Effects of Crop Diversity on Pests and Natural Enemies in Agricultural Fields: Postprint

Authors: Dong Wenxia, Xiao Chun, Li Chengyun

Date: 2017-11-06T00:00:00+00:00

Abstract

Crop diversity planting has an ancient and long-standing history in China, and continues to play an important role in modern agricultural production. In recent years, utilizing diversity planting to control insect pests has become one of the hotspots in agricultural research worldwide. Crop diversity planting directly influences the occurrence, damage, and behavior of agricultural pests. Numerous studies have shown that with crop diversity planting, both pest populations and damage levels are reduced to varying degrees. However, some studies have also demonstrated that crop diversity planting not only fails to reduce pest damage, but may even exacerbate it. Diversity planting affects not only the populations of natural enemy insects, but also their parasitism or predation rates, and influences their activity capacity by affecting their orientation behavior, searching behavior, dispersal behavior, etc. This paper summarizes recent research findings on the effects of crop diversity planting on agricultural pests and their natural enemies, and discusses the prospects and current challenges in this field. This paper also introduces seven hypotheses (physical barrier hypothesis, optomotor response hypothesis, host plant odor masking hypothesis, repellent chemical substance hypothesis, plant odor composition alteration hypothesis, natural enemy hypothesis, resource density hypothesis) and one theory (suitable/unsuitable landing theory) regarding the mechanisms by which crop diversity planting influences insects. These hypotheses and theories can elucidate the mechanisms of diversity planting effects on insects to a certain extent, but none can comprehensively explain the ecological mechanisms of pest control through diversity planting.

Full Text

Effect of Diversified Cropping on Insect Pests and Natural Enemies in Agroecosystems

DONG Wenxia, XIAO Chun, LI Chengyun

(National Key Laboratory for Conservation and Utilization of Biological Resources in Yunnan / College of Plant Protection, Yunnan Agricultural University, Kunming 650201, China)

Abstract: The history of diversified cropping can be dated back to the era of man' s evolution that followed hunting and gathering, and this form of cropping has stood the test of time to remain an important farming practice in modern agriculture. In recent years, controlling insect pests using diversified cropping has been the focus of agricultural research. Diversified cropping has direct effects on the occurrence, damage, and behaviors of insect pests. Many studies have indicated that diversified cropping reduces, to a large extent, the occurrence and damage caused by insect pests. It has been noted in some cases, however, that diversified cropping systems fail to reduce or even increase insect pest damage to crops. Diversified cropping affects not only natural enemy populations, but also parasitic and predation rates of these populations. Diversified cropping also influences natural enemies by disturbing the orientation, foraging, and dispersal behaviors of these beneficial organisms. This study summarized the effects of diversified cropping on insect pests and natural enemies in agroecosystems. From a review of domestic and international research reports, the study also highlighted current problems and future research directions on diversified cropping systems. Seven hypotheses (physical obstruction, visual camouflage, host plant odor masking, repellent chemicals, altering host plant odor profiles, enemy hypothesis, and resource concentration hypothesis) and one theory (appropriate/inappropriate landing) were introduced regarding the relationship between diversified cropping and insect pests. These hypotheses and theory largely explained the relationship, but none of them has fully elucidated the mechanisms of the effects of diversified cropping on insect pests and natural enemies in agroecosystems.

Keywords: Crop; Diversified cropping; Insect pest; Natural enemy; Agroecosystem; Population behavior

Diversified cropping has a long history in China and continues to play an important role in modern agricultural production. Applying the principles of biodiversity and ecological balance to optimize the layout and planting of crop genetic diversity and species diversity can increase species diversity and ecosystem stability in farmland [1], effectively reducing crop pest damage [2]. Particularly in recent years, with growing awareness of environmental safety, food safety, and resource protection, biodiversity has gained increasing attention. Utilizing diversified cropping to control pests and reduce chemical pesticide use has become a hot topic in agricultural research worldwide [3-5]. This paper synthesizes recent research findings on the effects of crop diversification on farmland pests and natural enemies, aiming to provide a reference for future in-depth research and technological development.

1.1 Effects of Crop Diversity on Pest Occurrence and Damage

Numerous studies have shown that rational intercropping of crops can reduce pest populations and damage to varying degrees. Many successful examples of pest control through intercropping have been documented (Table 1). It is generally believed that one reason intercropping can reduce pest damage is that diversified planting creates unfavorable microenvironments for pests, while also restricting their free movement among different crop species. More importantly, diversified planting may influence insect populations in four key ways: (1) pests are attracted to crops with lower economic value and lighter damage; (2) pest host-finding behavior may be disrupted by intercropped plants; (3) odoriferous plants repel pests; and (4) intercropped plants can enhance natural enemy effectiveness, particularly in vegetable systems, by providing nectar, pollen, or shaded, moist environments near the ground that favor predatory arthropods. Table 1 summarizes effective diversified planting patterns reported in the literature, covering major food crops such as maize (*Zea mays*) and wheat (*Triticum aestivum*), economic crops like sugarcane (*Saccharum sinense*) and legumes, and vegetables including cabbage (*Brassica oleracea*), tomato (*Solanum lycopersicum*), and cucumber (*Cucumis sativus*). The targeted pests are highly diverse, including stem borers, cotton bollworm (*Helicoverpa armigera*), Japanese beetle (*Popillia japonica*), aphids (Aphidoidea), flea beetles (*Phyllotreta striolata*), and termites (*Microtermes* spp.). Notably, pests such as stem borers and diamondback moth (*Plutella xylostella*) are difficult to control with conventional pesticides, making biodiversity-based control particularly advantageous. Moreover, a single crop combination can sometimes control multiple pest species simultaneously. These findings demonstrate that crop diversification holds great potential for pest control and natural enemy conservation, offering a cost-effective approach that protects both the ecological environment and beneficial insects, representing an important future direction for pest management.

However, some studies have shown that intercropping does not reduce pest damage and may even exacerbate it. For example, compared to monoculture maize fields, European corn borer (*Ostrinia nubilalis*) caused less early-season damage but more late-season damage in maize-potato (*Solanum tuberosum*) intercrops [41]. Banana (*Musa paradisiaca*) intercropped with legumes [*Canavalia ensiformis*, *Mucuna pruriens*, *Tephrosia vogelii*] had no effect on banana weevil (*Cosmopolites sordidus*) population density or damage levels [42]. Alfalfa weevil (*Hypera postica*) populations showed no significant difference between alfalfa (*Medicago sativa*) monoculture and alfalfa/smooth bromegrass (*Bromus inermis*) intercrops [37]. Intercropping snap beans (*Phaseolus vulgaris*) with winter wheat increased population densities of tarnished plant bug (*Lygus lineolaris*) and flea beetle (*Systena frontalis*) [19]. In oat (*Avena sativa*) and faba bean (*Vicia faba*) mixed stands, peak populations of bird cherry-oat aphid (*Rhopalosiphum padi*) were higher than in monocultures [43]. Leek moth (*Acrolepiopsis assectella*) laid the same number of eggs on cabbage (host plant) whether grown in monoculture or intercropped with red clover (*Trifolium pratense*, a non-host)

[44]. Strip intercropping with soybean or maize did not significantly reduce planthopper populations [*Sogatella furcifera*, *Nilaparvata lugens*, *Laodelphax striatellus*] [45]. Fruit-cotton intercropping [jujube (*Zizyphus jujuba*)-cotton, almond (*Amygdalus communis*)-cotton, walnut (*Juglans regia*)-cotton] led to severe aphid outbreaks [*Acyrthosiphon gossypii*, *Aphis gossypii*, *A. atrata*] [46]. Sugarcane intercropped with soybean did not reduce adult population density of the green weevil (*Hypomeces squamosus*); in fact, the richer host environment may have provided adequate nutrition for adults at different times, causing them to shift from soybean to sugarcane plants [47].

1.2 Effects of Crop Diversity on Pest Behavior

The impact and mechanisms of diversified cropping on farmland pests largely depend on pest biological characteristics and behavioral responses. Therefore, understanding how crop diversity affects pest behavior is essential for successful pest management. Many studies have shown that diversified planting primarily affects pest (herbivorous insect) settlement and reproduction by interfering with orientation, mating, oviposition, and dispersal behaviors, thereby influencing crop damage levels [48]. The authors have previously reviewed the effects of crop diversification on herbivorous insect behavior in detail [48], so this topic will not be elaborated here.

2.1 Effects of Crop Diversity on Natural Enemy Populations and Parasitism/Predation Rates

Crop diversification can significantly increase natural enemy populations. For example, compared to monocultures of carrot (*Daucus carota*) and onion (*Allium cepa*), predatory ground beetles (*Bembidion* spp.) and rove beetles (*Aleochara bipustulata*) that prey on carrot flies were captured in higher numbers in onion-carrot intercrops [32]. During the larval stage of cabbage root fly (*Delia brassicae*), although predatory ground beetles (Carabidae) and rove beetles (Staphylinidae) were captured at twice the rate in Brassica-non-Brassica intercrops compared to Brassica monocultures, their impact on reducing fly egg numbers was identical [49]. Sugarcane-maize intercropping significantly increased population densities of predatory lady beetles (Coccinellidae) [18], while pepper (*Capsicum annuum*) intercropped with sugarcane significantly increased populations of parasitoids attacking South American leafminer [*Diglyphus isaea*, *Opius* sp., *Hemiptarsenus varicornis*] [35]. In squash (*Cucurbita moschata*)-maize-pea (*Pisum sativum*) mixed stands, captured parasitoid numbers were more than double those in squash monoculture [38]. Intercropping tomato with cauliflower (*Brassica oleracea* var. *botrytis*) significantly increased numbers of the parasitoid *Cotesia plutellae* [34]. Intercropping wheat varieties with different resistance levels increased average numbers of aphid parasitoids [*Aphidius avenae*, *Aphidius gifuensis*] [25]. When cabbage was intercropped with faba bean and wild mustard (*Brassica kaber*), the field maintained six predatory and eight parasitic enemy species, whereas monoculture supported fewer natural enemies (only three predatory and three parasitic species) [50].

Crop diversification can also significantly enhance predation rates by predators and parasitism rates by parasitoids. For instance, onion and guar (*Cyamopsis tetragonoloba*) were identified as optimal intercrops for controlling major eggplant (*Solanum melongena*) pests. Acetone extracts of onion leaves and guar flowers significantly increased parasitism rates by *Trichogramma chilonis* (control: 50.3%; extract treatments: 82.7% and 74.3%) and predation rates by common green lacewing (*Chrysoperla carnea*) (control: 59.1%; extract treatments: 92.1% and 89.7%) [51]. Maize intercropped with sweet potato (*Ipomoea batatas*) also increased parasitism of Asian corn borer (*Ostrinia furnacalis*) eggs by *Trichogramma chilonis* [52]. In maize-chickpea (*Cicer arietinum*) intercrops, parasitism of stem borers by *Cotesia flavipes* increased with higher proportions of chickpea planting [10]. In squash-maize-pea mixed stands, 33% of melonworm (*Diaphania hyalinata*) eggs and 59% of larvae were parasitized, compared to only 11% and 29% in squash monoculture, respectively [38]. Summer maize intercropped with prostrate mung bean (*Vigna radiata*) significantly increased parasitism of Asian corn borer eggs by *Trichogramma ostriniae* [53], and pepper-sugarcane intercropping significantly increased parasitism of South American leafminer by parasitoids [*Diglyphus isaea*, *Opius* sp., *Hemiptarsenus varicornis*] [35].

However, some studies have found no effect of crop diversification on natural enemy numbers or parasitism/predation rates. For example, predation and parasitism rates showed no significant difference between cabbage-clover intercrops and cabbage monoculture [29]. Strip intercropping with soybean or maize also did not significantly increase populations of planthopper egg parasitoids [*Anagrus nilaparvatae*, *Anagrus paranilaparvatae*, *Anagrus longitubulosas*] [45].

2.2 Effects of Crop Diversity on Natural Enemy Behavior

The effects of crop diversification on natural enemies primarily manifest through impacts on mobility, orientation, searching behavior, and dispersal, which subsequently influence predation and parasitism rates.

Cage experiments with sorghum (*Sorghum bicolor*) intercropped with pigeon pea (*Cajanus cajan*) showed that the minute pirate bug (*Orius tantillus*) exhibited significantly higher mobility on sorghum flowers than on other plant parts or on pigeon pea. Consequently, predation of cotton bollworm larvae by *Orius tantillus* was stronger on sorghum than on pigeon pea [54]. In maize monoculture, the spotted lady beetle (*Coleomegilla maculata*) showed high predation rates on European corn borer egg masses, but this rate decreased when maize was intercropped with beans or squash. This occurred because *Coleomegilla maculata* spent more time searching for food on plants without egg masses (beans, squash), reducing foraging efficiency. Even when single-plant egg mass densities were identical between monoculture and intercropping, increased ineffective search time in intercropped systems significantly reduced predation rates on corn borer eggs. Another consequence of reduced searching efficiency was faster emigration of lady beetles from intercropped fields [55]. Predatory ground beetles and rove beetles attacking cabbage root fly were more active in cabbage monoculture than in cabbage-clover intercrops [29]. When cereal crops were intercropped with molasses grass (*Melinis minutiflora*), volatiles released by the grass attracted the stem borer parasitoid *Cotesia sesamiae* to hosts, significantly increasing parasitism rates [12,56]. Compared to soybean monoculture, fewer parasitoids (*Pediobius foveolatus*) of the Mexican bean beetle emigrated into and more emigrated out of soybean-tall maize intercrops. The height of maize was the main factor reducing parasitoid immigration into these intercropped systems [57].

3 Hypotheses and Theory on Mechanisms of Crop Diversity Effects on Insects

To date, seven hypotheses have been proposed to explain how diversified planting reduces populations of host-specific pests: (1) **physical obstruction**, (2) **visual camouflage**, (3) **masking of host plant odours**, (4) **repellent chemicals**, (5) **altering the profiles of host plant odours**, (6) **enemy hypothesis**, and (7) **resource concentration hypothesis**. The physical obstruction hypothesis suggests that tall non-host plants in intercrops can cover host plants, affecting visual orientation of pests and their dispersal in the field, thereby reducing herbivore numbers on host plants. The visual camouflage hypothesis proposes that pest landing during flight is determined by two visual stimuli: a direct response to color (typically green) and an optomotor response that causes pests to land on plants in their flight path. Other green plants or weeds above the background create competing visual stimuli with host plants, shortening the distance between host plants and background and creating visual camouflage. Host plant color becomes less conspicuous when surrounded by non-host plant leaves, ultimately reducing pest landings on host plants. The host plant odor masking hypothesis posits that odors released by non-host plants into the air can mask host plant volatiles, preventing pests from locating hosts and thereby protecting the host plants [58]. The repellent chemicals hypothesis suggests that odors released by non-host plants strongly repel host-seeking pests [32], reducing the number of pests orienting toward host plants. The plant odor profile alteration hypothesis proposes that host plants absorb certain chemicals from soil that they cannot produce themselves, which change the host' s physiological state and consequently affect pest populations on the host plant. The enemy hypothesis suggests that diversified cropping systems support greater numbers of parasitoids and predators with better predation and parasitism effects, thus suppressing herbivore outbreaks [59]. This is because, compared to monoculture, diversified cropping provides better living conditions for natural enemies, offers diverse pollen and nectar sources across multiple time periods to attract enemies and enhance their reproductive capacity, and provides alternative food sources that retain enemies in the system when primary pests are scarce. The resource concentration hypothesis proposes that pests prefer to settle and reproduce on concentrated host plant distributions. Diversified habitats containing both host and non-host crops result in less dense spatial distribution of host crops compared to monoculture, and the varying sizes, colors, and odors of different crops make it difficult for pests to land, remain, and reproduce on host crops [59].

Finch et al. [60] evaluated these seven hypotheses and proposed the **appropriate/inappropriate landings** theory. This theory suggests that host plant volatiles cause flying pests to land on them. If the area surrounding host plants consists of bare soil, pests land on the host plant as the only available landing object, since most pests avoid landing on brown surfaces like bare soil. When host plants are surrounded by bare soil, most landings are "appropriate landings," and host plants have an aggregating effect on pests. However, when non-host plants surround host plants, the entire ground is covered by both host and non-host vegetation, preventing flying pests from distinguishing between them. Pests also land on non-host plants, resulting in "inappropriate landings." Pests then use visual cues and perception of non-volatile plant compounds to decide whether to remain and oviposit on the landed plant. The presence of non-host plants interferes with these behaviors, leading to reduced pest numbers.

While these hypotheses and theories can partially explain the mechanisms by which diversified cropping affects pests, none can fully elucidate the ecological mechanisms of pest control through crop diversification.

4 Problems and Prospects

With increasing recognition of the urgency of biodiversity conservation, research on the effects of crop diversification on insects has advanced considerably in both depth and breadth in recent years. Notably, more studies are attempting to elucidate the mechanisms underlying the effects of diversified cropping on farmland pests and their natural enemies [24]. However, several aspects require strengthening: (1) There is a lack of effective field experimental evidence demonstrating that reduced pest numbers in diversified systems lead to increased crop yields, although some researchers are beginning to explore this [40]. (2) Many factors influence how crop diversification affects insects, yet most studies focus on only one or two factors. Comprehensive analysis of all factors is needed to identify both primary and secondary effects. (3) Global climate change is an undeniable reality that affects plant physiological functions, signaling molecules, and volatiles, severely impacting crop yields. Ozone also affects pest feeding preferences, behavior, growth, and development by altering plant primary and secondary metabolism, thereby influencing natural enemy fitness [61]. Climate change will inevitably affect pests and their enemies in diversified systems, but research on this topic remains scarce. (4) The scale of diversified planting and surrounding environmental features such as vegetation, buildings, and light/heat sources also significantly affect pests and natural enemies, but these aspects have received insufficient attention, particularly regarding accurate quantitative evaluation techniques. With advances in research technology, remote sensing, unmanned aerial vehicles, and image processing can now measure and assess the surrounding environment, enabling integrated analysis of environmental and crop factors. Incorporating habitat diversity factors alongside genetic and species diversity will yield more systematic and comprehensive understanding and facilitate development of more precise technical solutions for biodiversity-based pest management. (5) Quantitative studies on biodiversity effects on pests and enemies are needed. Pest control through diversified cropping can be slow or even delayed. Different plant growth stages affect different pest and enemy life stages differently, and crop effects on developmental processes are often quantitative. Therefore, research on diversified cropping requires systematic investigation of multiple factors and computer modeling to identify optimal spatiotemporal planting patterns that maximize the benefits of crop diversification. (6) Integration of diversified cropping with other environmentally friendly pest management techniques is essential. Multiple pest species may threaten a region within a single growing season, and single management techniques may not achieve effective control. Combining biodiversity-based approaches with other environmentally friendly techniques such as physical and biological control is necessary to effectively reduce chemical pesticide use while achieving high-quality, high-yield production.

References

[1] Zhu Y Y, Chen H R, Fan J H, et al. Genetic diversity and disease control in rice[J]. Nature, 2002, 406(6797): 718–722

[2] Li Z Y, Altieri M A, Zhu Y Y. Biodiversity and Integrated Pest Management[M]. Beijing: Science Press, 2009

[3] Hummel J D. Insect and agronomic responses in canola and wheat intercrops[D]. Edmonton, Alberta, Canada: University of Alberta, 2010: 4–9

[4] Bickerton M W. Intercropping for conservation biological control of European corn borer Ostrinia nubilalis Hübner (Lepidoptera: Crambidae) in bell peppers[D]. New Jersey, America: Rutgers, 2011: 1–20

[5] Wang Z Y, Su J P, Liu W W, et al. Effects of intercropping vines with tobacco and root extracts of tobacco on grape phylloxera, Daktulosphaira vitifoliae Fitch[J]. Journal of Integrative Agriculture, 2015, 14(7): 1367–1375

[6] Ugen M A, Wien H C. The effect of mixture proportions and fertilizer nitrogen on morphology, insect pest damage, competition and yield advantages in a maize/bean intercrop[J]. African Crop Science Journal, 1996, 4(l): 41–49

[7] Yue Y H. Preliminary observation on controlling cotton bollworm in soybean fields by intercropping with maize[J]. Bulletin of Agricultural Science and Technology, 1997(12): 22–23

[8] Chabi-Olaye A, Nolte C, Schulthess F, et al. Relationships of intercropped maize, stem borer damage to maize yield and land-use efficiency in the humid

forest of Cameroon[J]. Bulletin of Entomological Research, 2005, 95(5): 417-427

[9] Sekamatte B M, Ogenga-Latigo M, Russell-Smith A. Effects of maize-legume intercrops on termite damage to maize, activity of predatory ants and maize yields in Uganda[J]. Crop Protection, 2003, 22(1): 87-93

[10] Belay D, Schulthess F, Omwega C. The profitability of maize-haricot bean intercropping techniques to control maize stem borers under low pest densities in Ethiopia[J]. Phytoparasitica, 2009, 37(1): 43-50

[11] Skovgård H, Päts P. Reduction of stemborer damage by intercropping maize with cowpea[J]. Agriculture, Ecosystems & Environment, 1997, 62(1): 13-19

[12] Khan Z R, Ampong-Nyarko K, Chiliswa P, et al. Intercropping increases parasitism of pests[J]. Nature, 1997, 388(6643): 631-632

[13] Khan Z R, Pickett J A, van den Berg J, et al. Exploiting chemical ecology and species diversity: Stem borer and striga control for maize and sorghum in Africa[J]. Pest Management Science, 2000, 56(11): 957-962

[14] Holmes D M, Barrett G W. Japanese beetle (Popillia japonica) dispersal behavior in intercropped vs. monoculture soybean agroecosystems[J]. The American Midland Naturalist, 1997, 137(2): 312-319

[15] Mahadevan N R, Chelliah S. Influence of intercropping legumes with sorghum on the infestation of the stem borer, Chilo partellus (Swinhoe) in Tamil Nadu, India[J]. Tropical Pest Management, 1986, 32(2): 162-163

[16] Ampong-Nyarko K, Reddy K V S, Nyang' or R A, et al. Reduction of insect pest attack on sorghum and cowpea by intercropping[J]. Entomologia Experimentalis et Applicata, 1994, 70(2): 179-184

[17] Thirumurugan A, Koodalingam K. Management of borer complex in sugarcane through companion cropping under drought condition of Palar river basin area[J]. Sugar Tech, 2005, 7(4): 163-164

[18] Zhang H Y, Chen B, Li Z Y, et al. Effect of sugarcane plants intercropped with maize on population of Ceratovacuna lanigera Zehntner and Coccinellidae[J]. Southwest China Journal of Agricultural Sciences, 2011, 24(1): 124-127

[19] Tingey W M, Lamont W J Jr. Insect abundance in field beans altered by intercropping[J]. Bulletin of Entomological Research, 1988, 78(3): 527-535

[20] Basedow T, Hua L, Aggarwal N. The infestation of Vicia faba L. (Fabaceae) by Aphis fabae (Scop.) (Homoptera: Aphididae) under the influence of Lamiaceae (Ocimum basilicum L. and Satureja hortensis L.)[J]. Journal of Pest Science, 2006, 79(3): 177-181

[21] Li H J, Chen G H, Zhou H P, et al. Study on controlling Liriomyza sativae damage by intercropping broad bean with wheat in Kunming area[J]. Journal

of Yunnan Agricultural University, 2006, 21(6): 764-768

[22] Ma X M, Liu X X, Zhang Q W, et al. Assessment of cotton aphids, Aphis gossypii, and their natural enemies on aphid-resistant and aphid-susceptible wheat varieties in a wheat-cotton relay intercropping system[J]. Entomologia Experimentalis et Applicata, 2006, 121(3): 235-241

[23] Wang W L, Liu Y, Ji X L, et al. Effects of wheat-garlic or wheat-oilseed rape intercropping on population dynamics of Sitobion avenae and its main natural enemies[J]. Chinese Journal of Applied Ecology, 2008, 19(6): 1331-1336

[24] Zhou H B, Chen J L, Liu Y, et al. Influence of garlic intercropping or active emitted volatiles in releasers on aphid and related beneficial in wheat fields in China[J]. Journal of Integrative Agriculture, 2013, 12(3): 467-473

[25] Zhou H B, Chen J L, Liu Y, et al. Ecological regulation effect of wheat variety diversity on Sitobion avenae[J]. Acta Phytophylacica Sinica, 2009, 36(2): 151-156

[26] Forsythe T G. Successful Organic Pest Control: Environmentally Friendly Ways to Deal with Unwanted Garden Pests and Disease[M]. Wellingborough: Thorsons Publishers Ltd., 1990

[27] Madriaga C S. Abundance of diamondback moth Plutella xylostella L. and its natural enemies in different cabbage-based cropping systems[D]. Philippines: Philippines University, 1994

[28] Hooks C R R, Johnson M W. Population densities of herbivorous lepidopterans in diverse cruciferous cropping habitats: Effects of mixed cropping and using a living mulch[J]. BioControl, 2006, 51(4): 485-506

[29] Björkman M, Hambäck P A, Hopkins R J, et al. Evaluating the enemies hypothesis in a clover-cabbage intercrop: Effects of generalist and specialist natural enemies on the turnip root fly (Delia floralis)[J]. Agricultural and Forest Entomology, 2010, 12(2): 123-132

[30] Said M, Itulya F M. Intercropping and nitrogen management effects on diamondback moth damage and yield of collards in the highlands of Kenya[J]. African Crop Science Journal, 2003, 11(1): 35-42

[31] Adesiyun A A. Effects of intercrop on frit fly, Oscinella frit, oviposition and larval survival on oats[J]. Entomologia Experimentalis et Applicata, 1979, 26(2): 208-218

[32] Uvah I I I, Coaker T H. Effect of mixed cropping on some insect pests of carrots and onions[J]. Entomologia Experimentalis et Applicata, 1984, 36(2): 159-167

[33] Zhu P X, Liu M C, Qin Y C, et al. Control effects of intercropping celery in protected fields on greenhouse whitefly[J]. Chinese Bulletin of Entomology, 2011, 48(2): 375-378

[34] Xia N, Yang G, You M S. Regulation of dominant insect pests and natural enemies by intercropping tomato in cauliflower-based fields[J]. Acta Entomologica Sinica, 2015, 58(4): 391-399

[35] Chen B, Wang J J, Zhang L M, et al. Effect of intercropping pepper with sugarcane on populations of Liriomyza huidobrensis (Diptera: Agromyzidae) and its parasitoids[J]. Crop Protection, 2011, 30(3): 253-258

[36] Song J X, Shi A X, Zhang H X, et al. Effects of intercropping soybean and potato on control of Pseudaulacaspis pentagona and yield increase in Zanthoxylum bungeanum orchards[J]. Acta Phytophylacica Sinica, 2014, 41(2): 192-196

[37] DeGooyer T A, Pedigo L P, Rice M E. Effect of alfalfa-grass intercrops on insect populations[J]. Environmental Entomology, 1999, 28(4): 703-710

[38] Letourneau D K. The effects of vegetational diversity on herbivorous insects and associated natural enemies: Examples from tropical and temperate agroecosystems[D]. Berkeley: University of California, 1983

[39] Ramalho F S, Fernandes F S, Nascimento A R B, et al. Assessment of fennel aphids (Hemiptera: Aphididae) and their predators in fennel intercropped with cotton with colored fibers[J]. Journal of Economical Entomology, 2012, 105(1): 39-46

[40] de Sousa Ramalho F, Malaquias J B, dos Santos Brito B D, et al. Assessment of the attack of Hyadaphis foeniculi (Passerini) (Hemiptera: Aphididae) on biomass, seed and oil in fennel intercropped with cotton with colored fibers[J]. Industrial Crops and Products, 2015, 77: 511-515

[41] Umeozor O C, Bradley J R Jr, van Duyn J W, et al. Intercrop effects on the distribution of populations of the European corn borer, Ostrinia nubilalis, in maize[J]. Entomologia Experimentalis et Applicata, 1986, 40(3): 293-296

[42] McIntyre B, Gold C, Kashaija I, et al. Effects of legume intercrops on soilborne pests, biomass, nutrients and soil water in banana[J]. Biology and Fertility of Soils, 2001, 34(5): 342-348

[43] Helenius J. Insect numbers and pest damage in intercrops vs. monocrops: Concepts and evidence from a system of Faba bean, oats and Rhopalosiphum padi (Hornoptera, Aphididae)[J]. Journal of Sustainable Agriculture, 1991, 1(3): 57-80

[44] Åsman K, Ekbom B, Rämert B. Effect of intercropping on oviposition and emigration behavior of leek moth (Lepidoptera: Acrolepiidae) and the diamondback moth (Lepidoptera: Plutellidae)[J]. Environmental Entomology, 2001, 30(2): 288-294

[45] Yao F L, Zheng Y K, Lin S, et al. Effects of rice intercropped with soybean and maize in strips on the population abundance of rice planthoppers and their egg parasitoids, Anagrus spp.[J]. Journal of Fujian Agriculture and Forestry University: Natural Science Edition, 2012, 41(4): 459-464

[46] Cai Z P, Zhang D H, Li K F, et al. Effect of fruit-cotton intercropping on pest populations[J]. China Cotton, 2011, 38(4): 32-33

[47] Yang N B, Wu S R, Xiong G R, et al. Population distribution and food choice of Hypomeces squamosus in sugarcane-soybean intercropping[J]. Guangdong Agricultural Sciences, 2014, 41(13): 63-66

[48] Dong W X, Xu N, Xiao C. The effect of diversified cropping on phytophagous insect behavior[J]. Chinese Bulletin of Entomology, 2013, 50(4): 1133-1140

[49] Tukahirwa E M, Coaker T H. Effect of mixed cropping on some insect pests of brassicas; reduced Brevicoryne brassicae infestations and influences on epigeal predators and the disturbance of oviposition behaviour in Delia brassicae[J]. Entomologia Experimentalis et Applicata, 1982, 32(2): 129-135

[50] Altieri M A, Letourneau D K, Risch S J. Vegetation diversity and insect pest outbreaks[J]. Critical Reviews in Plant Sciences, 1984, 2(2): 131-169

[51] Elanchezhyan K, Baskaran R K M, Rajavel D S. Kairomone effect of acetone extracts of intercrops on Chrysoperla carnea (Stephens) and Trichogramma chilonis Ishii[J]. Journal of Entomological Research, 2009, 33(1): 51-54

[52] Nafus D, Schreiner I. Intercropping maize and sweet potatoes: effects on parasitization of Ostrinia furnacalis eggs by Trichogramma chilonis[J]. Agriculture, Ecosystems & Environment, 1986, 15(2/3): 189-200

[53] Zhou D R, Song Y Y, Wang Z Y, et al. Study on the preference habitat of Trichogramma ostriniae: Effect of summer corn intercropped with creeping type mungbean on parasitic rate[J]. Chinese Journal of Biological Control, 1997, 13(2): 49-52

[54] Sigsgaard L, Esbjerg P. Cage experiments on Orius tantillus predation of Helicoverpa armigera[J]. Entomologia Experimentalis et Applicata, 1997, 82(3): 311-318

[55] Wetzler R E, Risch S J. Experimental studies of beetle diffusion in simple and complex crop habitats[J]. Journal of Animal Ecology, 1984, 53(1): 1-19

[56] Gohole L S, Overholt W A, Khan Z R, et al. Effects of molasses grass, Melinis minutiflora volatiles on the foraging behavior of the cereal stemborer parasitoid, Cotesia sesamiae[J]. Journal of Chemical Ecology, 2003, 29(3): 731-745

[57] Coll M, Bottrell D G. Movement of an insect parasitoid in simple and diverse plant assemblages[J]. Ecological Entomology, 1996, 21(2): 141-149

[58] Tahvanainen J O, Root R B. The influence of vegetational diversity on the population ecology of a specialized herbivore, Phyllotreta cruciferae (Coleoptera: Chrysomelidae)[J]. Oecologia, 1972, 10(4): 321-346

[59] Root R B. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (Brassica olercea)[J]. Ecological Monographs, 1973, 43(1): 95-124

[60] Finch S, Collier R H. Host-plant selection by insects —A theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants[J]. Entomologia Experimentalis et Applicata, 2000, 96(2): 91-102

[61] Dong W X, Chen Z M. The effect of elevated ozone concentration on plants and insects[J]. Acta Ecologica Sinica, 2006, 26(11): 3878-3884

Note: Figure translations are in progress. See original paper for figures.