Reduviidae) preying on an adult *Hippodamia convergens* (J.P. Michaud). (See colour plate.)

Figure 11.2 The vedalia beetle *Rodolia cardinalis* with eggs and neonate larva on a mature cottony cushion scale (Jack Kelly Clark, courtesy UC Statewide IPM Program). (See colour plate.)

particular habitats. One the other hand, sometimes ladybirds, especially small species or immature stages, may have their effectiveness in biocontrol limited by intraguild predation from tertiary predators (e.g. Rosenheim et al. 2004; Fig. 11.1; Chapters 7 and 8).

11.3 SCALE INSECTS VERSUS APHIDS AS TARGETS OF EXOTIC INTRODUCTIONS

11.3.1 Coccidophagous coccinellids

In 1887 the vedalia beetle, **Rodolia cardinalis**, was introduced from Australia to combat the cottony cushion scale **Icerya purchasi** in the nascent California citrus industry (Fig. 11.2). The landmark success of this project became a textbook example of the great potential of classical biological control as a tactic for suppressing invasive pests (DeBach 1964). A total of 10,555 beetles were reared and released at a cost of $1500 and, within a year, the industry was saved from imminent destruction. The beetle was subsequently introduced to at least 29 other countries and control of the target was either complete or substantial in all locations. The success of the vedalia beetle, and the publicity surrounding its economic benefits, became a watershed event that catalyzed the introduction of many exotic coccinellids targeting other pests, although

rarely with the same degree of success (Caltagirone & Doutt 1989). Obrycki & Kring (1998) calculated that 18 ladybird species established in North America as a result of some 179 intentional introductions since 1900, an establishment rate of about 10%. In comparison, four exotic species became established in the UK over a similar period, although none were the result of intentional introductions (Majerus 1994). Neither does establishment equate to success in biological control. For example, the neotropical ladybirds *Diomus hennesseyi* and *Hyperaspis notata* were both established in a programme against the cassava mealybug, *Phenococcus manihoti*, in central and eastern Africa (Neuenschwander 2003), but neither became significant mortality factors. The high degree of specificity of *R. cardinalis* for *Icerya* species, in combination with a very short generation time, highly efficient detection of isolated host patches, and the ability of a larva to complete development on a single mature female scale are all thought to be key factors in the effectiveness of the vedalia beetle (Prasad 1990). Unfortunately, this ecological configuration is exceptional considering what is now known of the prey relationships of predatory Coccinellidae, and even atypical of other ladybird–coccid interactions. The importance of the rate of population increase of the predator relative to that of the prey has long been emphasized (Thorpe 1930, Hodek 1973, Hagen 1974), has recently been termed the 'generation time ratio' (Kindlmann & Dixon 1999, Dixon 2005) and is likely a key indicator of 'one on one' biocontrol potential.

Savoiskaya (1983) and Kuznetsov (1987) discussed examples of **coccinellid introductions across the Palearctic region** (Russia and Central Asia), many of which appeared to have failed because of climatic disparities between regions of collection and release. Similarly, introduction of a US strain of *Hip. convergens* to Kenya for control of *Schizaphis graminum* in 1911 failed despite a good history of the predator–prey association on wheat (Hunter 1909), probably because the source material was not adapted to tropical conditions (Greathead 1971). In contrast, many **introductions** of coccinellids **against scale** insects in tropical and subtropical habitats have been successful. DeBach (1964) listed introductions of nine coccidophagous coccinellids to which he attributed successful control of 11 coccid species other than *I. purchasi*. Of the 31 exotic species of Coccinellidae established in Hawaii, 17 are primarily scale-feeding species, five specialize on mealybugs and one on mites. The remainder feed on aphids or some combination of aphids, psyllids and other prey (Funasaki et al. 1988). Greathead (2003) reviewed classical programmes in Africa and listed nine coccinellid species successfully established, of which eight were scale-feeding species and the other the mealybug predator *Cryptolaemus montrouzieri*. In Fiji, successful control of the coconut scale, *Aspidiotus destructor*, was attributed to the introduction and establishment of *Cryptognatha nodiceps* Marshall from Trinidad (Singh 1976). Successful control of various scales in the subfamily Diaspidinae has been attributed to introductions of **Rhyzobius** (= *Lindorus*) **lophanthae** in Italy, the Black Sea coast of the Ukraine, and North Africa (Yakhontov 1960). This species is now considered an important introduced predator of citrus scale insects in both the United States (Flint & Dreisdadt 1998) and Australia (Smith et al. 1997), although it is less effective against heavily armoured species that are less vulnerable in later growth stages (Honda & Luck 1995).

Chilocorus bipustulatus is an effective predator of armoured scale insects and populations in the Middle East have been the source of successful introductions in North Africa (Iperti & Laudeho 1969), central Africa (Stansly 1984), Australia (Waterhouse & Sands 2001) and the USA (Huffaker & Doutt 1965). However, it failed to establish in New Zealand kiwi fruit orchards despite a vigorous release effort (Charles et al. 1995). Similarly, *Chil. nigritus* feeds on a variety of armoured scales and has been widely disseminated throughout tropical regions through both intentional and uninten-

tional introductions (Samways 1989). As early as 1940 it was introduced effectively against a complex of scale insects damaging coconuts in the Seychelles (Greathead 2003). This species is now mass-reared by various commercial suppliers of beneficial insects and widely used for augmentative biological control of armoured scales in glasshouses and interior plantscapes. *Chil. circumdatus*, a southeast Asian species, has been successfully introduced to Australia, South Africa, the USA and elsewhere (Samways et al. 1999) for control of citrus snow scale, *Unaspis citri*. It appears quite specific to its prey and is able to track it effectively at low densities, although in Hawaii it reportedly feeds on two additional species of Diaspididae (Funasaki et al. 1988). *Chil. circumdatus* is now considered to be the most important predator of *U. citri* in Australia (Smith et al. 1997) and appears to play a significant role in suppressing this pest in both Florida and California. Rosen (1986) reviewed natural enemies employed in biocontrol programmes against Diaspididae and concluded that, although useful, coccinellid species seldom provided adequate control without assistance from other natural enemies, especially parasitoids.

11.3.2   Aphidophagous coccinellids

Aphidophagous species have a long history of importation in classical biological control programmes, albeit with few recognized successes. As early as 1874, **C. undecimpunctata**, a relatively polyphagous species, was imported to New Zealand where it established to become an important predator of aphids and mealybugs in various fruit and forage crops (Dumbleton 1936). More recently, it established in various regions of North America (Wheeler & Hoebeke 1981) although its introduction there is thought to have been accidental. Dixon (2000) tallied 155 intentional introductions of coccinellid species worldwide that specifically targeted aphids and judged only one to be 'substantially successful'. The **high reproductive rate of aphids** is achieved through a combination of thelytoky and a telescoping of generations (live birth of pregnant daughters). Consequently, multiple aphid generations can be completed within the time required for a single generation of any coccinellid, forcing the numerical response of the predator to lag behind population growth of the prey. Borges et al. (2006) advanced the notion that the life history of ladybirds has evolved

within constraints dictated by the ecology and distribution of their prey. They suggest that scale-feeding species have evolved a slow pace of life (slow development, low voracity and fecundity) in order to effectively exploit slowly developing prey that are continuously available, but widely distributed in small colonies. In contrast to scales, aphid colonies develop quickly and become much larger, but can be harder to find and more ephemeral in availability, attributes that favour their exploitation by voracious species that have faster development and higher fecundity. These disparities in life history, whether derived from predator–prey relations or not, suggest that aphidophagous coccinellids cannot be manipulated in biological control programmes by the same means, or for the same ends, as coccidophagous species, even though they may emerge as key sources of natural aphid mortality in field studies (Costamagna et al. 2008).

Various species of *Adelgidae* have been targeted with introduced coccinellids in **arboreal habitats**. The larch ladybird, *Aphidecta obliterata* is a species of European origin that was introduced to South Carolina in 1960 (Amman 1966) to control the balsam woolly adelgid, *Adelges piceae*, an invasive pest that arrived in North America around 1900. Later, *A. obliterata* was introduced to British Columbia, Canada (Harris & Dawson 1979) where it has emerged as an important biological control of both *A. piceae* and the hemlock woolly adelgid, *Adelges tsugae* (Humble 1994, Montgomery & Lyon 1996). The Asian species *Sasajiscymnus tsugae* was introduced from Japan to target *A. tsugae* and has been established in various regions of the eastern USA as a result of release programmes initiated in 1997 (Cheah et al. 2004). Although established, the impact of *S. tsugae* on the pest population was not as great as originally hoped, resulting in the importation and release of a Chinese species, *Scymnus ningshanensis*, that purportedly exhibits a stronger numerical response to increasing prey density (Butin et al. 2003).

Biological control programmes involving **introductions** have become increasingly **controversial** in recent decades as attention has been drawn to their potential **non-target impacts** (Howarth 1991) and other associated risks (van Lenteren et al. 2006). The wisdom of using natural enemy introductions as a first response to invasive arthropod pests has also been challenged (Wajnberg et al. 2001, Michaud 2002a). Regulatory restrictions on exotic species introductions have become increasingly stringent and most developed countries now require that entomophagous species exhibit levels of prey specificity comparable to those previously required only for weed biocontrol agents (e.g. FAO 1996). Although few programmes currently seek to introduce exotic coccinellids into new regions, many displaced species (whether **intentionally or accidentally introduced**) now comprise a substantial proportion of the guild of aphidophagous insects in most Nearctic and Palearctic habitats. Many contribute significantly to control of pests in agricultural habitats, but others have been implicated in the **displacement of native species**. For example, the native species *Stethorus punctum* was replaced by the Palearctic *Stethorus pusillus* in Ontario around 1940 following its inadvertent establishment in Canada (Putman 1955).

11.3.3 Invasive coccinellids

Gordon (1985) listed over 150 species of Coccinellidae with records of intentional introduction to North America, mostly during the 20th century, with 19 successful establishments, and another 10 established apparently as a result of inadvertent introductions. However, species additional to these have been confirmed **established in the past 25 years**, including *P. quatuordecimpunctata*, *Har. axyridis*, *Har. quadripunctata* and *Hip. variegata* (Hoebeke & Wheeler 1996), *Curinus coeruleus* (Michaud 2002b), and probably others. Many of these species have gradually expanded their range through natural spread (e.g. *Hip. variegata*, Williams & Young, 2009) with mostly indeterminate ecological impacts. There is often a latent period before an introduced coccinellid assumes the status of an **invasive species**. Despite introductions to the USA as early as 1956, **C. septempunctata** was not confirmed established along the eastern seaboard until the late 1970s (Hoebeke & Wheeler 1980) and required another decade to expand its range westward to the Rocky Mountains. By the early 1990s, *C. septempunctata* had displaced the indigenous *Hip. convergens* as the dominant aphidophagous coccinellid in parts of the American Midwest and generated other non-target impacts (Horn 1991). Similar impacts were later attributed to *C. septempunctata* further west (Wheeler & Hoebeke 1995, Elliott et al. 1996, Hesler et al. 2005), although it has failed to displace *Hip. convergens* from dominance throughout much of the arid High Plains. Similarly, *A. bipunctata* remained confined to the Osaka region of Japan for about 10 years following its

introduction to Japan, but is now expanding its range and utilizing a greater number of tree and aphid species (Toda & Sakuratani 2006). In contrast, the spread of *Har. axyridis* in North America was much more rapid, requiring only 10 years to colonize most of the Nearctic region from Florida to California in the south, and from Nova Scotia to British Columbia in the north. No case history is perhaps more remarkable than that of *Har. axyridis* and it has the ignominious distinction of being the first predatory coccinellid to be indexed in the Global Invasive Species Database (ISSG 2008) and have its worldwide distribution mapped as a plant pest (CABI 2007).

Harmonia axyridis, referred to as the harlequin ladybird in the UK and the Asian multi-colored ladybeetle in the USA, is a voracious, highly polyphagous species of Asian origin with a long history of introductions worldwide, partly because it is so easily reared on factitious diets, because it readily attacks a wide range of pests, and because its diapause is not obligatory (Chapter 6). It is has proved an excellent biological control agent of scales and aphids occurring on a multitude of plants including alfalfa, apple, citrus, maize, cotton, hops, pecan, pines and soybean. For example, With et al. (2002) showed that *Har. axyridis* was more effective than the indigenous *Col. maculata* in tracking pea aphids to low densities on patches of red clover in a structurally fragmented landscape. *Har. axyridis* has also has been commercially produced and released in augmentation programmes throughout western Europe since the 1980s with little apparent concern for the establishment of feral populations (Adriaens et al. 2003). In 1993 it was introduced into citrus orchards in Greece (Katsoyannos et al. 1997) and many hundreds of thousands of beetles have since been released in various orchard and urban settings there, although establishment remains uncertain as yet. Towards the end of the 1990s, *Har. axyridis* was released in Mendoza province, Argentina and by 2003 it had become the dominant aphid predator in walnut orchards in Buenos Aires province (Saini 2004). Range expansion across much of South America is now expected (Koch et al. 2006).

Between 1999 and 2002, a large scale programme to rear-and-release *Har. axyridis* in the Yucatan peninsula of Mexico was initiated by federal agricultural agencies in an effort to delay movement of the **brown citrus aphid, *Toxoptera citricidus***, into the primary citrus growing regions to the north (Lopez-Arroyo et al. 2008). Once established in the states of Yucatan and Quintana Roo, populations became increasingly abundant in other horticultural habitats. Additional releases were made for purposes of aphid control in pecan orchards in northern Mexico (Quinones & Tarango 2005). In 2002, *Har. axyridis* appeared unexpectedly in the mountains near Mexico City, far from any release site, and spontaneous colonization of various coastal regions has since been confirmed. In 2004, it appeared in southeast England and spread at a rate of 58–144 km per year over the next 2 years (Brown et al. 2007).

Intentional **North American introductions** of *Har. axyridis* began in the early 1900s in California (Gordon 1985) and the most recent US introduction was in 1985 in North Carolina (McClure 1987). Despite evidence of life cycle completion in the field, none of these original American introductions appear to have resulted in established populations. Similarly, *Har. axyridis* failed to establish in the Azores despite a series of releases in the 1990s and earlier (Borges et al. 2005). Soares et al. (2008) hypothesized extrinsic ecological or environmental factors as potentially responsible, but such failures may simply be due to founder effects in the source material – i.e. the introduction of small groups of individuals coincidentally lacking genetic composition immediately suited to local conditions. More recently, it appeared unexpectedly on the relatively barren Sable Island off the coast of Nova Scotia (Catling et al. 2009) and has been detected as a hitchhiker on ornamental plants imported into Norway from western Europe (Sathre et al. 2010). The first established North American populations of *Har. axyridis* were discovered in Louisiana and Georgia (Chapin & Brou 1991), hundreds of miles from any release site. It is now thought by some that *Har. axyridis* was accidentally introduced in cargo containers arriving at a Gulf of Mexico seaport (Day et al. 1994) and genetic studies seemingly point to a single founding population in North America (Krafsur et al. 1997). A detailed history of *Har. axyridis* introductions worldwide can be found in Soares et al. (2008).

11.3.4 Competitive displacement

Competitive displacement of native ladybirds has often been inferred from their declining abundance following establishment of *Har. axyridis* (Brown & Miller 1998, Colunga-Garcia & Gage 1998, Michaud 2002c, Mizell 2007) and *C. septempunctata* (Turnock et al.

2003). Numerous laboratory studies have revealed the advantages enjoyed by *Har. axyridis* in intraguild predation interactions with native species (Yasuda & Shinya 1997, Cottrell & Yeargan 1998, Michaud 2002c, Snyder et al. 2004, Burgio et al. 2005, Cottrell 2005). Nevertheless, *Har. axyridis* has coexisted for many years in Japan with its sibling species *Har. yedoensis*, a habitat specialist on pine trees (Osawa & Ohashi 2008). Although declines in the abundance of native species in regions invaded by these large exotic species have raised concern among conservationists, the complete elimination of autochthonous coccinellid species has not yet been documented and seems unlikely. Rather, native species may simply equilibrate to lower population densities in the cultivated or disturbed habitats dominated by invasive species, or retreat to more feral, ancestral habitats (Evans 2004, Acorn 2007, Harmon et al. 2007).

Aside from the apparent impact of ***Har. axyridis*** on biodiversity, it has gained the **status of a pest** in North America, something that might have been anticipated based on the behavior of this species in its native China (Wang et al. 2011). Its aggregative hibernation behaviour has raised the ire of home-owners when massive hordes of overwintering beetles invade houses (Fig. 11.3), foul living quarters, **trigger allergic reactions** in susceptible individuals (Albright et al. 2006), and even 'pinch' exposed skin with their mandibles (Yarbrough et al. 1999, Huelsman et al. 2002, Koch 2003). Large swarms of *Har. axyridis* were first observed in the American Midwest in 2001 (Huelsman et al. 2002) apparently as a direct result of a numerical

Figure 11.3 Aggregation of *Harmonia axyridis* attempting to enter a house under a door (courtesy of Marlin Rice). (See colour plate.)

response to the large populations of *Aphis glycines* that developed in soybean fields in the years following the aphid's invasion, and where the beetle continues to be important for biological control (Fox et al. 2004). Elsewhere, a propensity for **feeding on ripening fruit** has resulted in *Har. axyridis* damaging peaches and other soft-skinned fruits (Koch et al. 2004), and led to its emergence as a serious flavour contaminant in grapes (Pickering et al. 2007) to the point of requiring insecticide treatment (Galvan et al. 2006a). Consequently, the recent establishment of *Har. axyridis* in southeast England in 2004 (Roy et al. 2006) and in South Africa in 2006 (Stals & Prinsloo 2007) have been causes for alarm.

11.4 AUGMENTATION OF COCCINELLIDS

The term 'augmentation' refers to the **periodic release or inoculation** of a natural enemy in contexts where only the released insects or their immediate descendants are expected to exert biological control. Recent reviews of the augmentation approach continue to indicate that coccinellids are rarely utilized in such programmes (Collier & van Steenwyck 2004, Powell & Pell 2007). Two **limiting factors** are the cost of their production and the education required for their effective application by end users. Thus many demonstration projects have shown potential efficacy, but have failed to evolve into tactics that are attractive or economically viable pest control alternatives. For example, Baker et al. (2003) successfully released overwintered adults of *Cleobora mellyi* and *Har. conformis* against the leaf beetle *Chrysophtharta bimaculata* on eucalyptus trees in Australia, but concluded this approach was only economically feasible in small, environmentally sensitive areas where pesticide use was not acceptable. The pest population was reduced below economic threshold levels, but beetle numbers declined to pre-release levels within 7 days.

Coccinellid augmentation programmes may sometimes be **useful in developing countries** where labour costs associated with rearing and distribution are low, but are unlikely to prove a viable method of pest suppression on the large-scale commercial farms of the developed world, especially in low value row crops. For example, Heinz et al. (1999) tested augmentative releases of *Delphastus catalinae* against *Bemisia tabaci* (as *B. argentifolii*) on cotton in the

Imperial Valley of **California**. Although measurable reductions of whitefly populations were obtained in exclusion cages, open field evaluations revealed no significant effects of releasing adult beetles at rates of 3.5–5.5 beetles per plant. The authors implicated intraguild predation as one factor possibly limiting the impact of released *D. catalinae*. In contrast, smaller scale organic farms producing high value fruits and vegetables provide a more likely setting for coccinellid augmentation to succeed, especially in greenhouses that afford environmental control and some containment of released insects. Powell and Pell (2007) listed augmentation trials of ladybirds against aphids reporting the target species, crop, life stages released, and degree of success obtained. Notably, a number of positive results were obtained when parasitoids or other predators were released in conjunction with a coccinellid species.

11.4.1   The mealybug destroyer

Cryptolaemus montrouzieri is a relatively voracious predator with a long history of use in biological control making it probably more widely utilized in augmentation than any other coccinellid species. Introduced into California in 1892, it has been used in augmentation programmes against various mealybug pests (Pseudococcidae) for many years (Smith & Armitage 1920, 1931, Fisher 1963). Mealybug infestations are notoriously resilient to pesticide applications, a factor that has favoured the commercial production and sale of *C. montrouzieri* in many countries. The larvae of *C. montrouzieri* produce copious wax filaments that mimic those of mealybugs and enable them to forage effectively in the presence of tending ants that may attack other predators and parasitoids (Daane et al. 2007). Mani et al. (2004) reported that releases of *C. montrouzieri* provided complete control of *Rastrococcus invadens* on sapodilla, *Manikara zapota*, trees in a two month period with no other sources of mortality evident; similar results have been reported on mango (Mani & Krishnamoorthy 2001). Open field releases of *C. montrouzieri* have also been made in citrus (Smith & Armitage 1920, Moore & Hattingh 2004) and coffee (Hutton 2007), although not always with favourable results (Villalba et al. 2006).

Cryptolaemus can also be useful for augmentation against soft scale species (Coccidae). Smith et al. (2004) reported effective reduction of *Pulvinaria urbicola* on *Pisonia* trees following releases of *C. montrouzieri* in combination with three parasitoid species. Mani and Krishnamoorthy (2007) reported that *C. montrouzieri* provided effective control of the green shield scale, *Pulvinaria psidii*, on guava, *Psidium guajava*, when released at a rate of 10 adults per tree. This ladybird is often employed in greenhouse systems where mealybugs can be especially problematic, although it requires relatively warm temperatures to be effective (Shrewsbury et al. 2004). Typically, periodic augmentation is necessary for continued pest suppression because *C. montrouzieri* numbers crash abruptly as their prey comes under control. However, this is of little concern when **inundative releases** are used to assist with **rapid suppression** of large pest populations during periods of parasitoid introduction. For example, the pink hibiscus mealybug, *Maconellicoccus hirsutus*, has a very effective specialist parasitoid, *Anagyrus kamali*, but mass releases of *C. montrouzieri* can reduce large populations on the primary woody host plants much more rapidly, allowing many trees to recover (Villa Castillo 2005, Santiago-Islas et al. 2008). Chemical treatments are far less effective and would interfere with establishment of the parasitoid, which is subsequently able to maintain the pest at densities too low to sustain the predator in any numbers. However, Chong and Oetting (2007) recommended that parasitoid releases against citrus mealybug, *Planococcus citri*, should precede those of *C. montrouzieri* by a period sufficient to ensure substantial mummification of the next generation so that intraguild predation on parasitoid larvae would be minimized.

11.4.2   Redistribution of coccinellids

In the mountains of the Sierra Nevada, California, the aggregation of large numbers of **overwintering Hip. convergens** has, for almost a century, facilitated their collection for purposes of redistribution in vegetable and row crops (Fink 1915; Chapter 6). This practice has been criticized, largely because overwintered beetles tend to have a strong dispersal tendency that results in the **immediate emigration** of most individuals **from release sites** (Obrycki & Kring 1998), but also because of their low fecundity (Bjornson 2008) and the potential for distribution and transmission to other species of diseases such as microsporidia

(Saito & Bjornson 2006). Starks et al. (1975) explored night-time releases and the provision of shelter and water to retain imported *Hip. convergens* in sorghum fields to prey on *S. graminum* but these efforts failed to inhibit the dispersal of the coccinellids significantly. Furthermore, greenhouse trials indicated that a locally adapted strain was more effective in controlling the greenbug. Dreistadt and Flint (1996) provided over-wintered *H. convergens* with an opportunity to fly in screen cages as a pre-release conditioning treatment, but retention of the beetles on aphid-infested chrysanthemums was only marginally improved. Flint and Dreistadt (2005) calculated that effective control of rose aphids, *Macrosiphum rosae*, could be obtained with a release rate of about 2300 adult *Hip. convergens* per metre-squared of shrub-covered surface, a rate corresponding to double that normally recommended by commercial suppliers. The authors suggested that the approach was economically feasible given costs comparable to an insecticide treatment, but did not address the possible impact of such collections on local populations. The large scale collection and sale of *Hip. convergens* from the Sierra Nevada mountains continues until present times, but represents a commercial enterprise that exploits the public appeal of biological control, usually without delivering the results (e.g. Randolph et al. 2002).

11.4.3   Selection of source material for augmentation

Care should be taken in extrapolating control potential from laboratory feeding experiments, because the range of prey acceptable to coccinellids in confinement is often much broader than that in the field (Chapter 5). This can be true for various reasons, including prey specificity, plant and habitat preferences or simple refuge effects that are eliminated in simplified feeding situations. For example, Corlay et al. (2007) observed that larvae of the swede midge, *Contarinia nasturtii*, were acceptable prey to both *C. septempunctata* and *Har. axyridis* when presented in small containers, but completely escaped predation when presented on potted broccoli plants. The export of mass-collected beetles for augmentation in dissimilar habitats (where they are often released against unfamiliar prey) may be misguided, even when locally indigenous species are involved. Such export is based on the implicit assumption that populations of a species are ecologically uniform across their range and ignores the likely importance of local adaptations in providing effective biological control.

11.4.4   Voltinism and diapause

Differences in voltinism and diapause behaviour have long been documented among European populations of *C. septempunctata* and other temperate species (Chapter 6) and such variation can pose a significant impediment to efficacy whenever augmentation programmes employ displaced material. In the New World, **Hip. convergens** is indigenous throughout tropical and sub-tropical America but has highly divergent ecology and prey relationships compared to populations inhabiting temperate regions.

11.4.5   Dietary requirements

The nutritional ecology of coccinellid species can also vary dramatically among geographically separated populations, probably reflecting underlying genetic divergence (Obrycki et al. 2001). *Curinus coeruleus* originates in Mexico and has been introduced to Florida, Hawaii and several Asian countries. Populations of *C. coeruleus* in Florida are unable to complete development on *T. citricidus* and rarely feed on this aphid, whereas in Hawaii they mature successfully on this prey and contribute substantially to its mortality on citrus trees (J.P. Michaud, unpublished). Similarly, Michaud (2000) was unable to obtain completed development of the introduced Eurasian species *Coelophora inaequalis* on *T. citricidus* using material collected in central Florida, despite observing successful maturation on this prey in Puerto Rico. Wang and Tsai (2001) obtained successful development of *Coelophora inaequalis* on *T. citricidus* using material from southern Florida and suggested this species had potential to control the pest. Intraspecific variation in prey utilization patterns probably arises from different founder effects in colonizing populations that are subsequently amplified by disruptive selection in local habitats. However widespread, such divergence of populations would seem to caution against augmentation efforts employing 'mail-order' beetles in favour of collecting and culturing
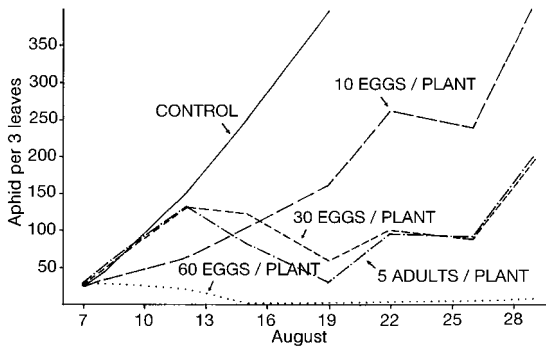
Figure 11.4 The effects of different rates of introduction of *Adalia bipunctata*, as either eggs or adults, on the numbers of *Myzus persicae* on sweet peppers in a greenhouse (from Hämäläinen 1977, with permission).

regionally adapted strains with proven local performance on the target.

11.4.6 Life stages for release

It is prudent to consider this in any particular coccinellid augmentation programme. Eggs are quite fragile and subject to a variety of mortality factors prior to hatching, especially predation and cannibalism, rendering them unsuitable for many applications. Nevertheless, Hämäläinen (1977) successfully used **egg masses** of *A. bipunctata* **for inundative control** of *M. persicae* on sweet peppers in a greenhouse (Fig. 11.4) and techniques have been developed for mass-producing eggs and applying them in the field (Shands et al. 1970). Kehrli and Wyss (2001) released *A. bipunctata* as eggs and **larvae** on apple trees over a range of dates in Switzerland and found that autumn releases of larvae could limit the deposition of overwintering eggs by aphids of the genus *Dysaphis*, leading to reductions in the numbers of fundatrices the following spring. By contrast, releasing egg masses was less effective due to the higher mortality. However, larvae are more costly to produce than eggs, especially if they require aphids for successful development, and they can suffer high levels of cannibalism in mass culture, depending on the species and the adequacy of the diet. Cannibalism is a particular problem in breeding strictly aphidophagous species and it is perhaps not surprising that most coccinellids mass-produced in commercial operations are species that can be reared on non-aphid prey or factitious diets. Pre-imaginal life stages are more practical for release in protected environments such as greenhouses and interior plantscapes where their survival can be enhanced by protection from natural enemies and control of the physical environment.

Adults are the most robust life stage for release. They are more **voracious** than larvae, but also the stage most prone to dispersal from release sites. Their effectiveness is enhanced if they can be induced to lay eggs prior to dispersal. Deng et al. (1987) claimed >90% reduction of sugar cane infestation by sugar cane woolly aphid, *Ceratovacuna lanigera*, by releasing field-collected adults of *Synonycha grandis* and *Coelophora biplagiata*. Yang (1985) reared and released between 600,000 and 800,000 *P. japonica* against *M. persicae* over a period of 4 years in cotton fields of Hubei, China. The study reported much lower aphid populations in release fields compared to control fields treated with insecticides, and at a lower cost. Ahmed et al. (2006) reported successful control of spider mites on cantaloupes in Egypt when releases of *Stethorus gilvifrons* were supplemented with applications of *Beauveria bassiana*, *Metarhizium anisopliae* (both entomopathogenic fungi) or insecticidal soap, none of which provided adequate control without the beetles. Presumably, the timing of field releases relative to pest population development is a critical factor influencing efficacy (10.1), as well as the elicitation of oviposition at release sites prior to emigration. Some progress in limiting emigration has been achieved by releasing flightless mutants, first discovered in *A. bipunctata* (Marples et al. 1993) and later mutagenically induced in *Har. axyridis* (Tourniaire et al. 2000). Weissenberger et al. (1999) showed that the flightless strain of *H. axyridis* has greater probability of laying eggs at a release site by virtue of its reduced dispersal capability. Unfortunately the flightless adults have significantly reduced fecundity (Ferran et al. 1998) and generally lower fitness. They appear more vulnerable to intraguild predation by tertiary predators such as Reduviidae (Heteroptera) and retain an urge to disperse, often wasting considerable time and energy on unsuccessful flight attempts (J.P. Michaud, unpublished).

11.5 CONSERVATION

In recent years, environmental concerns have given a renewed emphasis to the preservation and

enhancement of indigenous coccinellid species in order to improve their biocontrol contributions in natural and managed ecosystems. There are a wide variety of tactics for conserving coccinellids in horticultural and agricultural settings. In general, these aim to encourage immigration, discourage emigration, mitigate mortality caused by cultural activities including the application of pesticides, or improve survival during critical periods by the provision of specific resources, usually in the form of particular plant species. (See also 11.6.4 below.)

11.5.1   Alternative or supplementary food

The rationale for providing **additional food** for coccinellids is that food can be limiting to coccinellid survival or retention in the crop during critical periods, or can be used to attract immigrant beetles into crop fields earlier in the season or in larger numbers. The assumption is that provision of food can **alter the spatial distribution** of coccinellids in the landscape so as to improve subsequent biological control of a pest that is initially present at very low levels, or one that arrives in a crop with some predictability with respect to season or plant growth stage. There exists some experimental evidence to support the effectiveness of this approach, but the potential has been largely ignored in commercial agriculture. (See also 5.2.10.)

Artificial honeydews have been employed **successfully** to **attract** a variety of aphid predators, including coccinellids, into cropping systems (Hagen et al. 1971, Nichols & Neel 1977). Evans and Swallow (1993) demonstrated that sucrose sprays were more effective than protein supplements for attracting coccinellids and chrysopids into alfalfa fields. Predator responses to sucrose persisted up to 7 days in the absence of rain and resulted in reduced densities of *Acyrthosiphum pisum* in sprayed plots. Mensah and Madden (1994) successfully employed sucrose sprays and sugar granules in feeding stations to retain adult *Cleobora mellyi*, in target areas. Alhmedi et al. (2010) showed that limonene was attractive to gravid *Har. axyridis* females in both laboratory and field trials and increased their oviposition on plants. More recently, **herbivore-induced plant volatiles** have been synthesized that demonstrated activity in attracting beneficial insects into hop orchards, including the mite predator *Stethorus punctum picipes* (James 2003).

The ecological significance of **herbivory by coccinellids** in agricultural landscapes has probably not received adequate attention (but 5.2.9). Both adult and larval coccinellids have been observed consuming tender plant foliage, although this has often been dismissed as simply a means to obtain water. Moser et al. (2008) have shown that larvae of *Har. axyridis* and *Col. maculata* readily feed on maize seedlings even in the presence of animal prey. Coccinellids regularly utilize the **extrafloral nectaries** on wild and cultivated sunflowers, *Helianthus annuus* as a source of hydration and supplementary nutrition on the arid High Plains of Kansas (Michaud & Qureshi 2005, 2006). In spring, large numbers of first generation coccinellids (mostly *Hip. convergens*, *Hip. sinuata*, *C. septempunctata* and *Col. maculata*) mature on the aphids infesting winter wheat and emigrate *en masse* from the crop just prior to harvest in mid June. These beetles face hot dry conditions, a scarcity of essential prey (Fig. 5.1), and often a complete lack of free water, save the occasional dew. By maintaining a reproductive diapause, the beetles are able to sustain themselves throughout summer months on the extrafloral nectar of sunflowers (Fig. 11.5) and the occasional supplementary prey item until aphids become available once again as cooler weather returns in the autumn. Thus the presence of abundant sunflowers in the region, including substantial cultivated acreage, represents a valuable resource

Figure 11.5 Close-up of an adult *Hippodamia convergens* drinking extra-floral nectar from the petiole of a sunflower plant *Helianthus annuus* (J.P. Michaud). (See colour plate.)

that enables the beetle population to survive adverse summer conditions and subsequently limit aphid establishment on emergent winter cereals in autumn. Coccinellid consumption of plant material other than pollen has received little attention and could provide some novel opportunities for area-wide conservation, just as the planting of suitable flowers can enhance parasitoid foraging.

11.5.2   Hibernation refuges

In temperate regions where overwintering mortality can be high, the planting of hibernation refuges such as '**beetle banks**' (Fig. 11.6) has successfully enhanced coccinellid survival in various agricultural contexts including sugar beet (Bombosch 1965), Brussels sprouts (van Emden 1965) and potatoes (Galecka 1966). Iperti (1966) developed traps that **simulated rocky crevices** to shelter overwintering *Ceratomegilla (= Semiadalia) undecimnotata*, reduce their infection by *Beauveria bassiana*, and facilitate their collection for redistribution. **Bandages on branches** (Nohara 1962) or metal bands on tree trunks (Tamaki & Weeks 1968) have proven useful as artifical hibernation refuges for coccinellids in arboral settings. Construction of artificial shelters may sometimes be feasible in high-value vegetable crops, but is probably cost-prohibitive in most large scale agricultural settings and current approaches to enhancing overwintering survival tend to rely on recognizing and preserving natural hibernation sites.

Figure 11.6 A 'beetle bank' comprising a strip of perennial grasses forming dense tussocks to serve as overwintering habitat for coccinellids and other beneficial insects (Otago Regional Council, New Zealand). (See colour plate.)

11.5.3   Habitat management

Conservation of coccinellid populations hinges on understanding the full range of resources utilized by all life stages of a coccinellid species throughout a complete annual cycle. Potentially important considerations include the preservation of natural shelter or overwintering sites, the diversification of plant communities to improve availability of food and shelter, and modifications to conventional agricultural practices that minimize impacts on coccinellid populations. These modifications include tactics such as strip-harvesting, intercropping, reduced tillage, restriction of pesticide applications to spot or strip treatments, and the use of pesticides with selective modes of action. Unfortunately, the scaling up of commercial agriculture has generally resulted in larger fields of individual crops, reduced landscape complexity and increased habitat fragmentation for coccinellids, factors potentially reducing their ability to effectively track and control their prey (Elliott et al. 2002a, With et al. 2002). For example, Altieri and Todd (1981) showed that coccinellids remained **more concentrated in border rows** of soybean fields than in central parts. The floral composition of the surrounding landscape often explains a lot of observed variation in field-to-field coccinellid diversity and abundance (e.g. Elliott et al. 2002b). In addition, benefits observed in small-scale research plots may not be congruent with results obtained in larger scale commercial fields

(Corbett 1998). Thus, there is a need for continued study of coccinellid responses over various landscape scales if habitat management approaches to their conservation are to be successful.

11.5.3.1   Strip-harvesting

Strip-harvesting alfalfa (aka, lucerne) is one way to **prevent the post-harvest emigration** of local predator populations as a consequence of food deprivation, thus conserving natural enemies in fields and facilitating their rapid colonization of harvested areas when re-growth occurs. This approach has a long history of use in **alfalfa** production (Scholl & Medler 1947) where it functions to stabilize biological control of a range of pests and conserve coccinellids, among other beneficial species (Schlinger & Dietrick 1960, Hossain et al. 2001, Weiser et al. 2003). This approach has potential for conserving coccinellids in other perennial forage crops where aphids may cause losses. As with other forms of habitat management, even with proven results, the challenge in strip harvesting is one of implementation at farm level where the immediate convenience of conventional practices too often pre-empts consideration of future benefits that might be obtained with minor procedural modifications.

11.5.3.2   Floral diversity (non-crop plants)

Coccinellids demonstrate affinities for particular plants independent of prey availability but, although such preferences have been recognized, they have not been effectively exploited in biological control. For example, Schmid (1992) observed that coccinellids in Germany had consistent patterns of occurrence on particular **non-crop plant species**, mostly common weeds, and avoided others. These affinities were often independent of the presence of prey as fully 40% of the coccinellids were observed on plants without aphids. Lixa et al. (2010) demonstrated that six species of Coccinellidae were attracted to **aromatic species of Apiaceae** (dill, coriander and sweet fennel) particularly in their blooming seasons and Silva et al. (2010) found increased abundance of coccinellids and other beneficial insects in lemon orchards in response to ground cover vegetation.

   Although the potential exists to enhance coccinellid biological control via management of vegetative diversity, it will always be difficult in practice to encourage tolerance by farmers of plants considered weeds in other contexts. Kranz and Sengonca (2001) tested a range of plants for their relative attractiveness to *C. septempunctata* and successfully used preferred plants (*Medicago sativa* and *Artemisia vulgaris*) to influence the distribution and abundance of beetles in the field. Harmon et al. (2000) found that a **pollen-bearing weed** (dandelion, *Taraxacum officinale*) interspersed in alfalfa attracted sufficient concentrations of *Col. maculata* to locally reduce *A. pisum* densities relative to alfalfa patches lacking the weed. The work of Grez et al. (2010) in Chile illustrates just how species-specific coccinellid responses can be to various types vegetation bordering agricultural fields. However, border vegetation planted to provide supplementary food resources or alternative prey for coccinellids may sometimes impede their timely dispersal into adjacent crops, a phenomenon often referred to as 'apparent competition' (Frere et al. 2007). For example, stinging nettle, *Urtica dioica*, has long been recognized as a reservoir plant for coccinellids (Perrin 1975), but such reservoirs cannot benefit biological control unless beetles leave them and enter crop fields. Thus, Alhmedi et al. (2007) suggested **cutting border strips of nettle** to encourage timely movement of coccinellids into neighbouring field crops in Belgium, since nettle aphids colonized earlier in the season than species infesting green pea and wheat.

11.5.3.3   Intercropping

Fye and Carranza (1972) showed that intercropping grain sorghum with cotton could increase populations of *Hip. convergens* in the cotton due to the abundance of greenbug in sorghum early in the growing season. Patt et al. (1997) showed that intercropping aubergine (egg plant) with dill or coriander improved coccinellid diversity and abundance and increased mortality of *L. decemlineata* eggs and larvae, largely due to the attractiveness and suitability of these flowers for both *Col. maculata* and *Chrysoperla carnea*. Unfortunately, as mentioned above, manipulation of vegetation can have both positive and negative effects on biological control in a particular crop, depending on the plant and insect species involved. Andow and Risch (1985) found that densities of *Col. maculata* remained higher in monocultures of maize than in polycultures where maize was intercropped with beans, squash or red clover. Predation on *O. nubilalis* eggs by *Col. maculata* was also higher in the monoculture, apparently because maize

served as a better source of alternative foods (aphids and pollen) than did the other plants. Similarly, Seagraves & Yeargan 2006) used tomato as a companion plant to improve oviposition and egg survival of *Col. maculata* in corn plots, but this did not increase predation on *Helicoverpa zea* egg masses in the corn.

11.5.3.4   Reduced tillage

The widespread adoption of reduced tillage, or 'no-till' agriculture in the American High Plains over the past several decades was promoted to farmers for soil moisture conservation in this arid region. However, it also appears correlated with an area-wide reduction of cereal aphid problems in wheat and sorghum. Part of the effect may result from decreased rates of aphid colonization due to crop residues functioning as a mulch with reflective properties that reduce the 'apparency' of the crop plant (Burton & Krenzer 1985). There are also potential benefits for natural enemies such as coccinellids, the predators most often identified as responsible for biological control of cereal aphids in North America (Nechols & Harvey 1998, Michels et al. 2001). The structural complexity of habitats has been correlated with increased abundance and diversity of natural enemies, including coccinellids (Langellotto & Denno 2004). Crop residues in fields probably improve insect diversity by creating structural complexity on the soil surface, thus providing shelter for many species, as well as by providing food for detritivores and other non-pest insects, some of which may serve as alternative food for coccinellids. Although some studies have found no measurable effects of reduced tillage on coccinellid activity (Rice & Wilde 1991), others have noted favourable influences. Marti & Olson (2007) observed larger numbers of aphidophagous coccinellids in cotton fields under reduced tillage in Georgia, USA, although the treatment also increased populations of the red imported fire ant, *Solenopsis invicta*, a known antagonist of coccinellids and other aphid natural enemies (Eubanks et al. 2002). Although it is clear that coccinellids avoid tilled or bare soils, the extent to which they might utilize crop residues as overwintering sites has not been adequately explored.

Hesler and Berg (2003) observed that reduced tillage increased early season infestation by *Rhopalosiphum padi* in spring-sown cereals, an effect they inferred resulted from crop residues providing protection to the aphid which feeds preferentially on the lower stems of plants. However, this inference contrasts with the findings of Schmidt et al. (2004) who managed to improve biological control of *R. padi* in spring wheat using a **straw mulch treatment** that would have provided the aphids with physical protection similar to crop residues. These authors concluded that bare soil discouraged predators and rendered the crop more susceptible to pests. Given the similarity of the cropping systems, it seems unlikely that increased structural complexity alone can account for the contrasting results of these two studies, and the assemblages of natural enemies were also very different. Reduced tillage is also known to result in cooler soil temperatures and slower warming of the soil in spring, a factor that might impede the activity of coccinellids and other predators relative to aphids in specific situations. Thus it seems plausible that conditions may exist where the benefits of reduced tillage to coccinellids are offset by microclimatic effects.

Reports from **Mexico** suggest that adoption of no-till farming, known locally as 'direct seeding', has had a **long-term beneficial effect** on the abundance of aphidophagous coccinellids. In the Michoacán region of Mexico, summer crops of maize or sorghum are typically followed by winter crops of wheat or barley, a crop cycle similar to that seen across much of the Great Plains region to the north, albeit on an earlier seasonal schedule. Bahena and Fregoso (2007) sampled populations of beneficial insects annually in the winter crops of a number of fields that had been switched to continuous conservation tillage for periods as long as 10 years. Their data showed a trend toward increasing annual abundance of beneficial insects over time, particularly of *Hip. convergens* that comprised 80% of observed predators (Fig. 11.7). Reductions in the use of pesticides such as methyl parathion for aphids were also noted over this period although it is not clear to what extent they resulted from, or contributed to, the increase in *Hip. convergens* abundance.

11.6   ANCILLARY FACTORS INFLUENCING BIOLOGICAL CONTROL BY COCCINELLIDS

11.6.1   Ant-attendance of aphid colonies

Various ant species tend honeydew-producing insects and are notorious antagonists of coccinellids, repelling them from colonies of their prey (Cudjoe et al. 1993, Michaud & Browning 1999, Kaneko 2002) and even
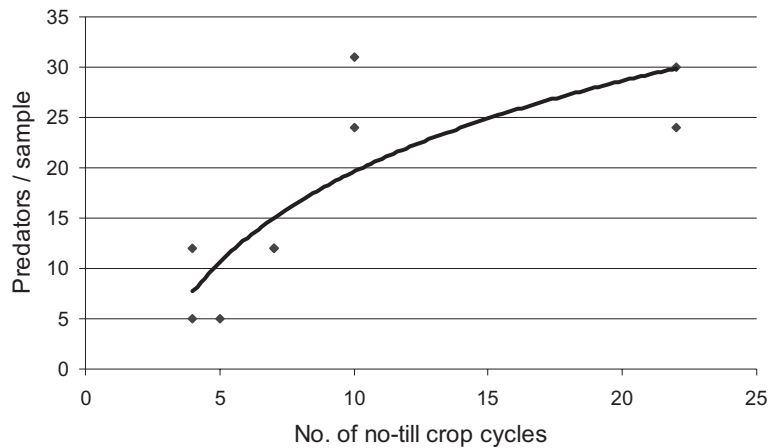
Figure 11.7 Mean numbers of predatory insects per sample (primarily *Hippodamia convergens*) in fields converted to reduced tillage cultivation in Michoacán, Mexico over a period of 10 years. The primary crop cycle was maize in summer followed by wheat in winter (courtesy of Bahena & Fregoso 2007). The logarithmic regression line obscures the fact that the maximum number of predators is actually reached in less than 10 cycles.

preying upon them (Sloggett et al. 1999). (See also 5.4.1.6 and 8.2.4) Where feasible, the **exclusion of ants** may improve biological control by coccinellids. For example, Itioka and Inoue (1996) obtained greatly improved control of citrophilus mealybug, *Pseudococcus cryptus*, by *Chil. kuwanae* when they excluded *Lasius niger* ants from citrus trees. In Hawaii, Reimer et al. (1993) obtained control of green scale, *Coccus viridis*, on coffee trees when they excluded tending *Pheidole megacephala* ants that preyed on larvae of four coccinellid species. Similarly, biological control of mealybugs on pineapples by parasitoids and predators, including the coccinellid *Nephus bilucernarius*, was substantially improved by the use of hydramethylnon **baits to reduce** populations of **tending ants**, primarily *P. megacephala* (Gonzalez-Hernandez et al. 1999). However, the larvae of some coccinellid species produce wax filaments that can provide protection against ant predation (e.g. *Scymnus lousianae*, Schwartzberg et al. 2010) and such species may actually benefit from ant attendance (e.g. *Azya orbigera*, Liere & Perfecto 2008).

11.6.2   Timing of arrival in annual crops

Timely immigration is often crucial to the impact of coccinellids on aphid populations and different species

exhibit different seasonal cycles (Elliott & Kieckhefer 1990). These cycles are affected by many factors, especially weather. For example, a cold snap in spring can de-couple biological control of aphids in winter cereals by slowing the development and reproduction of coccinellids and other predators relative to the aphids, and by delaying crop development that in turn extends the period of plant vulnerability to aphid feeding. Early recognition of conditions potentially disruptive to prey tracking by coccinellids can permit a **timely intervention** and prevent economic losses.

The importance of seasonal cycles of crop colonization by coccinellids is well illustrated in **sorghum** production on the High Plains of the USA (Kring et al. 1985, Kring & Gilstrap 1986, Michels & Burd 2007). Early season infestations of *Rhopalosiphum maidis* attract large numbers of aphid predators, mostly coccinellids (*Hip.* spp., but also *C. septempunctata*, *Col. maculata* and other native species) and chrysopids into sorghum fields where they complete a generation on this prey. Although a number of *R. maidis* colonies escape control and become large, they cause no economic damage to the plants and largely disappear before the panicles emerge. The predators attracted to *R. maidis* also feed on *S. graminum*, a pest that is highly damaging to sorghum (Rice & Wilde 1988). Alates of *S. graminum* arrive later in mid-summer and confront a population of newly emerged, hungry coccinellid

adults that exhaustively seek out and destroy greenbug colonies in their formative stages, usually preventing the development of economic populations. The generalist aphid parasitoid *Lysiphlebus testaceipes* is slower to respond, but eventually aids in maintaining the greenbug at low density. The risk of economic losses to greenbug is high only when *R. maidis* fails to colonize the crop in sufficient numbers to 'prime' the coccinellid population (Michels & Behle 1992). Thus, when relying on coccinellids to provide aphid control in annual field crops, agricultural producers should learn to **recognize and monitor the seasonal cycle of crop colonization** by these insects so that they can be prepared to intervene with supplementary controls in a timely manner in the event of any disruption.

11.6.3 Interaction of biological control by coccinellids with plant structure and chemistry

Since the plant is typically the theatre for biological control, plant architecture and chemistry may influence outcomes (5.4.1.1). Features such as **high structural complexity** (Grevstad & Klepetka 1992, Khan & Matin 2006) and **trichomes** (Belcher & Thurston 1982, Eisner et al. 1998, Heidari 1999) are known to impede coccinellid foraging ability, but may still be compatible with biocontrol. Shah (1982) demonstrated that varying the form and relative density of leaf trichomes had markedly divergent impacts on *A. bipunctata* larval foraging. Although larvae were unable to search leaves with dense upright or hooked hairs, searching efficiency was increased by widely scattered hairs that caused larvae to change direction frequently. In contrast, larval foraging on **waxy or highly glabrous leaves** was confined to edges and protruding veins. Obrycki et al. (1983) found that trichome density on potato cultivars was inversely correlated with aphid density when natural enemies (*Hip. convergens* and others) were excluded, but concluded that intermediate densities of trichomes would give the best combination of pest resistance and biocontrol in the field. Other plant features which discourage pests may also have unintended effects on coccinellid activity. Cotton cultivars lacking extrafloral nectaries reduce damage by *Lygus* spp. plant bugs, but such cultivars are also less attractive to natural enemies, including coccinellids (Scott et al. 1988). However, Katayama and Suzuki (2010) found that the presence of **extrafloral nectaries** on broad bean plants enhanced the survival of nuclear colonies of *Aphis craccivora* largely because of their greater attractiveness to two ant species that diminished the foraging activities of *C. septempunctata* larvae.

Certain plant characteristics may facilitate biological control by coccinellids. Kareiva and Sahakian (1990) found that a 'leafless' pea variety had higher than expected resistance to pea aphid in the field, simply because adult coccinellids were able to grasp the tendrils and forage more efficiently for the aphids than on **glossy leaves** from which they often slipped and fell. This tritrophic effect has been termed 'extrinsic resistance'. Eigenbrode et al. (1995) showed that a cabbage variety with glossy (as opposed to normal waxy) leaves reduced leaf mining by *Plutella xylostella* larvae, increasing their exposure to predation by *Hip. convergens* and other predators in addition to affording improved mobility for the predators. Similarly, Eigenbrode et al. (1998) showed that adult *Hip. convergens* foraged more effectively on pea cultivars with reduced epicuticular wax and Rutledge et al. (2003) found that such cultivars hosted lower pea aphid populations in field plots than isolines that lacked this trait. Comparing these isolines in cage and laboratory tests without predators revealed no differences between them in plant acceptance by aphids or their subsequent performance. The authors concluded that **higher foraging efficiency** was responsible for the greater coccinellid abundance and lower aphid populations on the reduced wax cultivar in the field.

The effectiveness of biocontrol is sometimes a function of plant susceptibility to the pest, creating the possibility for **synergism between plant resistance** factors **and natural enemies** such as coccinellids. In cereal breeding, much effort has been directed toward developing cultivars resistant to aphids, particularly *S. graminum* and the Russian wheat aphid *Diuraphis noxia*. Most sources of resistance available in commercial wheat, sorghum and barley cultivars express antibiosis that serves to impede aphid development and reproduction, coupled in some cases with a degree of antixenosis (van Emden 2007). Although such resistant cultivars ultimately succumb to uncontrolled aphid populations, they are able to survive longer than susceptible ones and effectively prevent yield losses when supported by the activities of natural enemies such as coccinellids. By slowing aphid growth and reproduction, they extend the period during which colonies remain small and vulnerable to elimination,
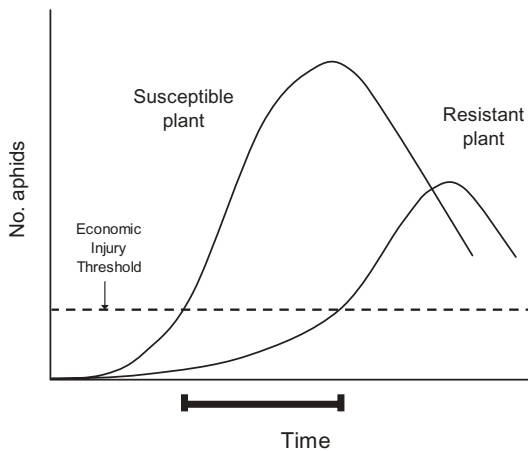
Figure 11.8 Hypothetical aphid colony growth trajectories on susceptible and resistant cereal plants in the absence of natural enemies. As the carrying capacity of the plant is reached, the plant begins to die and alate aphids develop and disperse. Since antibiosis delays aphid colony growth on the resistant plant, more time is required for the colony to reach the economic injury threshold (dashed line), and an incremental period (solid line) becomes available for the actions of coccinellids and other natural enemies to prevent economic damage.

and the time required for the economic injury level to be reached (Fig. 11.8). Wheat cultivars resistant to *D. noxia* are not selected simply for antibiosis, but also for resistance to leaf rolling, a plant response induced by aphid feeding that creates a physical refuge from foraging coccinellids and other natural enemies (Kauffman & LaRoche 1994). Farid et al. (1997) demonstrated that wheat **resistance to leaf rolling** by *D. noxia* was complementary to biological control by *Scymnus frontalis* because the suitability of *D. noxia* as prey was unaffected by resistance, while mortality of beetle larvae was lower on resistant plants due to the absence of rolled leaves that sometimes entrapped larvae on susceptible plants.

By definition, **plant antibiosis** has a negative impact on pest biology, leading to doubts about the suitability of prey fed on resistant plants. Most studies suggest only minor life history impacts of prey-mediated plant resistance factors on coccinellids that seem unlikely to significantly impact field populations or negate the benefits of such resistance in the field. Rice and Wilde (1989) fed *Hip. convergens* on *S.*

graminum reared on two resistant sorghum cultivars and found that larval survival was reduced by between 10 and 20% and development somewhat delayed. Martos et al. (1992) showed that survival and development of *Eriopis connexa* was reduced on a diet of *R. padi* raised on wheat seedlings containing the hydroxamic acid DIMBOA (also 5.2.6.1). Nevertheless, the deterrent flavour of the compound at higher concentrations causes beetles to avoid consuming aphids that contain a potentially lethal dose.

Aphids developing on resistant plants typically take longer to develop and have reduced reproductive rates (van Emden & Wearing 1965, Jyoti & Michaud 2005). They may move more and feed less, thus failing to achieve the size of those reared on susceptible plants. Smaller aphids are usually less profitable prey for coccinellids as they force a predator to spend more time searching and handling prey for a lower net energy return per unit foraging time. This could conceivably translate into delayed development for larvae or reduced clutch sizes for adult females. However, it is also possible for **reduced aphid size** to magnify the impact of coccinellid predation since a large number must be consumed before satiation occurs (Hassell et al. 1977). To date, there are no clear indications of negative effects of plant resistance on coccinellid abundance in the field. For example, Bosque-Perez et al. (2002) found no indications that *D. noxia*-resistant wheat had any adverse impact on the field abundance of coccinellids in Idaho.

With the widespread planting of **genetically modified** (GM) **insect-resistant crops** in many regions of the world, concern has been raised about possible impacts on coccinellids and other beneficial species. GM maize engineered to express *Bacillus thuringiensis* (Bt) toxins was considered a potential risk to coccinellids because the toxin was present in pollen (Harwood et al. 2007). Most studies have found no effect of Bt corn pollen consumption on fitness parameters of *Col. maculata* (Duan et al. 2002, Lundgren & Wiedenmann 2002) or other insect predators (Pilcher et al. 1997). Porcar et al. (2010) fed three types of solubilized Bt toxins directly to *A. bipunctata* and *Cryptolaemus montrouzieri* and obtained no increase in mortality compared to controls. However, (Moser et al. 2008) found that consumption of Bt maize leaf tissues by larvae resulted in a small delay in development relative to non-Bt maize. One study observed reductions in coccinellid abundance in Bt maize plots (Delrio et al. 2004), but McManus et al. (2005) found no reduction

in abundance of *Col. maculata* in pre- or post-anthesis Cry3Bb1 maize fields expressing the Bt subsp. *kumamatoensis* toxin that is Coleoptera specific. Similarly, Riddick et al. (2000) looked for changes in abundance of generalist predators in fields of Cry3A-transgenic potatoes with resistance to Colorado potato beetle and found no impact on coccinellids or predatory Heteroptera. Others have suggested that Bt crops may benefit coccinellid populations via reductions in broadcast insecticide applications (Wadhwa & Gill 2007), and the results of a comprehensive multi-year study in Bt cotton (Head et al. 2005) appear to support this conclusion. Nevertheless, it should be noted that **aphids do not acquire the Bt toxin**, whereas other prey species such as spider mites may accumulate and concentrate it in their bodies. Thus Obrist et al. (2006) found high concentrations of Bt toxin in *Stethorus* sp. nymphs sampled in GM maize in Spain, although the impact on fitness of the beetle population was not determined.

11.6.4   Selective use of pesticides

This has long been recognized as an important tactic for conserving coccinellids, and efforts have been made in recent years to determine indices of relative toxicity that can be used to rank materials for **compatibility with ladybirds in IPM programmes**. In general, eggs and young larvae are the most sensitive life stages, and adults the least. As sessile stages, eggs and pupae may have a somewhat reduced risk of exposure in the field relative to actively foraging larvae and adults. One problem in assessing the impact of insecticides in field studies is that materials highly effective against the pest population will also reduce numbers of coccinellids as a consequence of eliminating their food supply, even if they lack direct toxicity to the beetles (Poehling & Dehne 1984, Mateeva et al. 2001). However, **careful timing of insecticide applications** relative to crop development can sometimes serve to synergize, rather than disrupt, pest control by a complex of natural enemies that includes coccinellids (Fagan et al. 2010).

A literature review by Croft and Brown (1975) reported 33 citations where coccinellids were rated **more tolerant of pesticides than their prey**. However, these cases did not include examples of resistant pests and tested mostly older generations of halogenated hydrocarbon and organophosphate insecticides. More recently, Gesraha (2007) found that

pirimicarb, imidacloprid and thiamethoxam were all less toxic to *C. undecimpunctata* than to its prey, *B. brassicae*, although only adult beetles were tested. Broad-spectrum pyrethroids tend to be more destructive to coccinellids than organophosphates (e.g. Kumar & Bhatt 2002), although there is evidence that populations of *Hip. convergens* can evolve substantial resistance to pyrethroids in agroecosystems with heavy usage patterns (Ruberson et al. 2007). Some materials that have shown moderate to low toxicity to coccinellids are listed in Table 11.1. Disparities in procedures, formulations and concentrations across studies make objective comparisons of materials difficult, but there is obvious variation among species in sensitivity to particular compounds. Some materials have a **selective mode of action** that can spare coccinellids from toxic exposure. For example, **spinosad** is generally benign to coccinellids, although Galvan et al. (2005) found sub-lethal impacts on development and reproduction. Because spinosad requires ingestion to induce toxicity, residue trials typically yield high safety ratings, whereas direct topical applications may result in some mortality, probably due to ingestion via grooming behaviour (e.g. Michaud 2002d). Although potentially hazardous to Hymenoptera, certain spinosad-based fly baits have tested relatively safe for coccinellids (Michaud 2003), possibly because the formulation did not stimulate consumption.

Pymetrozine selectively inhibits aphid feeding behaviour, has reputedly low toxicity to coccinellids, and has been used effectively in conjunction with *C. septempunctata* for control of *B. brassicae* on broccoli (Acheampong & Stark 2004). However, despite observing low acute toxicity of pymetrozine to *C. leonina transversalis*, Cole et al. (2010) found that less than 3% of exposed larvae survived to maturity. Insecticides toxic to coccinellids may also be **selective by virtue of formulation** or mode of application. Systemic materials applied as granules, soil drenches or planting time 'in-furrow' applications can give good control of aphids without causing direct mortality to coccinellids. Most recently, the modern **neonicotinoids** thiamethoxam and imidacloprid display good systemic activity in plants and have become increasingly available as **seed treatments** that are very effective against seedling pests, especially aphids and flea beetles, while sparing coccinellids and other predators from direct impacts, except when they engage in herbivory (Moser & Obrycki 2009). Another systemic neonicotinoid, dinotefuran, was shown to provide good control

Table 11.1 List of some insecticides potentially compatible with predatory coccinellids in integrated pest management. Risk levels were assigned for particular species based on the results of individual reports since different studies employed various exposure methods in field and laboratory, different material concentrations and tested different beetle life stages.

Material	Species tested	Type of test	Risk level	Reference
carbofuran	*Ceratomegilla undecimnotata*	laboratory: fed treated prey	sub-lethal effects	Papachristos & Milonas (2008)
diflubenzuron	*Scymnus spp.*	field	low	Matrangolo et al. (1987)
	Cycloneda sanguinea L. *Harmonia axyridis*	laboratory, topical/residue	moderate/low low/low	Michaud (2002d)
dimethoate	*Brumoides suturalis* *Menochilus sexmaculatus* *Coccinella septempunctata*	field	low-moderate low-moderate low-moderate	Sandhu (1986)
endosulfan	*Menochilus sexmaculatus*	semi-field, foliar	low	Jalali & Singh (2001)
	Menochilus sexmaculatus	laboratory, residue	low	Dhingra et al. (1995)
	Menochilus sexmaculatus *Coccinella septempunctata* *Micraspis discolor*	field	low low low	Sharma et al. (1991)
	Cycloneda sanguinea *Hippodamia convergens* *Olla v-nigrum*	laboratory: residue	moderate moderate moderate	Mizell & Schiffhauer (1990)
	Hippodamia convergens	laboratory, fed treated prey	high	Hurej & Dutcher (1994)
fenvalerate	*Menochilus sexmaculatus* *Coccinella septempunctata* *Micraspis discolor*	field	moderate moderate moderate	Sharma et al. (1991)
	Cycloneda sanguinea *Hippodamia convergens* *Olla v-nigrum*	laboratory: residue	moderate moderate moderate	Mizell & Schiffhauer (1990)
imidacloprid	*Coccinella undecimpunctata*	laboratory: topical	moderate	Gesraha (2007)
	Ceratomegilla undecimnotata	laboratory: fed treated prey	sub-lethal effects	Papachristos & Milonas (2008)
indoxacarb	*Curinus coeruleus* *Cycloneda sanguinea* *Harmonia axyridis* *Olla v-nigrum*	laboratory: topical	moderate low low moderate	Michaud & Grant (2003)
	Harmonia axyridis	laboratory: topical	moderate	Galvan et al. (2005)
	Harmonia axyridis	laboratory: topical/ residue/fed treated prey	moderate/low/ moderate	Galvan et al. (2006b)
methidathion	*Curinus coeruleus* *Cycloneda sanguinea* *Harmonia axyridis* *Olla v-nigrum*	laboratory: topical	moderate moderate moderate moderate	Michaud & Grant (2003)
neem oil	*Cycloneda sanguinea*	laboratory: topical	low	da Silva & Martinez (2004)
	Menochilus sexmaculatus	laboratory: topical	low	Krishnamoorthy et al. (2005)
	Coccinalla septempunctata	field	low	Dhingra et al. (2006)
	Harmonia axyridis *Hippodamia convergens*	semi-field, foliar	low low	Tenczar & Krischik (2006)
oxydemeton-methyl	*Brumoides suturalis* *Menochilus sexmaculatus* *Coccinella septempunctata*	field	low-moderate low-moderate low-moderate	Sandhu (1986)

(*Continued*)

Table 11.1 (*Continued*)

Material	Species tested	Type of test	Risk level	Reference
phosalone	*Coccinella septempunctata*	laboratory: residue	moderate	Hao et al. (1990)
	Cycloneda sanguinea	laboratory: residue	moderate	Mizell & Schiffhauer
	Hippodamia convergens		moderate	(1990)
	Olla v-nigrum		low	
phosmet	*Curinus coeruleus*	laboratory: topical	high	Michaud & Grant
	Cycloneda sanguinea		moderate	(2003)
	Harmonia axyridis		high	
	Olla v-nigrum		low	
	Hippodamia convergens	laboratory, fed treated prey	high	Hurej & Dutcher (1994)
phosphamidon	*Brumoides suturalis*	field	low-moderate	Sandhu (1986)
	Menochilus sexmaculatus		low-moderate	
	Coccinella septempunctata		low-moderate	
pirimicarb	*Adalia bipunctata*	laboratory: topical	low	Kalushkov (1982)
	Coccinella quinquipunctata		low	
	Cycloneda sanguinea		low	
	Coccinella septempunctata	laboratory: residue	low	Hao et al. (1990)
	Coccinella septempunctata	field	moderate	Mateeva et al. (2001)
	Coccinella undecimpunctata	laboratory: topical	moderate	Gesraha (2007)
pyriproxyfen	*Cycloneda sanguinea*	laboratory: topical/residue	moderate/low	Michaud (2002c)
	Harmonia axyridis		low/low	
	Rodolia cardinalis	field (selectively timed)	moderate	Grafton-Cardwell et al. (2006)
pymetrozine	*Coccinella septempunctata*	laboratory, field	low	Acheampong & Stark (2004)
spinosad	*Cycloneda sanguinea*	laboratory: topical/residue	moderate/low	Michaud (2002c)
	Harmonia axyridis		low/low	
	Coccinella septempunctata	laboratory, greenhouse	low	Miles & Dutton (2000)
	Hippodamia convergens		low	
	Menochilus sexmaculatus	laboratory, residue	low	Elzen & James (2002)
	Harmonia axyridis	laboratory, topical	moderate	Galvan et al. (2005)
	Harmonia axyridis	laboratory: topical/ residue/fed treated prey	low/low/low	Galvan et al. (2006b)
	Harmonia axyridis	semi-field, foliar	low	Tenczar & Krischik
	Hippodamia convergens		low	(2006)
Spinosad GF 120®	*Rodolia cardinalis*	laboratory: bait	low	Medina et al. (2004)
	Curinus coeruleus	laboratory: bait	low	Michaud (2003)
	Cycloneda sanguinea		low	
	Harmonia axyridis		low	
sucrose octanoate	*Curinus coeruleus*	laboratory: topical	low	Michaud & McKenzie
	Cycloneda sanguinea		low	(2004)
	Harmonia axyridis		low	
	Olla v-nigrum		low	
thiamethoxam	*Coccinella undecimpunctata*	laboratory: topical	moderate	Gesraha (2007)

of armored scales on Christmas trees when applied in a band around the base of the trunk, without impacting the foraging activities of the scale predators *Chil. stigma* and *Cybocephalus nipponicus* (Cowles 2010). However, **coccinellids** can be **impaired behaviourally** or reproductively by non-lethal concentrations of insecticides that they may acquire when feeding on contaminated pollen or nectar (Smith & Krischik 1999) or contaminated prey (Singh et al. 2004, Eisenback et al. 2010). **Insect growth regulators** (IGRs) such as buprofezen and pyriproxyfen generally lack acute toxicity to coccinellids, but may impair development (Hattingh and Tate 1995) and fecundity (Olszak et al. 1994). Nevertheless, good knowledge of insect ecology can sometimes enable the judicious use of these compounds without disrupting coccinellid populations. Despite the high sensitivity of *Rodolia cardinalis* to IGRs, and residual activity longer than 6 months under California conditions, IGRs can be used to control pyrethroid-resistant scale insects in citrus, provided that applications are delayed until after *R. cardinalis* has exerted control of *Icerya purchasi* in spring (Grafton-Cardwell et al. 2006).

11.7 CONCLUSIONS

The role of coccinellids in classical biological control programmes has diminished as various unanticipated ecological impacts of exotic species have come to light and certain large, dominant coccinellids have gained recognition as invasive species. Consequently, regulatory authorities are likely to permit only highly specialized, non-aphidophagous species for use in classical programmes in future. Certain species will remain important for augmentation in specialized contexts, but few novel augmentation applications for coccinellids been developed recently. The future appears brighter for improving **conservation** and **enhancing the efficacy** of naturally occurring species in open systems. Advances will hinge on improved holistic understanding of the ecological roles of coccinellids and their ability to complement other beneficial species. This information is critical for the development of novel approaches to habitat management that could improve the efficiency of established coccinellid guilds in particular agroecosystems and enhance their ability to track economically important prey species in time and space.

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