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Biology, Ecology, and Management of Flea Beetles in *Brassica* Crops

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Abstract

Brassica vegetable and oilseed crops are attacked by several different flea beetle species (Chrysomelidae: Alticini). Over the past decades, most research has focused on two *Phyllotreta* species, *Phyllotreta striolata* and *Phyllotreta cruciferae*, which are major pests of oilseed rape in North America. More recently, and especially after the ban of neonicotinoids in the European Union, the cabbage stem flea beetle, *Psylliodes chrysocephala*, has become greatly important and is now considered to be the major pest of winter oilseed rape in Europe. The major challenges to flea beetle control are the prediction of population dynamics in the field, differential susceptibility to insecticides, and the lack of resistant plant cultivars and other economically viable alternative management strategies. At the same time, many fundamental aspects of flea beetle biology and ecology, which may be relevant for the development of sustainable control strategies, are not well understood. This review focuses on the interactions between flea beetles and plants and summarizes the literature on current management strategies with an emphasis on the potential for biological control in flea beetle management.

INTRODUCTION

Flea beetles (Chrysomelidae: Galerucinae: Alticini) of the genera *Phyllotreta* and *Psylliodes* are major pests of *Brassica* crops worldwide. Research has focused primarily on three species, the striped flea beetle (SFB), *Phyllotreta striolata* (F.); the crucifer flea beetle (CFB), *Phyllotreta cruciferae* (Goeze); and the cabbage stem flea beetle (CSFB), *Psylliodes chrysocephala* L. (**Figure 1**). All of them are considered Palearctic species, with SFB and CFB thought to have been introduced to North America (91, 112). However, recent molecular phylogenetic analyses indicate that SFB is in fact a Holarctic species (7).

SFB and CFB are major pests of spring oilseed rape (SOSR) in North America and occur sympatrically in most regions (113, 118). In Europe, several additional *Phyllotreta* spp. attack SOSR and other *Brassica* crops, whereas CSFB is the major flea beetle pest of winter oilseed rape (WOSR) (85, 99). In many regions of Southeast Asia, SFB is the dominant flea beetle pest of *Brassica* vegetables, although in some regions, other *Phyllotreta* species may be more important (7).

Flea beetle control relies mainly on conventional methods, with available insecticides having limited efficacy due to the development of resistance in flea beetle populations (121, 140). In addition, the complex biology and ecology of flea beetles make the development of alternative management methods difficult. For example, adult flea beetles are highly mobile and can thus not only move quickly from plant to plant but also escape from natural enemies (54). *Phyllotreta* flea beetles additionally possess an effective host plant–derived chemical defense, which might explain why some biological control agents are not effective (19, 122). Many aspects of flea beetle–plant interactions, such as factors influencing host plant preference and performance, are not well understood, despite their importance in the selection or development of flea beetle–resistant cultivars. With a focus on the three key species introduced above and their impact on oilseed rape, this review provides an overview of our current understanding of flea beetle–plant interactions and management and identifies specific gaps in the current literature that are important for the development of sustainable control strategies.

FLEA BEETLE DAMAGE IN OILSEED RAPE CROPS

The greatest economic damage in SOSR by *Phyllotreta* spp. is usually inflicted at the seedling stage by adult feeding on cotyledons, stems, and leaves (29, 45, 84). Depending on the level of infestation, flea beetle damage can cause uneven plant growth, delayed development, reduced yield, or even seedling death (73). SOSR losses from *Phyllotreta* flea beetle damage are recurrent and result in extensive use of insecticidal seed treatments in the Canadian prairies (113, 118), with an estimated average of 10% yield losses per year and damage costs that may exceed $300 million annually in North America (77).

In the case of CSFB, both adults and larvae can cause significant damage in WOSR, depending on the immigration time and beetle density (99). Similar to *Phyllotreta* adults, intense CSFB adult feeding can destroy seedlings, especially in dry conditions when plants are not able to compensate for feeding damage. Greater economic importance is usually attributed to the feeding damage of larvae, which mine in petioles and stems and may destroy the shoot apical meristem (99, 143).

FLEA BEETLE–PLANT INTERACTIONS

Host Plant Range

All three flea beetle species are specialists with a host plant range restricted to the Brassicaceae family and a few species from closely related plant families of the order Brassicales (16, 49, 101). Within Brassicales, flea beetles clearly discriminate among different plant species, with feeding

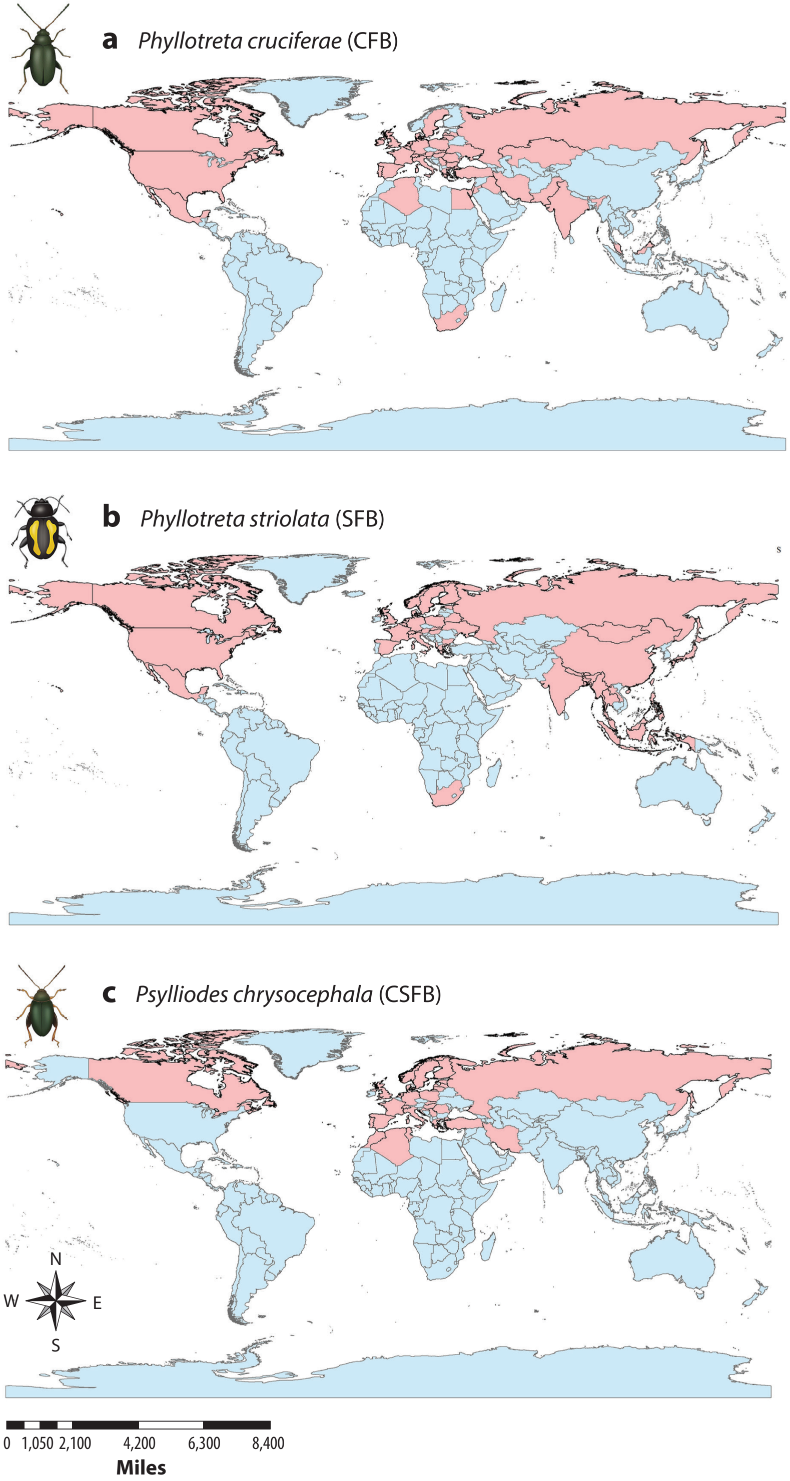

Figure 1

Distribution of the crucifer flea beetle (CFB), *Phyllotreta cruciferae*; the striped flea beetle (SFB), *Phyllotreta striolata*; and the cabbage stem flea beetle (CSFB), *Psylliodes chrysocephala*, based on the CABI Digital Library (**https://www.cabidigitallibrary.org**) and the EPPO Global Database (**https://gd.eppo.int/**).

preferences depending additionally on plant developmental stage and beetle life stage, among other factors (16, 59, 101, 137). Studies with CFB and SFB populations from North America suggest that both species have similar host preferences, with CFB possibly being less discriminating than SFB (76, 101).

Host plants of flea beetles contain mustard-oil glucosides (glucosinolates), which, together with plant β-thioglucosidase enzymes (myrosinases), form a two-component defense system characteristic of Brassicales (21). Upon herbivory, glucosinolates are hydrolyzed by myrosinases to an unstable aglucone intermediate from which different toxic and deterrent end products can arise. Isothiocyanates are particularly harmful for nonadapted herbivores because they impair nutrition and redox homeostasis (68, 69). Although specialist flea beetles are obviously adapted to this chemical plant defense, there is evidence that high levels of myrosinase activity can negatively influence CFB feeding in field conditions (93).

Flea Beetle Adaptations to the Glucosinolate–Myrosinase System

Recent research has demonstrated that *Phyllotreta* actively accumulate (sequester) ingested glucosinolates up to 2% of their body weight. Additionally, they possess endogenous myrosinase activity, which likely enables them to use sequestered glucosinolates for their own protection (19). The closely related horseradish flea beetle (*Phyllotreta armoraciae*) also possesses a glucosinolate–myrosinase system that was shown to protect larvae against a generalist predator (122). The sequestration of ingested glucosinolates is presumably facilitated by a rapid glucosinolate uptake mechanism and manipulation of plant myrosinase activity in the beetle gut, which may at least partially prevent glucosinolate hydrolysis by plant myrosinases (123, 151).

CSFB adults and larvae can also sequester ingested glucosinolates, but glucosinolate levels in this species are much lower than in *Phyllotreta*. Furthermore, there was no evidence for endogenous myrosinase activity in CSFB, which is therefore unlikely to benefit from sequestered glucosinolates as do *Phyllotreta* spp. (20). In addition to sequestration, CSFB adults are able to detoxify glucosinolates by enzymatic desulfation, whereas no glucosinolate sulfatase activity was detectable in *Phyllotreta* spp. (2, 19, 20). Although CSFB can prevent glucosinolate hydrolysis by plant myrosinases through sequestration and desulfation, some ingested glucosinolates are still hydrolyzed in the beetle gut, exposing adults to reactive isothiocyanates and other hydrolysis products. Isothiocyanates are mainly detoxified via the conserved mercapturic acid pathway, but the gut microbiota can also contribute to isothiocyanate detoxification (20, 114).

Impact of Glucosinolates on Flea Beetle–Plant Interactions

Both glucosinolates and their hydrolysis products play additional roles in flea beetle ecology. Glucosinolates stimulate flea beetle feeding (15, 63, 95) and are thus likely involved in host plant recognition and acceptance. Volatile glucosinolate hydrolysis products are known to attract *Phyllotreta* flea beetles and CSFB (49, 108). However, the doses of hydrolysis products required to attract high flea beetle numbers greatly exceed those emitted by individual or small groups of plants under natural conditions (108), making it unlikely that glucosinolate hydrolysis products released by intact or damaged host plants are important cues for host finding. Nevertheless, isothiocyanate-baited traps are still useful for monitoring flea beetle abundance in the field (139).

Several studies have investigated the impact of glucosinolates on host preference of flea beetles, but their findings are inconsistent. While field experiments with different *Brassica napus* lines revealed a positive correlation between CSFB feeding damage and total glucosinolate content in leaves (56), laboratory bioassays found no relationship between glucosinolate content in *B. napus* cotyledons and CSFB feeding (14). Moreover, the performance of CSFB larvae did not correlate with total glucosinolate levels in different brassicaceous plants (43). For CFB adults, *Brassica rapa* lines with intermediate glucosinolate contents showed the highest feeding damage in the field (115), whereas *Brassica juncea* lines differing in glucosinolate contents by up to 17-fold showed similar feeding damage (25). In addition, CFB adults did not discriminate between wild-type *Arabidopsis thaliana* and a transgenic line with fourfold higher glucosinolate content (96).

Other Plant Defenses

Several other classes of secondary metabolites are known to influence flea beetle feeding behavior. Cucurbitacins, cardiac glycosides, and saponins have been proposed to act as feeding deterrents and to be responsible for antixenosis resistance of several plant species, including *Iberis amara*, *Erysimum* spp., *Lunaria annua*, *Thlaspi arvense*, and *Capsella bursa-pastoris* (16, 49, 88, 95, 129). There is also evidence that flavonoids play a role in flea beetle feeding (59, 78, 98). In tests with commercially available flavonoid aglycones, some compounds deterred flea beetle feeding, while others stimulated feeding (98).

Several plant species, including *Crambe abyssinica* Hochst, *Camelina sativa* L., and some *Sinapis alba* L. cultivars, are not preferred by *Phyllotreta* flea beetles (5, 53, 64, 101, 107, 117), but the traits that are responsible for antixenosis resistance have not yet been identified. Analyses of the prefeeding behavior of CFB adults on host and nonhost plants suggest that volatile compounds deter feeding on *S. alba*, whereas nonvolatile compounds deter feeding on *C. abyssinica* (61). In a screening of 308 *S. alba* × *B. napus* hybrid lines obtained via embryo rescue, one line showed increased resistance against flea beetle feeding (53), indicating that *S. alba* is a promising resource for introgressing resistance into *Brassica* crops.

Leaf epicuticular waxes and trichomes are other traits that influence the susceptibility of plants to flea beetle herbivory (24, 100, 121). Thick and continuous layers of wax on the leaf make it difficult for the beetles to adhere to the surface and hinder access to nutritious leaf tissue (24, 46). Similarly, the presence of trichomes on the leaf surface can act as a physical barrier (100, 121). In laboratory and field experiments, CFB adults fed less on transgenic *B. napus* expressing *Arabidopsis GL3* with elevated trichome density on stems, petioles, and first and second true leaves than on the corresponding wild type (61, 121). Simultaneous knockdown of the regulatory gene *BnTTG1* resulted in a hairy *B. napus* line with yields that were comparable to those of the wild type in the field (3).

In addition to constitutive plant resistance, plants may also induce a defense response, which can deter herbivory or negatively affect herbivore performance. In Brassicaceae, the levels of induced resistance were shown to vary considerably between different plant species and even between different trials. For example, induced resistance was observed in *S. alba*, but not in *B. rapa* and *B. juncea* (23, 26, 102). In experiments using the same *B. napus* cultivar, two studies found reduced CFB feeding on damaged seedlings (23, 26), whereas a third study found no significant effects on damaged seedlings (102). In *Brassica nigra*, induced responses did not influence the feeding rate of CFB adults but did result in higher mortality of CFB adults compared to control plants (132). In addition, a weak negative impact on beetle growth was observed in one out of two maternal families (132). In a field study with wild radish, *Raphanus raphanistrum*, induced plants suffered increased flea beetle herbivory, suggesting that induced responses do not protect this plant against flea beetles (1).

Aggregation Behavior

Phyllotreta flea beetles are known to aggregate on host plants, a behavior that is mediated by a male-produced aggregation pheromone that attracts both males and females (18, 106). Beetle aggregations facilitate mate finding but may also be important in host plant location (51, 141). In addition, a role in host plant utilization has been proposed based on the observation that CFB adults feeding in groups consumed significantly more plant tissue per beetle compared to adults feeding individually (107). The underlying mechanism is still unknown, but suppression of plant defense responses could be one possible explanation.

Headspace analyses revealed that feeding males emit species-specific blends of sesquiterpenes that may function as aggregation pheromone components (12, 13, 17, 18, 130). For example, CFB males emit six different compounds (12), three of which elicited electrophysiological responses from beetle antennae (131). Synthetic blends comprising five out of six male-specific compounds attracted male and female CFB adults in field-trapping experiments in North America (119), while studies with different subsets of these five compounds indicated that one of them, (*6R*,7*S*)-himachala-9,11-diene, constitutes the major aggregation pheromone component of a European CFB population (131). The male-specific sesquiterpene blends of CFB and SFB males differ strongly, and there is additional evidence for minor differences between Asian and North American SFB populations (13, 17). The major sesquiterpene produced by SFB males, (*6R*,7*S*)-10-hydroxyhimachalan-9-one (hydroxyketone below), is unique to this species (12, 13) and is likely biosynthetically derived from (*6R*,7*S*)-himachala-9,11-diene, the second-most abundant compound found in headspace samples from SFB males (13, 17). Both compounds elicited electrophysiological responses from SFB adult antennae and were behaviorally active in laboratory and field experiments (13, 17, 139). SFB adults from an Asian population preferred a blend of (*6R*,7*S*)-himachala-9,11-diene and hydroxyketone over the individual compounds in two-choice assays, suggesting that the blend of both components constitutes the aggregation pheromone (17). A series of field trials in different locations in the United States suggested the hydroxyketone to be the major aggregation pheromone compounds of North American SFB populations and found a location-specific impact of (*6R*,7*S*)-himachala-9,11-diene on flea beetle responses (139).

Although there is clear evidence for a function of male-produced sesquiterpenes in aggregation behavior, synthetic blends of these compounds were often only marginally attractive in field-trapping experiments or even required combination with high doses of allyl isothiocyanate or 3-butenyl isothiocyanate to attract flea beetles (17, 119, 130, 131, 139). It is thus likely that attraction to the sesquiterpene aggregation pheromone requires the presence of additional currently unknown volatile compounds. Possible candidates are the green leaf volatiles *Z*-3-hexen-1-ol and 1-hexanol and the monoterpenes (+)-sabinene and *E*-β-ocimene, which attracted CFB adults in olfactometer studies (57).

Population Ecology

Several studies investigated the influence of habitat properties and patch size on the abundance of *Phyllotreta* flea beetles on host plants (32, 71, 125). A hallmark study published in 1972 demonstrated a higher abundance of CFB adults on *Brassica oleracea* (common cabbage) plants grown in monocultures than on *B. oleracea* grown in more diverse plant communities (125). In addition, monocultures were shown to be colonized more rapidly and suffer from higher feeding damage. The associational resistance of *B. oleracea* growing in complex plant communities was attributed primarily to odors from nonhost plants that interfered with host colonization, whereas natural enemies appeared to have a negligible influence on the differential abundance of flea beetles (125). In agreement with these findings, the cocultivation of some nonhost plant species with *Brassica* crops significantly reduced numbers of adult SFB and CFB on the main crop in field trials, which demonstrates the potential of nonhost plants in mixed cropping systems to control of *Phyllotreta* spp. (79).

Flea beetle abundance on host plants is influenced not only by colonization rates, but also by emigration rates. SFB and CFB adults that were released in single-plant patches were much less likely to stay on the plant than adults that were released on groups of plants, suggesting that *Phyllotreta* spp. require a critical patch size to establish a population (71). The impact of habitat and patch size on flea beetle abundance is consistent with the resource concentration hypothesis according to which "herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands" (111, p. 95).

Besides the spatial distribution of host plants, feeding by other herbivores also influences densities of *Phyllotreta* spp. on host plants. For example, higher densities of *Phyllotreta undulata* and *Phyllotreta atra* were recorded on *B. oleracea* plants that had been induced early in the season by feeding of *Pieris brassicae* L. (Lepidoptera: Pieridae) caterpillars than on undamaged plants (32). In contrast, significantly fewer adults of *P. undulata* and *Phyllotreta diademata* were recorded on *B. nigra* plants infested with the root herbivore *Delia radicum* (the cabbage root fly, Diptera: Anthomyiidae) than on uninfested plants (116). Which plant responses underlie the preference of *Phyllotreta* spp. for damaged or undamaged host plants is unknown.

MANAGEMENT OF FLEA BEETLES

Flea beetles are controlled mainly by using insecticides (85, 99, 118). Adult flea beetle damage to oilseed rape (OSR) is very fast and difficult to monitor in large fields (120), and there is currently a lack of forecasting models that allow growers to predict economically damaging populations that require treatment (99, 113). Therefore, farmers in North America and Europe traditionally used prophylactic applications of in-furrow granules or seed-coated systemic insecticides to control flea beetles in OSR (72, 74, 85, 118, 120, 134). Since the mid-1990s, nearly all OSR seeds planted in Canada have been treated with systemic neonicotinoid insecticides, which are effective in reducing flea beetle damage to seedlings, usually for up to three weeks (72, 113). Thus, protection against late-emerging flea beetles often requires 2–3 foliar insecticide applications or replanting of the field (72, 113). In China, seed treatments began after 2000 and are preferred by local growers over conventional foliar sprays because they provide extended protection of SOSR seedlings over three weeks and reduce labor costs (40). In Europe, neonicotinoid seed treatments were also the main method used to control adult CSFB in OSR until they were banned in 2013 (66, 99). Since then, farmers have opted to grow alternative crops due to severe infestations by CSFB, and the area planted with OSR has drastically decreased in several countries (6, 42), although in others, such as Sweden, the planted area has not changed (85). In this country, where *Phyllotreta* flea beetles are major pests in SOSR, a shift to WOSR maintained the total OSR production at similar levels as before the ban (85). However, shifting from SOSR to WOSR is more difficult in other regions with colder winters.

Economic thresholds are used in various crops to trigger foliar sprays of insecticide against flea beetles. When prophylactic seed insecticide treatments fail, a nominal threshold of 25% defoliation before the four-leaf stage of SOSR is used for foliar sprays against *Phyllotreta* flea beetles in North America (35); however, recent experiments suggest reducing this threshold to 15–20% defoliation (126). Similarly, an economic injury level of 11% defoliation has been recently proposed for Sweden, mainly based on the low price of pyrethroid insecticides (84). In Europe, economic thresholds for CSFB in OSR vary per country, in part due to variable resistance to insecticides, and are separate for adult and larval stages (99). For adult control, the most common economic thresholds used are 2 (range 1–3) adults/m^2, 0.5 adults per linear meter, 15 adults per day or 50 adults every 3 weeks in yellow water traps, 10% defoliation before the four-leaf stage, and 50% (range 25–80%) of plants damaged (99). For larval control, targeting newly emerged larvae or early stages moving between petioles, the most common economic thresholds are 2–3 larvae per plant, 7 out of 10 plants with larvae, and 50–100 adults every 3 weeks in yellow water traps (99). These thresholds are mainly based on insecticide costs and yield returns, with little knowledge on how OSR can compensate for CSFB damage and on the impact on natural enemies and pollinators (99).

Insecticide Resistance

Flea beetles were historically managed with seed dressings, granular applications, and foliar sprays of organochlorine, organophosphorus, and carbamate insecticides in Asia, Europe, and North America (82, 134, 142). However, due to the repeated use of these insecticides, which led to the development of resistance in various species (134, 147), and the high toxicity of some products, which led to their banning (99, 142), there was a shift toward the use of neonicotinoids, especially for seed treatments, and pyrethroids, especially for foliar applications, in most crops (99, 113).

More recently, the overuse of prophylactic controls of various pests in OSR, especially pollen beetle, lead to the development of pyrethroid resistance in CSFB in Europe (60, 66, 143). Resistance to pyrethroids was first reported in Germany in 2008, with a 81-fold resistance ratio for CSFB (60). Since 2013, neonicotinoid insecticides have been banned in Europe due to their alleged harmful effects on bees, which, along with the lack of effective alternative insecticides, has led to exacerbated resistance to pyrethroid insecticides (66, 143). CSFB resistance to pyrethroids has also been found in Denmark, the United Kingdom, France, and the Czech Republic (66, 99, 124). Today, despite multiple records of resistance, pyrethroids are the only class of insecticides whose use is permitted for chemical control of flea beetles in most European countries (85, 99, 143). Resistance of CSFB to pyrethroids is due to the L1014F kdr (knockdown resistance) mutation in the voltage-gated sodium channel (143, 153). Additionally, metabolic resistance, probably due to cytochrome P450 enzymes (66, 143), and resistance due to the L952I superkdr mutation (143) have been recently reported.

Despite mounting evidence of potential environmental issues associated with their persistence, high leaching and runoff potential, and toxicity to invertebrates (38, 94), neonicotinoids continued to be widely used in Canada as prophylactic systemic seed treatments against CFB and SFB (113, 118), resulting in a strong selection pressure on flea beetles. Laboratory studies have demonstrated that SFB has lower mortality and causes more damage to SOSR than CFB when exposed to the neonicotinoids thiametoxan and clothianidin, suggesting the development of tolerance to neonicotinoids in SFB (127, 128). Indeed, SFB has increased in frequency in various regions of the Canadian prairies that were previously dominated by CFB. This suggests that this tolerance may give it a competitive advantage over CFB and potentially reduce the effectiveness of neonicotinoid seed treatments to reduce flea beetle damage in OSR (118, 128). Additionally, tolerance of CSFB to the neonicotinoid thiacloprid has been shown in the Czech Republic (124). Alternative seed treatments, such as diamide and sulfoxamine, are currently available as seed treatments in Canada (85) and may contribute to reducing selection pressure on resistance to neonicotinoids.

Sustainable Control Strategies

Numerous studies have investigated sustainable management strategies to reduce the damage of flea beetles, including the development of resistant cultivars; alteration of seeding rates, planting dates, row spacing, and tillage regimes; mixed cropping; and use of natural enemies. Despite these efforts, most flea beetle species are managed using insecticides, with more sustainable techniques playing only a minor role in current integrated pest management (IPM) programs. In this section, we discuss some of the potential sustainable management methods that have received the most attention, including cultural controls and the use of biological control agents.

Cultural control. The development of resistant cultivars against flea beetle damage has been examined in OSR and related species. Early research has shown both antixenosis and tolerance in *S. alba*, antixenosis in *Brassica carinata* and some lines of OSR, and tolerance in *B. juncea* against CFB (28, 53, 75, 103, 117). As mentioned above, morphological traits such as trichomes and leaf epicuticular wax affect the behavior of flea beetles and reduce their feeding (24, 121). Transgenic SOSR expressing elevated hairiness (hairy canola) resulted in lower *Phyllotreta* damage than controls in both laboratory and field trials and could be used in the development of future resistant cultivars (3, 121). Despite the potential of resistant traits present in *Brassica* crops, no commercial cultivars of OSR with flea beetle resistance are currently available (62).

Higher seeding rates of OSR reduced *Phyllotreta* damage per plant in Canada (44, 45) and showed a similar trend in Sweden (86). In Europe, CSFB damage and abundance was reduced in fields with increased plant densities of OSR (99). This reduction in damage has been attributed to a dilution effect of more plants present per unit of area (45, 99). Although doubling seeding rates of untreated seed had produced the same yield as normal seeding rates with seed insecticidal treatments (45), the high cost of the seed, the potential for lodging and susceptibility to disease, and the potential increase of CSFB larvae are currently barriers to fully adopting this technique (86, 99).

Varying the planting date affects damage caused by flea beetles in various ways. In general, earlier SOSR planting dates resulted in lower flea beetle abundance in Manitoba, Canada (73) and a reduction in damage in southern Alberta, Canada (36) and in Sweden, even with measurable yield gains (86, 87). However, more flea beetles (90) and higher damage were observed with early planting dates in North Dakota (72) and in central and northern Alberta (36). These variable effects have been attributed to different species assemblages among regions, which could result in different responses to environmental conditions that affect flea beetle feeding and plant growth (36, 87). WOSR has the advantage that it grows very quickly in spring and typically receives less *Phyllotreta* damage (36, 45); however, the high risk of mortality due to harsh winters limits the use of this technique in much of the OSR planted area (87). Early planting of WOSR allows better crop establishment and reduces damage by adult CSFB but also increases susceptibility to larval damage, and more research is required before this technique can be adopted by farmers (99).

Zero-tillage regimes effectively reduced flea beetle abundance and damage in SOSR in North America (44, 81, 90) and Sweden (83) but did not affect yield (81, 83). Reduced tillage decreased abundance of CSFB in WOSR in France (136) but did not reduce flea beetle damage in SOSR in Sweden (87). Zero-tillage regimes may have more crop residues than reduced-tillage or conventional tillage regimes, which may interfere with the location of seedlings by flea beetles, and create a more humid and cooler environment, which limits flea beetle activity and increases populations of natural enemies (83, 99). Although studies of zero-tillage regimes show that they have great promise in reducing flea beetles in OSR, the adoption of this technique is limited by other agronomic factors, including negative effects on crop germination or emergence and yield, higher herbicide requirements, and increased potential for diseases (81, 83). Wider row spacing, both in zero-tillage regimes and conventional tillage, led to less flea beetle damage in Alberta, but the potential mechanisms behind this pattern remain unclear (44).

The use of nonhost plants (*Vicia faba* L., *Vicia villosa* Roth, *Allium fistulosum* L., *Solanum melongena* L., *Hordeum vulgare* L., *Artemisia abrotanum* L., *Artemisia absinthium* L., and *Tanacetum vulgare* L.) and wild hosts (*Sinapis arvensis* L.) on field borders or in intercropping practices reduced the abundance and damage of *Phyllotreta* flea beetles on vegetable *Brassica* crops (4, 52, 79). In addition, fields under mixed-crop regimes had higher abundance of natural enemies and higher evenness and diversity of the arthropod community (146). However, another study showed that, in cases of high flea beetle abundance and despite reduced damage, collards mixed with other vegetable crops showed a yield reduction compared to monocultures, probably due to competition between crops (80). Mixed-cropping of spring OSR with field peas or wheat failed to reduce flea beetle abundance and reduced OSR yield compared to monocultures in North America (140). By contrast, faba bean (*V. faba*) and grass pea (*Lathyrus sativus*) mixed with WOSR reduced CSFB larval abundance in Switzerland (30).

The use of *B. rapa* as a trap crop to manage flea beetles showed potential in several studies. Field experiments in the United Kingdom showed that a *B. rapa* border trap crop reduced the abundance of CSFB in OSR (11) and damage by *Phyllotreta* flea beetles on *B. oleracea* var. Lateman (55). In North America, trap crops mixing *B. juncea*, *B. napus*, and *B. rapa* improved yield of *B. oleracea* var. *italica* by changing the behavior but not the density of CFB (104). Similarly, mixtures of trap crops that remain attractive throughout the field season have been proposed to manage *Phyllotreta* flea beetles in SOSR in Estonia (*B. juncea*, *B. nigra*, *Eruca sativa* Mill., and *Raphanus sativus* L.) (89) and in *B. oleracea* convar. *capitata* in Slovenia (*S. alba*, *B. napus*, and *R. sativus*) (27).

Biological control. The overall reliance on insecticides to manage flea beetles in most crops resulted in relatively few studies on incorporating biological control agents into their IPM programs. Recent efforts have focused on using entomopathogenic nematodes (EPNs) and entomopathogenic fungi (EPFs), which can more easily be combined with current management techniques. Other microorganisms do not seem to be effective biological control agents. *Bacillus thuringiensis* subspecies *tenebrionis* caused low mortality on CSFB (99) and does not seem to be promising (65), although several strains have been patented against CFB in the United States (105). No effective protozoans have been reported against CSFB (99) or other flea beetles (47).

Commercially available EPNs in the genera *Steinernema* (Rhabditida: Steinernematidae) and *Heterorhabditis* (Rhabditida: Heterorhabditidae) have shown promising results against *Phyllotreta* spp. and CSFB. *Steinernema feltiae* reduced damage and protected SOSR yield against CFB when combined with a polymer gel in Montana (10, 31). This species also caused mortality of *Phyllotreta* flea beetles in laboratory trials in Slovenia (133) and in field trials in Estonia and Finland (67) and reduced CSFB numbers in field trials in the United Kingdom and Sweden (67). In Montana, *Steinernema carpocapsae* reduced CFB damage in some studies (110) but not in others (10). This species was also effective in controlling SFB numbers in laboratory experiments (148) and in field plots with cabbage (*B. rapa* and *Brassica campestris*) in China (149) and with radish in Japan and Thailand (65, 97). However, it failed to control SFB larvae and adults in plots with *B. campestris* in a more recent study (150). Additionally, *Steinernema pakistanense* suppressed SFB in both laboratory (148) and field conditions in China (150), and *Steinernema siamkayai* suppressed SFB in Thailand (97). *Heterorhabditis indica* increased mortality of SFB in the laboratory (97, 148) and reduced SFB abundance and damage in the field on *Brassica* crops in China (149, 150) and Thailand (97). Finally, both *Heterorhabditis bacteriophage* and *Heterorhabditis megidis* showed potential to control *Phyllotreta* spp. in laboratory studies (133). Although there is clear potential for using EPNs to control flea beetles, more studies are needed to assess how they interact with insecticides and fungicides, other biological control agents, and abiotic factors before farmers can implement them into IPM programs (65).

Relatively few studies have explored the potential of EPFs against flea beetles. A laboratory study showed 50–90% mortality of CFB exposed to *Beauveria bassiana* (Balsamo) Vuillemin (92), but mortality was below 40% in other laboratory studies (8), and no reduction of OSR damage was found in field studies in Montana using the commercial form of *B. bassiana*, BotaniGard ES (Emerald BioAgriculture Corp., Lansing, Michigan) (9). However, a follow-up field study found that two sprays with combined *B. bassiana* and *Metarhizium brunneum* (Metchnikov) reduced CFB damage and protected OSR from yield loss (110). The fungi *Isaria javanica* (IsjaHN3002), *Aspergillus* spp., *Fusarium falciforme*, *Lecanicillium* spp., *Metarhizium* spp., and *Talaromyces* spp. showed pathogenicity against SFB in China (152). *Isaria javanica* caused the highest mortality and has the highest potential as a biocontrol agent (152). Two isolates of *M. anisopliae* s. l. (*brunneum*) (Metchnikov) also caused high mortality in CSFB (73–88% mortality) in laboratory studies (34), and further studies are in progress with additional EPF isolates and species (99).

Parasitoids and predators are not currently incorporated into any management system for flea beetles. Six species of parasitoids were found in Europe attacking CSFB (70, 135). The most abundant one, *Tersilochus microgaster* (Szépligeti) (Hymenoptera: Ichneumonidae), had a strong spatial association with CSFB (50) and resulted in up to 57% parasitism across Europe (135). Other species, including the ichneumonid *Aneuclis melanaria* (Holmgren), the braconids *Diospilus morosus* (Reinhardt) and *Diospilus oleraceus* (Haliday), and the pteromalid *Trichomalus lucidus* (Walker), caused negligible parasitism (135). More recently, the braconid *Microctonus brassicae* (Haeselbarth) resulted in 44% parasitism on CSFB in laboratory conditions and shows promise as a potential biological control agent for this pest in OSR in the United Kingdom (70). In North America, several parasitoid species attack flea beetles, including the braconids *Townesilitus psylliodis* (Loan) and *Microctonus punctulatae* sp. n., which attack *Psylliodes punctualata* Melsh, and *Microctonus pusillae* Muesebeck and *Microctonus brevipetiolatus* (Thomson), which attack CFB, SFB, and *Phyllotreta conjuncta* Gent (145). In Canada, the most common parasitoid of *Phyllotreta* flea beetles in SOSR is *Microctonus brevipetiolatus* (previously *Microctonus vittatae* Muesebeck; 109), but this species typically causes only <5% parasitism (144, 145). The braconid *Townesilitus bicolor* (Wesmael) parasitizes up to 50% of *Phyllotreta* flea beetles in Europe but failed to establish in North America (144).

Little is known about predators attacking flea beetles. Using molecular methods, Ekbom et al. (48) found that 19.4% of the spiders *Pardosa* spp. (Aranae: Lycosidae) and 10% of the spiders *Phylloneta impressa* (Koch) (Aranae: Theridiidae) were positive for *Phyllotreta* spp. DNA in OSR in Sweden. The carabids *Trechus quadristriatus* (Schrank) and *Pterostichus madidus* (Fabricius) showed strong spatial associations with CSFB larvae in OSR in the United Kingdom, and *T. quadristriatus* consumed CSFB eggs in the laboratory (138). In North America, field observations indicate predation of flea beetles by big-eyed bugs, lacewings, nabids and pentatomids, and crickets (33, 41). In addition, the activity density and evenness of noninvasive ground predators (predatory beetles, spiders, and ants) have negative associations with the abundance of CFB in organic broccoli crops in North America (22). Agronomic activities, such as tillage, crop rotation, and high insecticide use, are likely the main factors associated with the low impact of parasitoids and predators on flea beetle populations (70, 99). Further studies are needed on the integration of natural enemies into IPM programs, especially within conservation biological control strategies.

CONCLUSIONS AND OUTLOOK

In this article, we review many significant advances in our understanding of plant–flea beetle interactions and of sustainable agricultural practices that can be used to reduce flea beetle damage to crops. However, more research on how to incorporate this knowledge into IPM programs for *Brassica* crops is warranted. For example, management strategies such as mixed-cropping systems have only been tried in vegetable *Brassica* crops, and other techniques, such as cover crops, have not yet been investigated. First, more research on the molecular genetics and neurotoxicology of flea beetles is needed to elucidate the molecular mechanism of resistance of flea beetles to insecticides and to lay the theoretical foundation for developing new methods of resistance management. Second, more efforts should be allocated to using our extensive understanding of flea beetle–plant interactions to develop resistant varieties that reduce flea beetle damage to *Brassica* crops. Currently, although morphological traits have been found to reduce feeding by flea beetles in OSR, these are not yet available in commercial cultivars. Third, more research is needed into incorporating natural enemies, including of EPNs and EPFs, into IPM programs and the role of habitat management in conservation biological control programs at local and landscape scales. Fourth, emerging technologies such as RNA interference, based on lethal genes found in SFB (39, 58) and CSFB (37), should be explored to develop more specific biopesticides. Fifth, effective control of flea beetles requires the establishment of a comprehensive prediction and forecasting system. In terms of field monitoring and early warning, modern information technology such as big data analysis, cloud computing, and machine learning can be used to support the improvement of prediction accuracy and, combined with sustainable control methods, decrease the current reliance on prophylactic insecticidal controls.

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LITERATURE CITED

1. Agrawal AA, Sherriffs MF. 2001. Induced plant resistance and susceptibility to late-season herbivores of wild radish. *Ann. Entomol. Soc. Am.* 94:71–75
2. Ahn S-J, Betzin F, Gikonyo MW, Yang Z-L, Köllner TG, Beran F. 2019. Identification and evolution of glucosinolate sulfatases in a specialist flea beetle. *Sci. Rep.* 9:15725
3. Alahakoon U, Adamson J, Grenkow L, Soroka J, Bonham-Smith P, Gruber M. 2016. Field growth traits and insect-host plant interactions of two transgenic canola (Brassicaceae) lines with elevated trichome numbers. *Can. Entomol.* 148:603–15
4. Altieri MA, Schmidt LL. 1986. Population trends and feeding preferences of flea beetles (*Phyllotreta cruciferae* Goeze) in collard-wild mustard mixtures. *Crop Prot.* 5:170–75
5. Anderson MD, Peng C, Weissl MJ. 1992. Crambe, *Crambe abyssinica* Hochst., as a flea beetle resistant crop (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 85:594–600
6. Andert S, Ziesemer A, Zhang H. 2021. Farmers' perspectives of future management of winter oilseed rape (*Brassica napus* L.): a case study from north-eastern Germany. *Eur. J. Agron.* 130:126350
7. Anooj SS, Raghavendra KV, Shashank PR, Nithya C, Sardana HR, Vaibhav V. 2020. An emerging pest of radish, striped flea beetle *Phyllotreta striolata* (Fabricius), from Northern India: incidence, diagnosis and molecular analysis. *Phytoparasitica* 48:743–53
8. Antwi FB, Olson DL, Carey DR. 2007. Comparisons of ecorational and chemical insecticides against crucifer flea beetle (Coleoptera: Chrysomelidae) on canola. *J. Econ. Entomol.* 100:1201–9
9. Antwi FB, Olson DL, Knodel JJ. 2007. Comparative evaluation and economic potential of ecorational versus chemical insecticides for crucifer flea beetle (Coleoptera: Chrysomelidae) management in canola. *J. Econ. Entomol.* 100:710–16
10. Antwi FB, Reddy GVP. 2016. Efficacy of entomopathogenic nematodes and sprayable polymer gel against crucifer flea beetle (Coleoptera: Chrysomelidae) on canola. *J. Econ. Entomol.* 109:1706–12
11. Barari H, Cook SM, Clark SJ, Williams IH. 2005. Effect of a turnip rape (*Brassica rapa*) trap crop on stem-mining pests and their parasitoids in winter oilseed rape (*Brassica napus*). *BioControl* 50:69–86
12. Bartelt RJ, Cossé AA, Zilkowski BW, Weisleder D, Momany FA. 2001. Male-specific sesquiterpenes from *Phyllotreta* and *Aphthona* flea beetles. *J. Chem. Ecol.* 27:2397–423
13. Bartelt RJ, Zilkowski BW, Cossé AA, Schnupf U, Vermillion K, Momany FA. 2011. Male-specific sesquiterpenes from *Phyllotreta* flea beetles. *J. Nat. Prod.* 74:585–95

14. Bartlet E, Mithen R, Clark S. 1996. Feeding of the cabbage stem flea beetle *Psylliodes chrysocephala* on high and low glucosinolate cultivars of oilseed rape. In *Proceedings of the 9th International Symposium on Insect-Plant Relationships*, pp. 87–99. Berlin: Springer
15. Bartlet E, Parsons D, Williams I, Clark S. 1994. The influence of glucosinolates and sugars on feeding by the cabbage stem flea beetle, *Psylliodes chrysocephala*. *Entomol. Exp. Appl.* 73:77–83
16. Bartlet E, Williams I. 1991. Factors restricting the feeding of the cabbage stem flea beetle (*Psylliodes chrysocephala*). *Entomol. Exp. Appl.* 60:233–38
17. Beran F, Jimenez-Aleman GH, Lin MY, Hsu YC, Mewis I, et al. 2016. The aggregation pheromone of *Phyllotreta striolata* (Coleoptera: Chrysomelidae) revisited. *J. Chem. Ecol.* 42:748–55
18. Beran F, Mewis I, Srinivasan R, Svoboda J, Vial C, et al. 2011. Male *Phyllotreta striolata* (F.) produce an aggregation pheromone: identification of male-specific compounds and interaction with host plant volatiles. *J. Chem. Ecol.* 37:85–97
19. Beran F, Pauchet Y, Kunert G, Reichelt M, Wielsch N, et al. 2014. *Phyllotreta striolata* flea beetles use host plant defense compounds to create their own glucosinolate-myrosinase system. *PNAS* 111:7349–54
20. Beran F, Sporer T, Paetz C, Ahn S-J, Betzin F, et al. 2018. One pathway is not enough: The cabbage stem flea beetle *Psylliodes chrysocephala* uses multiple strategies to overcome the glucosinolate-myrosinase defense in its host plants. *Front. Plant Sci.* 9:1754
21. Blažević I, Montaut S, Burčul F, Olsen CE, Burow M, et al. 2020. Glucosinolate structural diversity, identification, chemical synthesis and metabolism in plants. *Phytochemistry* 169:112100
22. Blubaugh CK, Asplund JS, Judson SM, Snyder WE. 2021. Invasive predator disrupts link between predator evenness and herbivore suppression. *Biol. Control* 153:104470
23. Bodnaryk RP. 1992. Effects of wounding on glucosinolates in the cotyledons of oilseed rape and mustard. *Phytochemistry* 31:2671–77
24. Bodnaryk RP. 1992. Leaf epicuticular wax, an antixenotic factor in Brassicaceae that affects the rate and pattern of feeding of flea beetles, *Phyllotreta cruciferae* (Goeze). *Can. J. Plant Sci.* 72:1295–303
25. Bodnaryk RP. 1997. Will low-glucosinolate cultivars of the mustards *Brassica juncea* and *Sinapis alba* be vulnerable to insect pests? *Can. J. Plant Sci.* 77:283–87
26. Bodnaryk RP, Rymerson RT. 1994. Effect of wounding and jasmonates on the physicochemical properties and flea beetle defense responses of canola seedlings, *Brassica napus* L. *Can. J. Plant Sci.* 74:899–907
27. Bohinc T, Trdan S. 2013. Sowing mixtures of Brassica trap crops is recommended to reduce *Phyllotreta* beetles injury to cabbage. *Acta Agric. Scand. B* 63:297–303
28. Brandt RN, Lamb RJ. 1993. Distribution of feeding damage by *Phyllotreta cruciferae* (Goeze) (Coleoptera, Chrysomelidae) on oilseed rape and mustard seedlings in relation to crop resistance. *Can. Entomol.* 125:1011–21
29. Brandt RN, Lamb RJ. 1994. Importance of tolerance and growth rate in the resistance of oilseed rapes and mustards to flea beetles, *Phyllotreta cruciferae* (Goeze) (Coleoptera, Chrysomelidae). *Can. J. Plant Sci.* 74:169–76
30. Breitenmoser S, Steinger T, Baux A, Hiltpold I. 2022. Intercropping winter oilseed rape (*Brassica napus* L.) has the potential to lessen the impact of the insect pest complex. *Agronomy* 12:723
31. Briar SS, Antwi F, Shrestha G, Sharma A, Reddy GVP. 2018. Potential biopesticides for crucifer flea beetle, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) management under dryland canola production in Montana. *Phytoparasitica* 46:247–54
32. Bukovinszky T, Gols R, Kamp A, de Oliveira-Domingues F, Hambäck PA, et al. 2010. Combined effects of patch size and plant nutritional quality on local densities of insect herbivores. *Basic Appl. Ecol.* 11:396–405
33. Burgess L, Hinks CF. 1987. Predation on adults of the crucifer flea beetle, *Phyllotreta cruciferae* (Goeze), by the northern fall field cricket, *Gryllus pennsylvanicus* Burmeister (Orthoptera, Gryllidae). *Can. Entomol.* 119:495–96
34. Butt TM, Ibrahim L, Ball BV, Clark SJ. 1994. Pathogenicity of the entomogenous fungi *Metarhizium anisopliae* and *Beauveria bassiana* against crucifer pests and the honey bee. *Biocontrol Sci. Technol.* 4:207–14
35. Cárcamo HA, Blackshaw RE. 2007. Insect pest incidence and injury to herbicide-tolerant canola in western Canada. *Agron. J.* 99:842–46

36. Cárcamo HA, Otani JK, Dosdall LM, Blackshaw RE, Clayton GW, et al. 2008. Effects of seeding date and canola species on seedling damage by flea beetles in three ecoregions. *J. Appl. Entomol.* 132:623–31
37. Cedden D, Güney G, Scholten S, Rostás M. 2023. Lethal and sublethal effects of orally delivered double-stranded RNA on the cabbage stem flea beetle, *Psylliodes chrysocephala*. *Pest Manag. Sci.* In press
38. Chagnon M, Kreutzweiser D, Mitchell EA, Morrissey CA, Noome DA, Van der Sluijs JP. 2015. Risks of large-scale use of systemic insecticides to ecosystem functioning and services. *Environ. Sci. Pollut. Res.* 22:119–34
39. Chen D, Yan R, Xu Z, Qian J, Yu Y, et al. 2022. Silencing of *dre4* contributes to mortality of *Phyllotreta striolata*. *Insects* 13:1072
40. Chen H, Gu M, Li L, Li S, Wen G. 2006. Preliminary report on a trial of 5% fipronil seed treatment for control of *Phyllotreta striolata* (Fabricius) in seedlings of Chinese flowering cabbage. *Guangdong Agric. Sci.* 1:58–59
41. Culliney TW. 1986. Predation on adult *Phyllotreta* flea beetles by *Podisus maculiventris* (Hemiptera: Pentatomidae) and *Nabicula americolimbata* (Hemiptera: Nabidae). *Can. Entomol.* 118:731–32
42. Dewar AM. 2017. The adverse impact of the neonicotinoid seed treatment ban on crop protection in oilseed rape in the United Kingdom. *Pest Manag. Sci.* 73:1305–9
43. Döring A, Ulber B. 2020. Performance of cabbage stem flea beetle larvae (*Psylliodes chrysocephala*) in brassicaceous plants and the effect of glucosinolate profiles. *Entomol. Exp. Appl.* 168:200–8
44. Dosdall LM, Dolinski MG, Cowle NT, Conway PM. 1999. The effect of tillage regime, row spacing, and seeding rate on feeding damage by flea beetles, *Phyllotreta* spp. (Coleoptera: Chrysomelidae), in canola in central Alberta, Canada. *Crop Prot.* 18:217–24
45. Dosdall LM, Stevenson FC. 2005. Managing flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae) in canola with seeding date, plant density, and seed treatment. *Agron. J.* 97:1570–78
46. Eigenbrode SD, Espelie KE. 1995. Effects of plant epicuticular lipids on insect herbivores. *Annu. Rev. Entomol.* 40:171–94
47. Ekbom B. 2010. Pests and their enemies in spring oilseed rape in Europe and challenges to integrated pest management. In *Biocontrol-Based Integrated Management of Oilseed Rape Pests*, ed. IH Williams, pp. 151–65. Berlin: Springer
48. Ekbom B, Kuusk A-K, Malsher G, Astrom S, Cassel-Lundhagen A. 2014. Consumption of flea beetles (*Phyllotreta*, Coleoptera: Chrysomelidae) by spiders in field habitats detected by molecular analysis. *Can. Entomol.* 146:639–51
49. Feeny P, Paauwe KL, Demong NJ. 1970. Flea beetles and mustard oils: host plant specificity of *Phyllotreta cruciferae* and *P. striolata* adults (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* 63:832–41
50. Ferguson AW, Barari H, Warner DJ, Campbell JM, Smith ET, et al. 2006. Distributions and interactions of the stem miners *Psylliodes chrysocephala* and *Ceutorhynchus pallidactylus* and their parasitoids in a crop of winter oilseed rape (*Brassica napus*). *Entomol. Exp. Appl.* 119:81–92
51. Fernandez P, Hilker M. 2007. Host plant location by Chrysomelidae. *Basic Appl. Ecol.* 8:97–116
52. Gao Z, Wu W, Cui Z. 2004. The effect of intercrop on the densities of *Phyllotreta striolata* (F.). *Chin. Agric. Sci. Bull* 20:214–16
53. Gavloski JE, Ekuere U, Keddie A, Dosdall L, Kott L, Good AG. 2000. Identification and evaluation of flea beetle (*Phyllotreta cruciferae*) resistance within Brassicaceae. *Can. J. Plant Sci.* 80:881–87
54. Ge D, Chesters D, Gomez-Zurita J, Zhang L, Yang X, Vogler AP. 2011. Anti-predator defence drives parallel morphological evolution in flea beetles. *Proc. R. Soc. B* 278:2133–41
55. George D, Port G, Collier R. 2019. Living on the edge: using and improving trap crops for flea beetle management in small-scale cropping systems. *Insects* 10:286
56. Giamoustaris A, Mithen R. 1995. The effect of modifying the glucosinolate content of leaves of oilseed rape (*Brassica napus* ssp. *oleifera*) on its interaction with specialist and generalist pests. *Ann. Appl. Biol.* 126:347–63
57. Gruber M, Xu N, Grenkow L, Li X, Onyilagha J, et al. 2009. Responses of the crucifer flea beetle to *Brassica* volatiles in an olfactometer. *Environ. Entomol.* 38:1467–79
58. Guo M, Gao R, Nanda S, Li Y, Guo C, et al. 2023. RNAi assays in the striped flea beetle (*Phyllotreta striolata*) suggest *Psγ-COPI* and *PsArf1COPI* as potential molecular targets for pest control. *Pestic. Biochem. Physiol.* 193:105428

59. Hallett RH, Ray H, Holowachuk J, Soroka JJ, Gruber MY. 2005. Bioassay for assessing resistance of *Arabidopsis thaliana* L. (Heynh.) to the adult crucifer flea beetle, *Phyllotreta cruciferae* (Goeze) (Coleoptera: Chrysomelidae). *Can. J. Plant Sci.* 85:225–35
60. Heimbach U, Müller A. 2013. Incidence of pyrethroid-resistant oilseed rape pests in Germany. *Pest Manag. Sci.* 69:209–16
61. Henderson AE, Hallett RH, Soroka JJ. 2004. Prefeeding behavior of the crucifer flea beetle, *Phyllotreta cruciferae*, on host and nonhost crucifers. *J. Insect Behav.* 17:17–39
62. Hervé MR. 2018. Breeding for insect resistance in oilseed rape: challenges, current knowledge and perspectives. *Plant Breed.* 137:27–34
63. Hicks KL. 1974. Mustard oil glucosides: feeding stimulants for adult cabbage flea beetles, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* 67:261–64
64. Hiiesaar K, Metspalu L, Jõgar K. 2006. Attractiveness and susceptibility of *Brassica rapa*, *B. napus* and *Sinapis alba* to the flea beetles (Coleoptera: Chrysomelidae). *Agron. Res.* 4:191–96
65. Hoarau C, Campbell H, Prince G, Chandler D, Pope T. 2022. Biological control agents against the cabbage stem flea beetle in oilseed rape crops. *Biol. Control* 167:104844
66. Højland DH, Nauen R, Foster SP, Williamson MS, Kristensen M. 2015. Incidence, spread and mechanisms of pyrethroid resistance in European populations of the cabbage stem flea beetle, *Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae). *PLOS ONE* 10:e0146045
67. Hokkanen H, Zec-Vojinovic M, Husberg G-B, Menzler-Hokkanen I, Büchs W, et al. 2006. Effectiveness of entomopathogenic nematodes in the control of oilseed rape pests. In *Proceedings of the International Symposium on Integrated Pest Management in Oilseed Rape*, *3–5 April*, *Göttingen*, *Germany*, pp. 96–99. Cambridge, UK: Br. Crop Prod. Counc.
68. Jeschke V, Gershenzon J, Vassão DG. 2016. Insect detoxification of glucosinolates and their hydrolysis products. *Adv. Bot. Res.* 80:199–245
69. Jeschke V, Gershenzon J, Vassão DG. 2016. A mode of action of glucosinolate-derived isothiocyanates: Detoxification depletes glutathione and cysteine levels with ramifications on protein metabolism in *Spodoptera littoralis*. *Insect Biochem. Mol. Biol.* 71:37–48
70. Jordan A, Broad GR, Stigenberg J, Hughes J, Stone J, et al. 2020. The potential of the solitary parasitoid *Microctonus brassicae* for the biological control of the adult cabbage stem flea beetle, *Psylliodes chrysocephala*. *Entomol. Exp. Appl.* 168:360–70
71. Kareiva P. 1985. Finding and losing host plants by *Phyllotreta*: patch size and surrounding habitat. *Ecology* 66:1809–16
72. Knodel JJ, Olson DL, Hanson BK, Henson RA. 2008. Impact of planting dates and insecticide strategies for managing crucifer flea beetles (Coleoptera: Chrysomelidae) in spring-planted canola. *J. Econ. Entomol.* 101:810–21
73. Lamb RJ. 1984. Effects of flea beetles, *Phyllotreta* spp. (Chrysomelidae, Coleoptera), on the survival, growth, seed yield and quality of canola, rape and yellow mustard. *Can. Entomol.* 116:269–80
74. Lamb RJ. 1989. Entomology of oilseed *Brassica* crops. *Annu. Rev. Entomol.* 34:211–29
75. Lamb RJ, McVetty PBE, Palaniswamy P, Bodnaryk RP, Jeong SE. 1993. Susceptibility of inbred lines of oilseed rape, *Brassica napus*, to feeding damage by the crucifer flea beetle, *Phyllotreta cruciferae* (Goeze) Coleoptera, Chrysomelidae, and its inheritance. *Can. J. Plant Sci.* 73:615–23
76. Lamb RJ, Palaniswamy P. 1990. Host discrimination by a crucifer-feeding flea beetle, *Phyllotreta striolata* (F) (Coleoptera, Chrysomelidae). *Can. Entomol.* 122:817–24
77. Lamb RJ, Turnock WJ. 1982. Economics of insecticidal control of flea beetles (Coleoptera, Chrysomelidae) attacking rape in Canada. *Can. Entomol.* 114:827–40
78. Larsen LM, Nielsen JK, Sørensen H. 1982. Identification of 3-*O*-[2-*O*-(β-D-xylopyranosyl)-β-D-galactopyranosyl] flavonoids in horseradish leaves acting as feeding stimulants for a flea beetle. *Phytochemistry* 21:1029–33
79. Latheef MA, Ortiz JH. 1984. Influence of companion herbs on *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) on collard plants. *J. Econ. Entomol.* 77:80–82
80. Latheef MA, Ortiz JH, Sheikh AQ. 1984. Influence of intercropping on *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) populations on collard plants. *J. Econ. Entomol.* 77:1180–84

81. Lenssen AW, Johnson GD, Blodgett SL, Goosey HB. 2007. Influence of tillage system, oilseed species, and insecticidal seed treatment on flea beetle (Coleoptera: Chrysomelidae) damage, oilseed production, and postharvest residue cover. *J. Entomol. Sci.* 42:1–10
82. Lin R, Zhuang J, Zou H, Fu J, Chen H. 2007. Control effect of several insecticides on striped flea beetle. *Nongyao Kexue Yu Guanli* 11:29–32
83. Lundin O. 2019. No-till protects spring oilseed rape (*Brassica napus* L.) against crop damage by flea beetles (*Phyllotreta* spp.). *Agric. Ecosyst. Environ.* 278:1–5
84. Lundin O. 2020. Economic injury levels for flea beetles (*Phyllotreta* spp.; Coleoptera: Chrysomelidae) in spring oilseed rape (*Brassica napus*; Brassicales: Brassicaceae). *J. Econ. Entomol.* 113:808–13
85. Lundin O. 2021. Consequences of the neonicotinoid seed treatment ban on oilseed rape production—what can be learnt from the Swedish experience? *Pest Manag. Sci.* 77:3815–19
86. Lundin O, Malsher G, Högfeldt C, Bommarco R. 2020. Pest management and yield in spring oilseed rape without neonicotinoid seed treatments. *Crop Prot.* 137:105261
87. Lundin O, Myrbeck Å, Bommarco R. 2018. The effects of reduced tillage and earlier seeding on flea beetle (*Phyllotreta* spp.) crop damage in spring oilseed rape (*Brassica napus* L.). *Crop Prot.* 107:104–7
88. Meisner J, Mitchell B. 1983. Phagodeterrency induced by two cruciferous plants in adults of the flea beetle *Phyllotreta striolata* (Coleoptera: Chrysomelidae). *Can. Entomol.* 115:1209–14
89. Metspalu L, Kruus E, Ploomi A, Williams IH, Hiiesaar K, et al. 2014. Flea beetle (Chrysomelidae: Alticinae) species composition and abundance in different cruciferous oilseed crops and the potential for a trap crop system. *Acta Agric. Scand. B* 64:572–82
90. Milbrath LR, Weiss MJ, Schatz BG. 1995. Influence of tillage system, planting date, and oilseed crucifers on flea beetle populations (Coleoptera: Chrysomelidae). *Can. Entomol.* 127:289–93
91. Milliron HE. 1953. A European flea beetle injuring crucifers in North America. *J. Econ. Entomol.* 46:179
92. Miranpuri GS, Khachatourians GG. 1995. Entomopathogenicity of *Beauveria bassiana* toward flea beetles, *Phyllotreta cruciferae* Goeze (Col., Chrysomelidae). *J. Appl. Entomol.* 119:167–70
93. Mitchell-Olds T, Siemens D, Pedersen D. 1996. Physiology and costs of resistance to herbivory and disease in *Brassica*. *Entomol. Exp. Appl.* 80:231–37
94. Morrissey CA, Mineau P, Devries JH, Sanchez-Bayo F, Liess M, et al. 2015. Neonicotinoid contamination of global surface waters and associated risk to aquatic invertebrates: a review. *Environ. Int.* 74:291–303
95. Nielsen JK. 1978. Host plant discrimination within Cruciferae: feeding responses of four leaf beetles (Coleoptera: Chrysomelidae) to glucosinolates, cucurbitacins and cardenolides. *Entomol. Exp. Appl.* 24:41–54
96. Nielsen JK, Hansen ML, Agerbirk N, Petersen BL, Halkier BA. 2001. Responses of the flea beetles *Phyllotreta nemorum* and *P. cruciferae* to metabolically engineered *Arabidopsis thaliana* with an altered glucosinolate profile. *Chemoecology* 11:75–83
97. Noosidum A, Mangtab S, Lewis EE. 2021. Biological control potential of entomopathogenic nematodes against the striped flea beetle, *Phyllotreta sinuata* Stephens (Coleoptera: Chrysomelidae). *Crop Prot.* 141:105448
98. Onyilagha J, Gruber M, Hallett R, Holowachuk J, Buckner A, Soroka J. 2012. Constitutive flavonoids deter flea beetle insect feeding in *Camelina sativa* L. *Biochem. Syst. Ecol.* 42:128–33
99. Ortega-Ramos PA, Coston DJ, Seimandi-Corda G, Mauchline AL, Cook SM. 2022. Integrated pest management strategies for cabbage stem flea beetle (*Psylliodes chrysocephala*) in oilseed rape. *Glob. Change Biol. Bioenergy* 14:267–86
100. Palaniswamy P, Bodnaryk RP. 1994. A wild brassica from Sicily provides trichome-based resistance against flea beetles, *Phyllotreta cruciferae* (Goeze) (Coleoptera, Chrysomelidae). *Can. Entomol.* 126:1119–30
101. Palaniswamy P, Lamb RJ. 1992. Host preferences of the flea beetles *Phyllotreta cruciferae* and *P. striolata* (Coleoptera, Chrysomelidae) for crucifer seedlings. *J. Econ. Entomol.* 85:743–52
102. Palaniswamy P, Lamb RJ. 1993. Wound-induced antixenotic resistance to flea beetles, *Phyllotreta cruciferae* (Goeze) (Coleoptera, Chrysomelidae), in crucifers. *Can. Entomol.* 125:903–12

103. Palaniswamy P, Lamb RJ, McVetty PBE. 1992. Screening for antixenosis resistance to flea beetles, *Phyllotreta cruciferae* (Goeze) (Coleoptera, Chrysomelidae), in rapeseed and related crucifers. *Can. Entomol.* 124:895–906
104. Parker JE, Crowder DW, Eigenbrode SD, Snyder WE. 2016. Trap crop diversity enhances crop yield. *Agric. Ecosyst. Environ.* 232:254–62
105. Payne JM, Michaels TE, Bradfisch GA, Muller-Cohn J, Fu J. 2000. Bacillus thuringiensis *isolates, toxins, and genes selectively active against certain coleopteran pests*. US Patent 6,071,511
106. Peng C, Bartelt RJ, Weiss MJ. 1999. Male crucifer flea beetles produce an aggregation pheromone. *Physiol. Entomol.* 24:98–99
107. Peng CW, Weiss MJ, Anderson MD. 1992. Flea beetle (Coleoptera, Chrysomelidae) response, feeding, and longevity on oilseed rape and crambe. *Environ. Entomol.* 21:604–9
108. Pivnick KA, Lamb RJ, Reed D. 1992. Response of flea beetles, *Phyllotreta s*pp, to mustard oils and nitriles in field trapping experiments. *J. Chem. Ecol.* 18:863–73
109. Pucci TM. 2013. Contributions to the classification of North American *Microctonus* (Braconidae, Euphorinae). *Zootaxa* 3725:1–150
110. Reddy GVP, Tangtrakulwanich K, Wu S, Miller JH, Ophus VL, Prewett J. 2014. Sustainable management tactics for control of *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) on canola in Montana. *J. Econ. Entomol.* 107:661–66
111. Root RB. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43:95–120
112. Rousseau M, LeSage L. 2016. Earliest North American occurrence of *Phyllotreta striolata* (Coleoptera: Chrysomelidae) from Québec, Canada. *Can. Entomol.* 148:476–78
113. Sekulic G, Rempel CB. 2016. Evaluating the role of seed treatments in canola/oilseed rape production: integrated pest management, pollinator health, and biodiversity. *Plants* 5:14
114. Shukla SP, Beran F. 2020. Gut microbiota degrades toxic isothiocyanates in a flea beetle pest. *Mol. Ecol.* 29:4692–705
115. Siemens DH, Mitchell-Olds T. 1996. Glucosinolates and herbivory by specialists (Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae): consequences of concentration and induced resistance. *Environ. Entomol.* 25:1344–53
116. Soler R, Schaper SV, Bezemer TM, Cortesero AM, Hoffmeister TS, et al. 2009. Influence of presence and spatial arrangement of belowground insects on host-plant selection of aboveground insects: a field study. *Ecol. Entomol.* 34:339–45
117. Soroka J, Grenkow L. 2013. Susceptibility of brassicaceous plants to feeding by flea beetles, *Phyllotreta* spp. (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 106:2557–67
118. Soroka J, Grenkow L, Otani J, Gavloski J, Olfert O. 2018. Flea beetle (Coleoptera: Chrysomelidae) species in canola (Brassicaceae) on the northern Great Plains of North America. *Can. Entomol.* 150:100–15
119. Soroka JJ, Bartelt RJ, Zilkowski BW, Cossé AA. 2005. Responses of flea beetle *Phyllotreta cruciferae* to synthetic aggregation pheromone components and host plant volatiles in field trials. *J. Chem. Ecol.* 31:1829–43
120. Soroka JJ, Grenkow LF, Irvine RB. 2008. Impact of decreasing ratios of insecticide-treated seed on flea beetle (Coleoptera: Chrysomelidae, *Phyllotreta* spp.) feeding levels and canola seed yields. *J. Econ. Entomol.* 101:1811–20
121. Soroka JJ, Holowachuk JM, Gruber MY, Grenkow LF. 2011. Feeding by flea beetles (Coleoptera: Chrysomelidae; *Phyllotreta* spp.) is decreased on canola (*Brassica napus*) seedlings with increased trichome density. *J. Econ. Entomol.* 104:125–36
122. Sporer T, Körnig J, Beran F. 2020. Ontogenetic differences in the chemical defence of flea beetles influence their predation risk. *Funct. Ecol.* 34:1370–79
123. Sporer T, Körnig J, Wielsch N, Gebauer-Jung S, Reichelt M, et al. 2021. Hijacking the mustard-oil bomb: how a glucosinolate-sequestering flea beetle copes with plant myrosinases. *Front. Plant Sci.* 12:13
124. Stara J, Kocourek F. 2019. Cabbage stem flea beetle's (*Psylliodes chrysocephala* L.) susceptibility to pyrethroids and tolerance to thiacloprid in the Czech Republic. *PLOS ONE* 14:e0214702

125. Tahvanainen JO, Root RB. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10:321–46
126. Tangtrakulwanich K, Reddy GVP, Wu S, Miller JH, Ophus VL, Prewett J. 2014. Developing nominal threshold levels for *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) damage on canola in Montana, USA. *Crop Prot.* 66:8–13
127. Tansey JA, Dosdall LM, Keddie BA. 2009. *Phyllotreta cruciferae* and *Phyllotreta striolata* responses to insecticidal seed treatments with different modes of action. *J. Appl. Entomol.* 133:201–9
128. Tansey JA, Dosdall LM, Keddie BA, Sarfraz RM. 2008. Differences in *Phyllotreta cruciferae* and *Phyllotreta striolata* (Coleoptera: Chrysomelidae) responses to neonicotinoid seed treatments. *J. Econ. Entomol.* 101:159–67
129. Tattersall DB, Bak S, Jones PR, Olsen CE, Nielsen JK, et al. 2001. Resistance to an herbivore through engineered cyanogenic glucoside synthesis. *Science* 293:1826–28
130. Tóth M, Csonka É, Bartelt RJ, Cossé AA, Zilkowski BW. 2012. Similarities in pheromonal communication of flea beetles *Phyllotreta cruciferae* Goeze and *Ph. vittula* Redtenbacher (Coleoptera, Chrysomelidae). *J. Appl. Entomol.* 136:688–97
131. Tóth M, Csonka É, Bartelt RJ, Cosse AA, Zilkowski BW, et al. 2005. Pheromonal activity of compounds identified from male *Phyllotreta cruciferae*: field tests of racemic mixtures, pure enantiomers, and combinations with allyl isothiocyanate. *J. Chem. Ecol.* 31:2705–20
132. Traw BM, Dawson TE. 2002. Reduced performance of two specialist herbivores (Lepidoptera: Pieridae, Coleoptera: Chrysomelidae) on new leaves of damaged black mustard plants. *Environ. Entomol.* 31:714–22
133. Trdan S, Vidrih M, Valič N, Laznik Ž. 2008. Impact of entomopathogenic nematodes on adults of *Phyllotreta* spp. (Coleoptera: Chrysomelidae) under laboratory conditions. *Acta Agric. Scand. B* 58:169–75
134. Turnock WJ, Turnbull SA. 1994. The development of resistance to insecticides by the crucifer flea beetle, *Phyllotreta cruciferae* (Goeze). *Can. Entomol.* 126:1369–75
135. Ulber B, Williams IH, Klukowski Z, Luik A, Nilsson C. 2010. Parasitoids of oilseed rape pests in Europe: key species for conservation biocontrol. In *Biocontrol-Based Integrated Management of Oilseed Rape Pests*, ed. IH Williams, pp. 45–76. Berlin: Springer
136. Valantin-Morison M, Meynard JM, Doré T. 2007. Effects of crop management and surrounding field environment on insect incidence in organic winter oilseed rape (*Brassica napus* L.). *Crop Prot.* 26:1108–20
137. Vaughn TT, Hoy CW. 1993. Effects of leaf age, injury, morphology, and cultivars on feeding-behavior of *Phyllotreta cruciferae* (Coleoptera, Chrysomelidae). *Environ. Entomol.* 22:418–24
138. Warner DJ, Allen-Williams LJ, Warrington S, Ferguson AW, Williams IH. 2003. Mapping, characterisation, and comparison of the spatio-temporal distributions of cabbage stem flea beetle (*Psylliodes chrysocephala*), carabids, and Collembola in a crop of winter oilseed rape (*Brassica napus*). *Entomol. Exp. Appl.* 109:225–34
139. Weber DC, Konstantinov AS, Khrimian A, Bier AD, Lubenow LA, et al. 2022. Trapping of crucifer-feeding flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae) with pheromones and plant kairomones. *J. Econ. Entomol.* 115:748–56
140. Weiss MJ, Schatz BG, Gardner JC, Nead BA. 1994. Flea beetle (Coleoptera: Chrysomelidae) populations and crop yield in field pea and oilseed rape intercrops. *Environ. Entomol.* 23:654–58
141. Wertheim B, van Baalen EJ, Dicke M, Vet LE. 2005. Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. *Annu. Rev. Entomol.* 50:321–46
142. Williams IH. 2010. The major insect pests of oilseed rape in Europe and their management: an overview. In *Biocontrol-Based Integrated Management of Oilseed Rape Pests*, ed. IH Williams, pp. 1–43. Berlin: Springer
143. Willis CE, Foster SP, Zimmer CT, Elias J, Chang XM, et al. 2020. Investigating the status of pyrethroid resistance in UK populations of the cabbage stem flea beetle (*Psylliodes chrysocephala*). *Crop Prot.* 138:105316
144. Wylie HG. 1988. Release in Manitoba, Canada of *Townesilitus bicolor* [Hym, Braconidae], an European parasite of *Phyllotreta* spp. [Col, Chrysomelidae]. *Entomophaga* 33:25–32
145. Wylie HG, Loan C. 1984. Five Nearctic and one introduced Euphorine species (Hymenoptera, Braconidae) that parasitize adults of crucifer-infesting flea beetles (Coleoptera, Chrysomelidae). *Can. Entomol.* 116:235–46

146. Xia N, Yang G, You M. 2015. Regulation of dominant insect pests and natural enemies by intercropping tomato in cauliflower-based fields. *Acta Entomol. Sin.* 58:391–99
147. Xiong TF, Nanda S, Jin FL, Lin QS, Feng X. 2022. Control efficiency and mechanism of spinetoram seed-pelleting against the striped flea beetle *Phyllotreta striolata*. *Sci. Rep.* 12:9524
148. Xu C, De Clercq P, Moens M, Chen S, Han R. 2010. Efficacy of entomopathogenic nematodes (Rhabditida: Steinernematidae and Heterorhabditidae) against the striped flea beetle, *Phyllotreta striolata*. *BioControl* 55:789–97
149. Yan X, Han R, Moens M, Chen S, De Clercq P. 2013. Field evaluation of entomopathogenic nematodes for biological control of striped flea beetle, *Phyllotreta striolata* (Coleoptera: Chrysomelidae). *BioControl* 58:247–56
150. Yan X, Lin YY, Huang ZM, Han RC. 2018. Characterisation of biological and biocontrol traits of entomopathogenic nematodes promising for control of striped flea beetle (*Phyllotreta striolata*). *Nematology* 20:503–18
151. Yang Z-L, Seitz F, Grabe V, Nietzsche S, Richter A, et al. 2022. Rapid and selective absorption of plant defense compounds from the gut of a sequestering insect. *Front. Physiol.* 13:846732
152. Zhang K, Zhang XF, Hu QB, Weng QF. 2022. Entomopathogenic fungi in the soils of China and their bioactivity against striped flea beetles *Phyllotreta striolata*. *Diversity* 14:464
153. Zimmer CT, Müller A, Heimbach U, Nauen R. 2014. Target-site resistance to pyrethroid insecticides in German populations of the cabbage stem flea beetle, *Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae). *Pestic. Biochem. Physiol.* 108:1–7