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Pest Status, Bio-Ecology, and Area-Wide Management of Mirids in East Asia

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Abstract

Mirids (Hemiptera: Heteroptera: Miridae) feed upon a wide variety of cultivated and wild plants and can be economically important crop pests. They have traditionally been perceived as innocuous herbivores in East Asia; however, population levels of various mirid species have dramatically increased over the past decades. High-profile pests such as *Apolygus* spp., *Adelphocoris* spp., and *Lygus* spp. are now widely distributed across the region, and their infestation pressure is associated with climate, agroecological conditions, and farming practices. This review outlines how an in-depth understanding of pest biology, a systems-level characterization of pest ecology, and a comprehensive evaluation of integrated pest management tactics have enabled sustainable management of mirids across crop boundaries and harvest cycles. This work underscores how more holistic, integrative research approaches can accelerate the implementation of area-wide management of generalist pests, effectively prevent pest population build-up and yield impact, and shrink the environmental footprint of agriculture. In addition to highlighting the merits of interdisciplinary systems approaches, we discuss prospects and challenges for the sustainable management of polyphagous mirid pests in landscape matrices.

1. INTRODUCTION

Mirids (Hemiptera: Heteroptera: Miridae) are widely distributed across the Palearctic, Oriental, Nearctic, and other biogeographic regions and include more than 11,000 species worldwide (6). They are polyphagous herbivores on a diverse range of wild herbs, shrubs, and trees; a subset of mirid species recurrently attained pest status in agricultural crops. One group of prominent pests, including *Lygus lineolaris*, *Lygus hesperus*, *Lygus elisus*, and *Lygus rugulipennis*, affect cotton, alfalfa, legume, fruit tree, and vegetable crops in North America and Europe. Feeding damage, biology, ecology, and management options for these *Lygus* spp. have been extensively reviewed (20, 41, 125). These valuable reference materials have helped researchers devise sustainable management solutions for pestiferous mirids across the globe.

In contrast to other piercing-sucking pests, such as aphids, planthoppers, or whiteflies, and pestiferous Lepidoptera, there is scant information on the feeding damage, bio-ecology, and management of mirids. This knowledge gap is ascribed to their concealed behavior, distinct feeding habits, and rather inconspicuous damage (125). In East Asia, the bulk of mirid research has been conducted in China, Japan, and South Korea. Yet, as compared to stemborers and locusts, which have been locally studied for more than 3,000 years, mirid pests have only received scientific attention subsequent to the first records of their feeding damage in the early twentieth century (69, 169). Mirid research has been intermittent and fragmentary over space and time; aside from piecemeal progress over the period 1950–1980 (69), comprehensive ecological research and pest management programs were only initiated from the 1990s onward.

2. TEMPORAL SHIFTS IN MIRID ABUNDANCE, CROP INJURY, AND IMPACT

In the Palearctic Region, 2,808 mirid species from 397 genera have been recorded (38). In China, there are more than 1,000 mirid species from 219 genera of 8 subfamilies (59, 60, 161, 169), including economically important pests such as *Apolygus lucorum*, *Adelphocoris suturalis*, *Adelphocoris lineolatus*, *Adelphocoris fasciaticollis*, and *Lygus pratensis* (68, 71). Among these, *Ap. lucorum* is omnipresent in China's farming landscapes and mostly occurs in the Yangtze River and Yellow River Regions. *Adelphocoris suturalis* is the main species in the Yangtze River Region, *Ad. fasciaticollis* is dominant in the Yellow River Region, *Ad. lineolatus* is restricted to the Yellow River and Northwestern Region, and *L. pratensis* primarily occurs in the Northwestern Region (69, 169). The community composition of crop-feeding mirids is thus geographically variable and mediated by the seasonal feeding habits, host plant ranges, and climatic preferences of individual species. Their pest status has changed over the past decades, from insignificant herbivores or secondary pests on cotton to major crop pests of local and regional allure. In recent years, mirids have attained high infestation levels, inflicted important feeding damage, and thus become key pests of local cotton, legume, fruit trees, and tea crops (71, 74). For example, mirid-induced yield losses increased three- to fivefold in China's cotton crop from 1991 to 2010 (71). When left uncontrolled, mirids occasionally reduce yields by 30% in cotton and alfalfa and by 50–80% in grape and jujube and can even cause total crop loss in tea (33). Mirid feeding further affects the susceptibility of various crops to phytopathogenic or fruit spoilage fungi (101). In Japan and South Korea, *Apolygus spinolae* and *Ap. lucorum* are common pests on fruit trees, tea, and cultivated herbs (39, 42, 43, 124). In addition, *Stenotus rubrovittatus* and *Trigonotylus caelestialium* are important rice pests that have increased their distribution range and population density across Japan over the past two decades (88, 136).

3. MIRID BIOLOGY AND BEHAVIOR

3.1. Life History

Mirids are hemimetabolic organisms that pass through three development stages: egg, nymph, and adult. Species such as *Ap. lucorum*, *Ap. spinolae*, *Ad. suturalis*, *Ad. lineolatus*, and *Ad. fasciaticollis* overwinter as diapausing eggs on dead plant material, crop stubble, weeds, woody branches (e.g., of fruit trees and tea), and the soil surface (65, 78). Egg clusters of *Ap. lucorum* are deposited on old stems of jujube and grape (92), while *S. rubrovittatus* and *T. caelestialium* oviposit in grasses, where eggs undergo overwintering diapause (28, 40). Meanwhile, *L. pratensis* overwinters as adults on weeds, tree bark crevices, and fissures and in the soil (69). Photoperiod and temperature synergistically regulate diapause induction in *Ap. lucorum* and *Ad. suturalis*, with first-instar nymphs being sensitive to shortening day length (13, 14). Both factors affect egg diapause and subsequent development; for example, a slight temperature increase (2°C) induces diapause termination and egg eclosion for *Ap. lucorum*. During the postdiapause phase, temperature and photoperiod equally mediate egg development time and hatching in this species (171). Similarly, *T. caelestialium* egg diapause is induced by shortening day length in the parental generation (40), and high temperatures cause females to deposit nondiapause eggs (25).

Several mirids possess a well-developed flight apparatus and fly over large distances. Tethered flight mill assays showed that young (i.e., 5–15-day-old) adults of *Ap. lucorum*, *Ad. suturalis*, *Ad. lineolatus*, and *Ad. fasciaticollis* exhibit the strongest flight performance. Under laboratory conditions, 10-day-old adults cover 25–45 km per day, with *Ap. lucorum* adults undertaking the longest flights (72, 75). In the field, mark-recapture trials using rubidium markers found that *Ap. lucorum* and *Ad. suturalis* adults move between 850 and 1,280 m per day (103). The former species moves over larger distances during autumn as compared to spring, when food sources are more abundant (86). This flight capability facilitates the seasonal exploitation of ephemeral food resources and even enables transmaritime migration. Every year, *Ap. lucorum* adults are monitored on islands in the Bohai Gulf 40–60 km from China's mainland, where they fly at airspeeds of 0.5–2.5 m/s and at 100–150 m altitude. By relying on shifting wind patterns, *Ap. lucorum* adults thus seasonally colonize areas in northern and northeastern China (16).

Mirids employ a repertoire of chemical cues for interspecific communication. Behavioral assays have shown that sexually mature virgin females attract conspecific males. For five species of *Apolygus* spp., *Adelphocoris* spp., and *Lygus* spp., binary or ternary blends of (E)-4-oxo-2-hexenal, hexyl butyrate, (E)-2-hexenyl butyrate, and hexyl hexanoate act as sex pheromones. In *Ad. fasciaticollis*, (E)-4-oxo-2-hexenal and hexyl butyrate (1:11 ratio) constitute the main components of the female sex pheromone (156); for *Ad. suturalis*, a 10:1 ratio blend of (E)-4-oxo-2-hexenal and hexyl hexanoate attracts males (164).

Ternary blends of hexyl butyrate, (E)-2-hexenyl butyrate, and (E)-4-oxo-2-hexenal act as a sex pheromone of *L. pratensis*, with a 20:1:30 ratio blend showing high levels of attraction in the field (158). These compounds are also the main constituents of *Ap. lucorum*, *Ad. lineolatus*, and *Ap. spinolae* sex pheromones. Yet the exact composition of the most attractive blends differs markedly. While 1:1 to 1:2 blends of (E)-4-oxo-2-hexenal and (E)-2-hexenyl butyrate prove attractive to *Ad. lineolatus* (155), 3:2 blends of these compounds yield high capture rates of *Ap. lucorum* (157). For *Ap. spinolae*, a 10:1 blend of (E)-2-hexenyl butyrate and (E)-4-oxo-2-hexenal provides levels of male attraction equal to those of live virgin females (137). Ternary blends of hexyl hexanoate, (E)-2-hexenyl hexanoate, and octyl butyrate (100:40:3 ratio) are most attractive to *T. caelestialium* males (37), while a 5:10:1 blend of hexyl butyrate, (E)-4-oxo-2-hexenal, and (E)-2-hexenyl butyrate elicits high male attraction in *S. rubrovittatus* (143, 145). Among the 38 putative odorant-binding proteins (OBPs) identified in *Ap. lucorum*, AlucOBP7 is a pheromone-binding protein

(31, 146), and in vitro electrophysiological recordings have uncovered how the receptors AlucOR4, AlucOR40, and AlucOR59 correspond to specific pheromone blends (1, 154, 170).

Although mirids are primarily day active for feeding, they usually mate and oviposit at night. Females of *Ap. lucorum* deposit eggs upon inserting their ovipositor into different plant tissues, e.g., stem, petiole, shoot, bud, and fruit (9). Shortly after egg eclosion, nymphs of *Ap. lucorum* and other species disperse onto suitable host plants. Within a 10–30°C range, egg and nymphal development rates for *Ap. lucorum*, *Ad. suturalis*, *Ad. lineolatus*, *Ad. fasciaticollis*, and *L. pratensis* increase with temperature (57, 76, 79). At 25°C, *Ap. lucorum* eggs and nymphs require 8 days and 12 days to complete their respective development, and adults live on average 34 days (males) and 31 days (females). Females normally initiate oviposition approximately 6–8 days after eclosion, but the preoviposition period can be extended to more than 2 months (79). Females of *Ap. lucorum* oviposit over most of their adult lifespan and lay an average of 81 eggs per individual (79). Oviposition dynamics of *Ad. suturalis*, *Ad. lineolatus*, and *Ad. fasciaticollis* are similar (76). Thus, successive mirid generations routinely overlap, and multiple developmental stages co-occur in the field (33, 69).

3.2. Host Plant Selection and Feeding Behavior

Many mirid species are generalists: 288 host plant species (54 families) have been logged for *Ap. lucorum*, 270 species (49 families) for *Ad. suturalis*, 127 species (32 families) for *Ad. fasciaticollis*, 245 species (47 families) for *Ad. lineolatus*, and 71 species (22 families) for *L. pratensis*. Hosts include annual arable crops, perennial fruit trees, ornamentals, and wild (herbaceous, woody) plants. As many mirid species undertake seasonal host plant shifts, the above numbers are likely underestimates, and new hosts are continually being described (33, 66, 94, 95).

A decade-long common garden trial involving nearly 200 plant species in Langfang (China) uncovered the seasonal host selection and use of four mirid species. This trial uncovered species-specific preferences for multiple wild and cultivated plants. For example, *Ap. lucorum* prefers *Vigna radiata*, *Ricinus communis*, *Impatiens balsamina*, *Artemisia lavandulaefolia*, and *Artemisia annua*. *Adelphocoris suturalis* exhibits a preference for *Astragalus complanatus*, *Medicago sativa*, *Agastache rugosa*, and *Nepeta cataria*. For *Ad. fasciaticollis* and *Ad. lineolatus*, preferences were logged for *Lablab purpureus* and *Leonurus japonicus* and for *M. sativa* and *Melilotus suaveolens*, respectively (33). Adults of these mirids are primarily encountered on flowering stages of their preferred hosts, and host selection is mediated by infochemicals (97, 135). Similarly, *T. caelestialium* adults preferentially forage on the flowering panicles of rice (*Oryza sativa*) and graminaceous weeds as compared to their nonflowering stages (17). Volatile compounds (m-xylene, butyl acrylate, butyl propionate, and butyl butyrate) extracted from 18 preferred host plants elicited behavioral responses in *Ap. lucorum* adults. These volatiles reached 2–8 times higher concentrations during the flowering stage as compared to the vegetative phase. Thus, volatile release during flowering elicits attraction of *Ap. lucorum* adults (98), and the same volatiles likely mediate foraging processes during the fruit ripening stage of jujube and grape crops (100). Electrophysiological, olfactometer, and field studies revealed how adults of the three *Adelphocoris* species were variably attracted to the above-listed four volatiles and n-butyl ether (135).

Mirid adults and nymphs feed on plant tissues by lacerating the cell wall with their stylets and secreting a watery saliva into ruptured cells. This saliva contains enzymes such as polygalacturonase that cause plant cell lysis (148, 160). For *Ad. suturalis*, direct current-electrical penetration graph (DC-EPG) assays characterized feeding behavior on various plant hosts, i.e., green bean, alfalfa, cauliflower, wheat, and cotton. Four waveforms correspond with distinct steps of the feeding process: (*a*) stylet insertion into plant tissues, (*b*) cell wall laceration and saliva secretion, (*c*) ingestion, and (*d*) stylet withdrawal. The duration of the entire probing event and waveform *c* is longest on alfalfa—reflecting alfalfa's status as a host. DC-EPG assays also showed how *Ad.*

suturalis feeds mainly on the cotyledons and young leaves of cotton, with a preference for apical meristem tissue (3).

3.3. Physiological Determinants of Omnivory

During the 1950s, *Ap. lucorum* was observed preying on aphids (7), and recent work has confirmed that this mirid is a common predator of the cotton aphid *Aphis gossypii* and cotton bollworm *Helicoverpa armigera*. Its predation rate generally increases with mirid development stage and prey density (51). Molecular gut content analyses and exclusion cage assays further revealed that *Ap. lucorum* contributes to *A. gossypii* biological control (51). The zoophytophagous feeding habits of *Ap. lucorum* have major life history implications. Mirids that feed on a mixed diet of green bean and *H. armigera* eggs have higher fitness than those feeding on single-plant diets. In addition, *Ap. lucorum* is unable to complete its life cycle in the sole presence of insect prey (52, 147). Individuals that exclusively feed on a plant diet exhibit high amylase activity, while those consuming insect prey or a mixed diet possess high titers of proteases, i.e., trypsin- and chymotrypsin-like enzymes (53). Compared to other hemipterans, *Ap. lucorum* has a broader set of digestive enzymes with substantially more serine proteases. These enable omnivorous feeding habits, in which *Ap. lucorum* complements a mainly plant-based diet with the occasional intake of insect prey (62). The remaining mirid species (i.e., *Ad. suturalis*, *Ad. fasciaticollis*, *Ad. lineolatus*, and *L. pratensis*) all engage in omnivory and likely possess the same underlying physiological determinants as *Ap. lucorum*.

4. LANDSCAPE-LEVEL FLOWS AND OUTBREAK DYNAMICS

4.1. Seasonal Host Transfer

Mirid population dynamics are dictated mainly by the identity and (flowering) phenology of locally available host plants. Throughout their life cycle, individual mirids engage in extensive host plant switching in which adults track a succession of flowering plant species in the agro-landscape (7, 94, 97). Adult females mainly oviposit on flowering plants, where adult lifespan, fecundity, nymphal development rate and survival are markedly higher than on their nonflowering counterparts (10). On various key host plants, flower nectar rich in carbohydrates (e.g., sucrose, fructose, glucose) directly enhances *Ap. lucorum* fitness (99).

Landscape-scale dynamics reflect host plant use, which varies geographically due to locally prevailing mirid species and the distribution, phenology, and relative occurrence of host plants. In China's Yellow River Region, mirid populations are primarily found in flowering fruit orchards, tea plantations, alfalfa fields, and weedy Lamiaceae and legumes during spring. The population shifts to cotton or alfalfa fields and cultivated legumes during summer and then colonizes fruit orchards, tea plantations, alfalfa and maize fields, and composite and mulberry weeds in autumn. In the Yangtze River Region, mirids are primarily found in fruit orchards, tea plantations, broad bean fields, and leguminous and umbelliferous weeds during spring. The population shifts to fields with cotton and cultivated legumes in summer and then colonizes fruit orchards, tea plantations, maize fields, and composite and goosefoot (*Chenopodium* spp.) weeds in autumn. In northwestern China, mirid populations move from fruit orchards, alfalfa fields, and leguminous weeds in spring, to cotton, alfalfa, and other cultivated legume fields and tamarisk shrubs in summer, to fruit orchards, alfalfa fields, and various composite and goosefoot weeds in autumn (33).

4.2. Biotic and Abiotic Mediating Factors

Various biotic and abiotic variables affect mirid development and population build-up within agricultural landscape mosaics. The relative contributions of local (agro-)climatic conditions, natural

enemies, identity and spatial coverage of (crop and non-crop) host plants, and anthropogenic factors such as landscape-level insecticide use are described below.

4.2.1. Climate. Mirid development, distribution, and behavior are shaped by temperature, and temperature optima and thermal tolerances are species specific. Under constant temperatures, optimum development of *Ap. lucorum*, *Ad. suturalis*, *Ad. lineolatus*, *Ad. fasciaticollis*, and *L. pratensis* occurs between 20°C and 30°C (57, 76, 79, 113). Temperature also dictates activity patterns. Mirids actively forage on the canopy in the morning and evening. Once dew disappears from the leaves and temperature or light intensity increases, they either move to the underside of leaves, flowers, and bracts on lower parts of plants or disperse to noncrop habitats with ample shade, e.g., wood plots or weed patches (18, 69).

Many mirids are associated with shady, moist environments, and humidity is a prime determinant of their population fitness. Under laboratory conditions, high levels of relative humidity (RH) (70–80%) result in high egg and nymphal survival, increased adult longevity, and raised fecundity of *Apolygus* spp. and *Adelphocoris* spp. Drier conditions (40–50% RH) negatively impact nymphal survival, adult longevity, fecundity, and other demographic parameters (57, 70, 93). These effects are also reflected in field- or landscape-level dynamics. Mirid infestation pressure and crop damage are consistently higher in years or seasons with high rainfall (113, 114), and cotton fields in irrigated locations in the desert regions of northwestern China experience high levels of mirid feeding damage (33). However, in Japanese paddy rice systems, feeding damage caused by *S. rubrovittatus* negatively relates to overall precipitation (105).

Overwintering egg survival is strongly affected by climatic conditions. Abundant rainfall is critical for egg development and nymphal emergence of *Ap. lucorum*, acting as a trigger for egg hatching and mediating overall nymphal density; few nymphs emerge from overwintering eggs in the absence of rainfall (92, 123). In addition to rainfall, elevated springtime temperatures lead to high egg hatching, while cold spells delay the initial onset (and size) of mirid spring populations (171).

4.2.2. Natural enemies. Numerous natural enemies affect mirids in different crops, habitats, and farming contexts. Generalist predators such as ladybeetles, lacewings, spiders, and predatory bugs attack early-instar nymphs in experimental arenas. In laboratory settings, adults of the spider *Misumenops tricuspidatus* consume 57 individuals of second-instar *Ap. lucorum* nymphs per day (117). However, gut content analysis reveals that only a fraction (2%) of resident predators actually consume mirids under field conditions. Various species of lacewings, ladybeetles, and spiders are positive for *Ap. lucorum* DNA, with the highest positive proportion (6%) occurring in *Harmonia axyridis* larvae. Given that exclusion cage assays confirm this low predation rate, e.g., by *H. axyridis* larvae, predation likely plays a relatively minor role in mirid population regulation (48). Predation in noncrop habitats (e.g., during early spring or fall) may exert important impacts on mirid population dynamics, but this remains to be empirically assessed and is likely mediated by habitat type or agro-landscape composition.

Surveys of *Ap. lucorum*, *Ad. suturalis*, *Ad. fasciaticollis*, *Ad. lineolatus*, and *L. pratensis* nymphs in crop and noncrop habitats discovered two parasitoid species, *Peristenus spretus* and *Peristenus relictus*. The former nymphal parasitoid species accounts for an average of 13% parasitism in experimental plots with 13 different host plants, attaining respective parasitism levels of 43% and 16% in buckwheat and cotton, whereas *P. relictus* occurs at markedly lower levels, i.e., 0–12% (46). The egg parasitoid *Telenomus* sp. affects *Ap. lucorum* overwintering eggs in jujube orchards, providing (spatially clustered) parasitism rates of 13–24%, as recorded through molecular assays (47). In Japan, *Oligosita* sp. and *Telenomus* sp. attack the eggs of *T. caelestialium*, although parasitism levels exhibit large seasonal variation (23).

4.2.3. Host plant suitability. Inter- and intraspecific differences exist in plants' susceptibility to mirid attack. Cotton varieties exhibit variable tolerance to mirids; varieties with high densities of gossypol glands and high titers of tannins and total terpenoids in leaves are less susceptible to *Ap. lucorum* (54–56). A similar phenomenon has been recorded for grape (120), although there is no evidence of full host plant resistance (54, 56). Mirid development and population growth do not vary between conventional and *Bacillus thuringiensis* (Bt) transgenic cotton cultivars; the latter have been locally deployed in China against lepidopteran pests such as *H. armigera* (44, 45). For a given plant species, cultivar, or phenological stage, mirid population growth and crop damage can be inferred from adult feeding preferences or field-level abundance (10, 19). Differences in host plant suitability directly relate to crop damage and management action. As mirids seasonally switch hosts (91, 94), close proximity of preferred (flowering) host plants can raise the odds of crop damage but may also enable spatiotemporal targeting of curative management.

4.2.4. Insecticide use. Mirid infestation pressure is affected by field- and landscape-level insecticide application regimes and resistance development. Several common insecticides (e.g., organochlorines, organophosphates, pyrethroids, carbamates, neonicotinoids) inflict mortality on mirid adults and nymphs and are extensively used by Asian farmers (11, 63, 165). Many insecticides negatively affect resident natural enemies and favor resistance development (63, 166), although novel compounds such as sulfoxaflor selectively conserve some arthropod predators (2). Chemical pest control has resulted in field-evolved resistance of mirids to multiple insecticide classes (61, 110, 150) and popular compounds such as chlorpyrifos, malathion, or cyhalothrin (119, 167, 168). While prophylactic insecticide applications, e.g., as soil granulates or seed treatment, may slow pest establishment or population build-up early in the season (149, 162), these practices routinely hamper natural biological control and degrade ecological resilience (15).

4.3. Regional Population Outbreaks

In several crops, mirids are controlled through recurrent insecticide sprays—often directed against other crop antagonists. Following the nationwide adoption of Bt cotton in China during the late 1990s, a concomitant reduction in insecticide use triggered mirid population build-up and crop damage over extensive areas (71, 74). Adult mirids colonize cotton fields during the budding and flowering stages, a critical time period for *H. armigera* management. Prior to the adoption of Bt cotton, insecticide sprays directed against *H. armigera* also impacted mirid colonists, slowing their population build-up (71). Since the late 1990s, Bt cotton enables *H. armigera* control and reduced insecticide usage levels (127, 159), while several broad-spectrum organochlorine and organophosphate insecticides have been banned (151). The reduction of insecticide applications led to escalating mirid pest outbreaks in cotton and multiple other crops, e.g., jujube and grape in cotton agro-landscapes (74, 126, 159). Mirid outbreaks covered broad geographic areas and inflicted severe losses in noncotton crops from 2010 onward. Shifting cultivation patterns further led to an increased cultivation of high-value horticultural crops in China's traditional cotton-growing regions, while insecticide usage in those noncotton crops largely continued unabated. The year-long abundance of flowering host plant resources and weakened ecological regulation ultimately translated into recurring mirid population outbreaks (50, 71, 73). Landscape composition affects *Ap. lucorum* populations at broad spatial scales (50), a finding that is consistent with earlier work on *L. hesperus* (5). Global warming exacerbates these dynamics. Increasingly warm winters and wet summers favor mirid overwintering survival and development, potentially deepening the ensuing socioeconomic and environmental impacts. Similar dynamics were recorded in Japan for *S. rubrovittatus* and *T. caelestialium*. Since 2000, both species have expanded their geographic distribution and attained higher population densities. This can be directly ascribed to global warming

(89) and heightened coverage of fallow land and meadow fields, i.e., key source habitats for both mirids (30, 90).

5. TOWARD AREA-WIDE INTEGRATED PEST MANAGEMENT

5.1. Pest Monitoring and Forecasting

Field-level monitoring was initially done through labor-intensive methods such as visual observation or drop-tray or sweep-net sampling (34, 115). Feeding damage on young leaves was also used to infer timing and extent of crop damage (33, 80), and a linear relationship was found between mirid population density and leaf damage in cotton (34). Following their identification and synthesis, sex pheromones have been widely used in pan traps for monitoring (4, 29, 142). For *S. rubrovittatus* and *T. caelestialium*, mixed lures proved attractive to males of either species (141, 144). Pheromone-based trapping now constitutes a cost-effective method to gauge the onset of crop colonization and assess mirid population dynamics at field, farm, or landscape scales and is complemented by light trapping (33, 107); these practices tend to be preferred over more labor-intensive methods. An analysis of 16-year-long *Ap. lucorum* monitoring data helped to identify key meteorological determinants of the species' seasonal abundance and predict seasonal population peaks (134).

The above sampling techniques and predictive models are presently employed in a monitoring platform and early warning network that covers 15 provinces in China. Through this network, the identity and infestation pressure of multiple mirid species are systematically assessed using standardized protocols, periodic population forecasts are generated, and crop-specific management guidelines are suggested (32).

5.2. Preventative and Curative Measures

Given their long lifespan, dispersal capabilities, and damage potential, mirid adults constitute prime targets for area-wide integrated pest management (IPM). At present, a wide suite of IPM tactics is available to manage mirid populations in Asian cotton landscapes. These comprise preventative measures such as semiochemicals; physical, agroecological, or agronomic practices; and curative practices such as chemical control, biopesticides, or parasitoid augmentation.

5.2.1. Use of semiochemicals. Behavior-modifying semiochemicals such as sex pheromones can be used to mass-trap adult males and thus slow population build-up (82), e.g., by using bucket traps baited with a 3:1 ratio blend of butyl acrylate and butyl propionate for *Ap. lucorum* (12). Products such as the acaricide dimethyl disulfide (DMDS) provide a repellent action; adult populations in cotton fields are lowered for 6 days following a DMDS foliar spray (96).

5.2.2. Biological control. The nymphal parasitoid *P. spretus* is commercially available (as pupae) for field-level release. Under laboratory conditions, *P. spretus* females oviposit up to 670 eggs over 32 days (85). As parasitoids attain optimum fitness when developing on second- to third-instar nymphs (81, 84), releases are scheduled to coincide with peak mirid egg hatching. In an assessment of mirid infestation levels, 2–3 subsequent releases at 5–7-day intervals and a 1:100 ratio (parasitoid pupae versus mirids) resulted in 80% parasitism levels (83). Many systemic insecticides such as imidacloprid are highly toxic to *P. spretus* (63), and their usage is incompatible with biological control (36, 131). Instead, selective compounds or entomopathogenic fungi such as *Beauveria* spp. are recommended to conserve released and naturally occurring natural enemies (118). Buckwheat strips, sown in or near cotton fields, provide carbohydrate resources for foraging *P. spretus* and substantially raise *Ap. lucorum* parasitism levels (46, 132). The actual establishment of buckwheat strips or deployment of buckwheat floral volatiles bolsters rates of natural biological control, e.g.,

in cotton fields, and potentially can be paired with augmentative releases in different crop contexts (133).

5.2.3. Agronomic practices. Insights into mirid foraging and oviposition behavior have been used to devise preventative pest management tactics. As *Ap. lucorum* adults preferentially deposit overwintering eggs on dead jujube branches, sanitary practices (i.e., branch removal and burning) reduce the ensuing spring population (49, 82, 92). Along the same lines, the removal of dead host weeds during winter is recommended for control of *Ap. lucorum* and *Adelphocoris* spp. (7, 78, 116). Population build-up during spring is further mitigated through manual, mechanical, or herbicidal control of host weeds (94, 95). Mowing alfalfa plots during nymphal population peaks lowers infestation levels of several mirid species (116), a tactic that has been used in the United States against *Lygus* spp. for several decades (104). In small-scale farming systems, pest spillover and population build-up can be averted by not establishing preferred host plants such as alfalfa, sunflower, jujube, or legumes near (or within) cotton fields (33, 49, 50). Conversely, by establishing strips of insecticide-treated mung bean, sunflower, or safflower in cotton fields, mirid infestation levels are kept below economic threshold (77, 122, 152). Lastly, a timely mowing of graminaceous weeds at the field border lowers *S. rubrovittatus* and *T. caelestialium* densities in rice (102, 108, 138–140). By pairing some of these practices with biological control at the landscape level, effective mirid pest control has been attained, e.g., in Japan's organic paddy rice (106).

5.2.4. Physical control. Physical and mechanical control is well-developed in high-value commodities such as tea and perennial fruits. The application of 3–5-cm-wide glue strips on the trunks of fruit trees reduces *Ap. lucorum* nymphal density during early spring (33, 49). In tea plantations, fine-mesh insect netting prevents the (autumn) immigration of *Ap. lucorum* adults from nearby weed or crop patches. By deploying net covers in September and removing them in late October, overwinter egg laying and feeding damage during the subsequent spring can be reduced economically (33, 87).

5.2.5. Chemical control. In most major crops, mirids are regularly treated with synthetic insecticides, and economic thresholds have been defined (22, 27, 33, 163). Insecticide sprays are guided by monitoring, e.g., physical scouting or pheromone trapping, and infestation peaks of early developmental stages are targeted. In China, organophosphates, pyrethroids, and neonicotinoids are widely used for mirid control, and their actual usage depends on crop-specific product registration. Yet, given mirids' dispersal capabilities, the efficacy of chemical control is limited in small-scale, diversified production systems (33). In addition, many chemical insecticides negatively impact nontarget biota and weaken biological control. Botanical pesticides such as Matrine and Veratrine or microbial pesticides are thus preferred for curative interventions, especially where the environmental or human health impacts of synthetic insecticides are of concern (121).

5.3. Implementing Area-Wide Pest Management

Regular monitoring is the foundation of effective mirid management in China, but this practice differs among farming systems and agro-ecological contexts. In large-scale monocultures, monitoring is mainly conducted in the affected crop. In diversified farming systems, mirid population densities are tracked on multiple host plants and habitats. The fact that mirids sequentially colonize different crop and noncrop habitats and exhibit seasonal affinities with particular crops allows for timely forecasts of local and regional population emergence, helps pinpoint source habitats, and guides curative or preventative management (33).

As landscape composition and cropping structure differ geographically, certain practices (e.g., weed removal) are more suitable to some farming regions than others. Infestation levels are also

mediated by the geographical proximity and spatial coverage of cultivated host plants, which facilitate seasonal host switching and gradual population build-up. In diverse landscapes with a mixture of perennial fruit and cotton fields, a systematic implementation of sanitary practices in fruit orchards during autumn can thus mitigate pest pressure in alfalfa or cotton field crops in the following year. Similarly, a characterization of mirid population abundance in blooming fruit orchards during spring can aid in anticipating colonization dynamics of nearby cotton fields and scheduling parasitoid releases. By thus tailoring both preventative and curative management interventions to specific contexts, one can disrupt the annual mirid life cycle and avert pest-induced losses in one or more target crops (**Figure 1**).

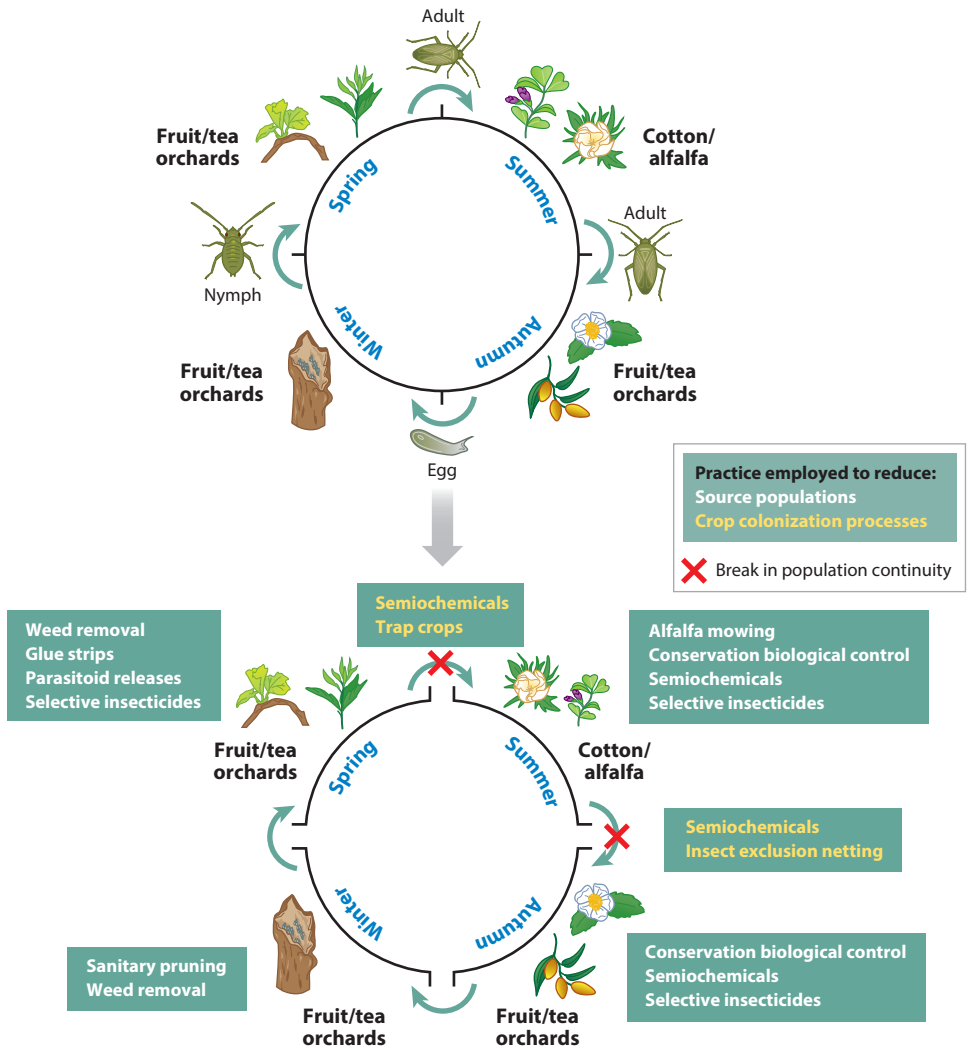

Figure 1

Preventative and curative practices constitute the basis of area-wide pest management in China's cotton landscapes. These measures are tailored to specific crops, seasons, and stages in the annual mirid life cycle. Practices highlighted in white and yellow aim to reduce source populations and crop colonization processes, respectively.

The above principles and the underlying mirid population phenology thus constitute the basis of area-wide management programs, as tailored to the Yellow River, Yangtze River, and Northwestern farming regions (33). At present, these programs are annually implemented and cover millions of hectares of cotton, fruit tree, tea, and alfalfa crops in China. Area-wide management programs have also been devised for *S. rubrovittatus* and *T. caelestialium* in Japan's rice-growing regions; these programs comprise monitoring and management actions in various (rice or nonrice) habitats (24, 109).

5.4. Social-Ecological Outcomes

In the late 1990s, mirid infestation levels escalated in multiple cropping systems across East Asia. By 2010, mirids negatively affected primary productivity, harvest quality, and farmer income on more than 8 million hectares of cotton, alfalfa, perennial fruit, and tea plantations across China. Yet, over the period 2010–2020, a systematic implementation of area-wide IPM reduced mirid-affected cropping area by 45% nationwide, i.e., from a peak of more than 8.0 million hectares to the present approximately 4.5 million hectares (67); lowered overall infestation pressure; and enhanced yield and harvest quality of multiple crops (8, 67, 82). Furthermore, a 30% reduction was achieved in insecticide use (as directed against mirids), with spillover benefits in terms of averted carbon emissions and biodiversity conservation (130) and a (possible) deceleration of insecticide resistance development. The area-wide IPM program also increased the unit price of harvested produce and total farm income, especially for high-quality tea and stone or pome fruit (35, 82). Lastly, the replacement of chemical control with a battery of preventative and ecologically based measures likely provided major, though unquantified, benefits for human health and the environment. These achievements can be further consolidated, and area-wide IPM can be taken to scale in China and neighboring East Asian countries, through awareness raising, stakeholder education, and policy change (26).

6. CONCLUSION AND FUTURE OUTLOOK

Since the early 2000s, polyphagous mirid species have attained recurrent population outbreaks and inflicted major crop losses in East Asian farming systems (74). As mirid population dynamics relate to the seasonal exploitation of different host plants and habitats, reductionist approaches and management action at the level of single fields or crops are ineffective to resolve pest issues. Instead, a sound understanding of mirid ecology, systems thinking, and landscape-level action are crucial to devising effective management strategies. Losses in specific crops can be averted by controlling mirid populations in source habitats during the preceding spring or winter. Similarly, a coordinated implementation of both curative and preventative management in summer crops such as cotton or alfalfa can reduce colonization flows into high-value crops such as grape or jujube during autumn (33, 94). Pheromone-based monitoring across crops and agro-landscapes helps to orchestrate the deployment of such tactics.

Effective mirid IPM hinges on farmers' agro-ecological knowledge, routine field scouting, and timely management. Local farmers traditionally disregarded mirids on (flowering) weeds at the field border or in noncotton crops. As a consequence, their unchecked population build-up in these settings often preceded extensive crop damage. Mirid host plant use and habitat switching, however, can be exploited for preventative pest management aimed at disrupting their annual life cycle. For instance, *Ap. lucorum* feeding preferences served as a basis for the design of (mung bean) trap crops. By directing spray applications of chemical or biological insecticides to these trap crops, mirid numbers can be reduced in neighboring cotton fields (77, 152). For other mirid species, a tactical deployment of flowering plants in or near cropping fields can divert colonization

flows, enable spatially targeted interventions, and provide foraging resources for resident natural enemies (46).

Parasitoids regulate mirid populations and exert varying degrees of biological control in crop and noncrop habitats (23, 46), but farmers are largely unaware of their existence and ecological role (128). Thus, engaging farmers through discovery-based learning is paramount to the effective promotion of parasitoid-mediated biological control and other biodiversity-driven tactics. By consciously conserving parasitoid populations, e.g., through insecticide avoidance or providing nectar-bearing plants and performing augmentative releases, pest infestation levels can be lowered substantially (82, 83). In temporally stable habitats, e.g., fruit orchards or tea plantations, habitat management plays a central role in promoting biological control. Natural pest regulation can thus be effectively wielded to achieve sustainable pest control at the landscape level and attain a progressive phasedown of synthetic insecticide use across crops.

Mirids rely extensively on volatiles for sexual communication. The identification and synthesis of their sex pheromones has unlocked the potential for volatile-based mass trapping and population monitoring (141, 157, 158). The incorporation of plant volatiles such as m-xylene or butyl butyrate (98, 100, 153) in pheromone lures could further enhance the efficiency of current trapping, monitoring, and mating disruption schemes.

In several farming systems in China, cotton fields assume a pivotal role in mirids' annual population cycle. Similarly to *H. armigera*, mirids colonize cotton at the onset of summer but feed on many crop and noncrop host plants during the remainder of the year. Varietal resistance, i.e., Bt transgenic cotton cultivars, enabled a suppression of *H. armigera* populations over extensive areas (74). Similarly, mirid-resistant cotton cultivars developed through conventional breeding or transgene, RNA interference, or gene-editing techniques (21, 58, 111), as well as biologically or chemically (aerial or soil-directed) primed defenses and agronomic practices such as plant training for induced defense, could become part of area-wide IPM schemes in the future (64, 129). Given that China's cotton crop largely consists of genetically uniform monocultures, the potential of inter- and intraspecific crop diversification has yet to be tapped. These approaches ideally should be combined with conservation biological control; parasitoid releases; and microbials, e.g., *Beauveria* spp. Along the same lines, amended (cotton) fertilization, irrigation, and cultivation schemes can contribute to mitigating mirid infestation pressure over space and time (33, 112, 115).

SUMMARY POINTS

1. For several mirid species in China, cotton constitutes a preferred (summer) host and modulates region-wide pest population growth and crop damage. Following the commercial adoption of *Bacillus thuringiensis* cotton in China and the concomitant reduction in insecticide usage during the 1990s, mirids exhibited secondary pest outbreaks. Given mirids' dispersal capabilities and extensive host switching, these outbreaks are not confined to cotton but also affect forage, perennial fruit, and tea production systems. Infestation pressure is further aggravated by shifting cultivation patterns, low levels of (genetic) diversity in China's cotton crop, farmers' over-reliance on (broad-spectrum) synthetic insecticides, and climate change.
2. Mirids exhibit volatile-mediated preferences for flowering plants. This behavior assumes a central role in mirids' annual life cycle, and the flowering phenology of crop and noncrop hosts shapes adult foraging dynamics, crop damage, and ensuing economic losses. By methodically tracking and disrupting mirids' sequential host usage in entire farming landscapes, area-wide pest management can be attained.

3. Mirids' host plant usage patterns differ among geographies and agro-ecological contexts. Population growth is mediated by the prevailing climatic conditions; landscape composition; and crop management, e.g., insecticide usage. A scientific elucidation of locality-specific mirid population ecology and host plant phenology, coupled with routine, multihabitat monitoring, has allowed for tailoring integrated pest management programs to key farming regions.
4. Farmers still regularly revert to chemical insecticides for mirid control. Yet an in-depth evaluation of the relative contribution of biological control across habitats has opened new vistas for biodiversity-driven alternatives. Diversification schemes, agroecological measures, and parasitoid releases could bolster natural pest regulation and may in future be tactically deployed at field, farm, and landscape levels.
5. Although mirid population dynamics are complex, mediated by multiple biotic and abiotic forces and determined by the local presence of hundreds of host plants, interdisciplinary science has unlocked unprecedented opportunities for ecologically based, preventative management. This review chronicles how (basic, applied) research uncovered critical aspects of a pest's biology and ecology and enabled an effective, environmentally responsible management of polyphagous pests at a macroscale. Awareness raising and policy change can now consolidate the initial gains in terms of pest mitigation, pesticide phasedown, and the ensuing social-ecological benefits.

DISCLOSURE STATEMENT

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