

Differences in *Phyllotreta cruciferae* and *Phyllotreta striolata* (Coleoptera: Chrysomelidae) Responses to Neonicotinoid Seed Treatments

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ABSTRACT Insecticidal seed treatments are used commonly throughout the Northern Great Plains of North America to systemically protect seedlings of canola (*Brassica napus* L. and *Brassica rapa* L.) from attack by the flea beetles *Phyllotreta cruciferae* (Goeze) and *Phyllotreta striolata* (F.) (Coleoptera: Chrysomelidae). Here, we investigated differential responses by the two flea beetle species to the neonicotinoid seed treatments thiamethoxam (Helix and Helix Xtra) and clothianidin (Prosper 400) in greenhouse experiments. *P. cruciferae* experienced higher mortality and fed less when exposed to these compounds than did *P. striolata*. Beetles of the overwintered and the summer generations responded differently when feeding on seedlings that developed with insecticidal seed treatments, with mortality higher for *P. cruciferae* in May than in August. When the two flea beetle species were held together at equal densities and allowed to feed on seedlings affected by the seed treatments, mortality of *P. cruciferae* significantly exceeded that of *P. striolata*. Differences in efficacies of these compounds for these beetles have ramifications for management strategies in regions where these insects occur sympatrically. Competitive release of *P. striolata* was previously reported to occur when *P. cruciferae* was excluded from brassicaceous crops; consequently, the consistent use of these seed treatments over millions of hectares of canola cropland may be a factor that contributes to a shift in prevalence of flea beetle pest species from *P. cruciferae* toward *P. striolata*.

KEY WORDS canola, flea beetles, neonicotinoid, seed treatment, species composition shift

Throughout North America, the flea beetles *Phyllotreta cruciferae* (Goeze) and *Phyllotreta striolata* (F.) (Coleoptera: Chrysomelidae: Alticinae) are serious pests in the production of brassicaceous crops, especially canola (*Brassica napus* L. and *Brassica rapa* L.), where they are estimated to cause economic losses of >\$300 million (Canadian) annually (Madder and Stemeroff 1988). Both species are usually univoltine in North America (Westdal and Romanow 1972). Overwintering occurs in leaf litter and turf often beneath shelterbelts, and in spring emergence of *P. striolata* adults usually precedes *P. cruciferae* by a few days and coincides with the germination of spring-planted canola (Burgess 1977). Adults of both species feed on canola cotyledons and early leaves, creating a distinct “shot-hole” appearance, and they occasionally cut seedling stems (Feeny et al. 1970). Damaged seedlings cannot mount a compensatory response if apical meristems are damaged (Gavloski and Lamb 2000). Even moderate feeding can delay plant development and reduce yield (Lamb 1984). Oviposition by *Phyllotreta*

spp. occurs at the soil–stem interface of host plants in late spring. Larvae feed on fine roots and root hairs and pupate in the soil (Feeny et al. 1970, Burgess 1977). New generation adults of both species emerge simultaneously in mid- to late summer and feed on foliage and pods of mature canola before migrating to overwintering sites (Feeny et al. 1970; Hicks and Tahvanainen 1974, and references therein). The crucifer flea beetle (*P. cruciferae*) is considered the dominant pest of newly germinated *B. napus* and *B. rapa* L. in Canada (Lamb and Turnock 1982) and in the United States (Weiss et al. 1991). Crucifer flea beetles are considered much more abundant throughout most of the Northern Great Plains of North America although local *P. striolata* numbers can be very high, particularly in northern production areas in Canada (Burgess 1977, 1980).

Insecticidal seed treatments with systemic activity are used routinely to protect canola seedlings from herbivory by *Phyllotreta* spp. (e.g., Dosdall and Stevenson 2005). The neonicotinoid insecticides thiamethoxam (marketed as Helix with 200 g active ingredient [AI]/100 kg, and Helix Xtra with 400 g [AI]/100 kg, Syngenta Crop Protection, Calgary, AB, Canada) and clothianidin (marketed as Prosper 400 with 400 g [AI]/100 kg, Bayer CropScience, Monheim, Germany) were registered in 2001 and 2004, respec-

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tively, for use as canola seed treatments in Canada to replace lindane, a chlorinated hydrocarbon phased out by the end of 2004 due to unacceptable risks associated with occupational exposure; lindane was previously the only compound used for flea beetle control in canola in Canada (Pest Management Regulatory Agency 2001, 2002, 2004). Neonicotinoids are nicotinic acetylcholine receptor "super" agonists; these receptors occur in high densities in insect nervous tissue (Brown et al. 2006). Although clothianidin and thiamethoxam seed treatments have been proven effective for reducing *P. cruciferae* feeding damage to *B. napus* in field trials (Elliott et al. 2004), unacceptable seedling losses can still occur with their use. For example, $\approx 1,500$ ha treated with either clothianidin or thiamethoxam were reseeded in the Peace Lowland Ecoregion of Alberta in 2004 due to flea beetle attack (Western Committee on Crop Pests 2004), where *P. striolata* is the dominant species (Burgess 1977) and responsible for most damage (Western Committee on Crop Pests 2004).

Interspecific competition can bias distributions of organisms that occur sympatrically and exploit the same resources. Dominance of *P. cruciferae* in most regions is likely the product of such competitive interactions. Kareiva (1982) demonstrated that *P. striolata* benefits from competitive release in the absence of *P. cruciferae*. Numbers of *P. striolata* were significantly higher on collards from which *P. cruciferae* were removed. In the absence of an effectual competitor, *P. striolata* could prosper.

This study was undertaken to test the responses of these two flea beetle species to neonicotinoid compounds under controlled greenhouse conditions. Interactions of both interspecific and intraspecific competition and the seed treatments also were investigated, and effectiveness of the seed treatments was compared for spring and fall generations of each species. Possible effects of differential responses to the ecology and management of these species, including the potential for a shift in dominant species, are discussed.

Materials and Methods

Beetles were swept from canola fields near Fairview (118° 22' 32" W; 56° 04' 17" N), and Edmonton (112° 32' 25" W; 53° 22' 13" N) and maintained on potted canola (*B. napus* 'InVigor 5020') in 60- by 60- by 90-cm mesh cages. Both beetle species were collected from both sites and catches were pooled. Canola seeds were sown in 7-dram (25.88-ml) cylindrical plastic vials filled with a commercial potting mix (Sunshine Professional, SunGro Horticulture, Vancouver, BC, Canada) containing sphagnum peat moss, fertilizer, lime, and a wetting agent and grown for 6 d. Vials had perforated bottoms to allow irrigation from below. Seed treatments included an untreated control, Prosper 400 (400 g [AI]/100 kg clothianidin), Helix (200 g [AI]/100 kg thiamethoxam), and Helix Xtra (400 g [AI]/100 kg thiamethoxam). Treatments are hereafter referred to by their trade names.

Beetles were introduced within 1 wk of capture to 25 caged seedlings with fully expanded cotyledons. Seedlings were arranged in 5 by 5 arrays with no spaces between vials. Beetles were introduced in conspecific groups of 50 and 100 (two and four beetles per plant) and mixed (congeneric) groups of 50. Densities of two *Phyllotreta* spp. per seedling are common in European and North American production regions, and densities of four per plant are not exceptional (Hiiesaar et al. 2003; J.A.T., unpublished data). These densities were tested to assess effects of crowding. After 72 h, numbers of dead beetles and damage to plants were recorded. Defoliation was assessed by methods similar to those used by Palaniswamy et al. (1992): visual estimation of proportion of plant material consumed was rated on a scale of 0–9, with 0 corresponding to 0–10% and 9 to 91–100% defoliation and/or a cut seedling stem. The same worker rated all plants. Experiments were conducted in 2006 in a greenhouse chamber at the Alberta Research Council, Vegreville (ambient light, photoperiod of $\approx 16:8$ [L:D]h mid-May, photoperiod of $\approx 15:9$ [L:D] h mid-August, and 60–80% RH).

Three experiments were conducted using a randomized complete block design with four replications each. The first compared feeding damage to canola seedlings subjected to the different seed treatments (untreated control seedlings, and seedlings treated with Prosper 400, Helix, and Helix Xtra), by *P. cruciferae* and *P. striolata* from the overwintered (May) and summer-emerging (August) generations. Mortality levels of beetles of the two species also were compared in this study. The second experiment compared feeding damage to treated and untreated seedlings at two densities of each flea beetle species, either two or four beetles per seedling. Beetle mortalities also were determined. The third experiment compared mortality levels of *P. cruciferae* and *P. striolata* when placed in cages with treated or untreated canola seedlings when the beetles were either in conspecific groups of two beetles per seedling, or in congeneric groups consisting of equal components of each species at densities of two beetles per seedling.

Relatively low *P. striolata* numbers in May 2006 prevented assessment of feeding damage and mortality on treatments at high densities (four beetles per plant) at that time. Assessment of interactions of fixed factors were limited to beetle species by density by seed treatment in August, beetle species by generation by seed treatment at densities of two beetles per plant in May and August, and composition (beetles in mixed species or conspecific groups) by beetle species by seed treatment in August. Mortalities associated with control groups were used to calculate Abbott's correction for mortality (Abbott 1925) due to natural causes. Corrected mortalities, expressed as a percentage of beetles introduced, and feeding damage ratings were compared by analysis of variance (ANOVA) by using SAS version 9.1 (SAS Institute 2005) MIXED procedure. Block was considered a random factor for all comparisons. Three-way least square means were compared using pairwise *t*-tests ($P = 0.05$) with a

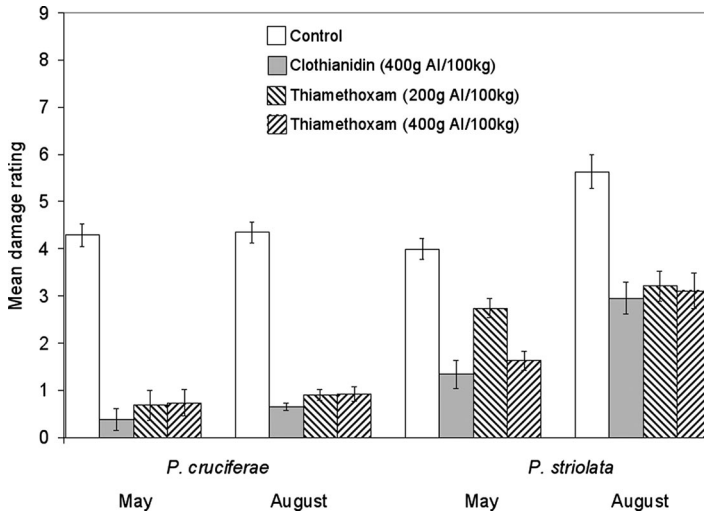


Fig. 1. Mean feeding damage ratings mean \pm SEM for *P. cruciferae* and *P. striolata* after 72 h on treated (Helix with 200 g [AI] (thiamethoxam)/100 kg; Helix XTra with 400 g [AI] (thiamethoxam)/100 kg; and Prosper 400 with 400 g [AI] (clothianidin)) seedlings at densities of two beetles per plant in May and August 2006.

pooled variance estimate from the ANOVA (PDIFF option in the MIXED procedure).

Results

General Feeding Damage by *Phyllotreta* spp. Feeding by both *P. cruciferae* and *P. striolata* adults resulted in the typical shot-hole damage observed in the field: small holes were chewed in the adaxial surfaces of cotyledons and occasionally seedling stems were cut. Several control plants and some treated seedlings had cotyledons partially or completely destroyed by both beetle species in the allotted 72 h. Damage was rarely distributed evenly among caged plants, although no obvious edge effects were apparent. Both beetle species appeared to feed in tight aggregations at the scale of these experiments. Damage associated with adults of the two species was indistinguishable.

Seed Treatment Effects on Spring and Summer Generation Feeding. Feeding damage ratings were significantly higher for *P. striolata* than for *P. cruciferae* ($F = 134.45$; $df = 1, 45$; $P < 0.0001$) (least squares means 3.0812 and 1.6125, respectively) (Fig. 1). Although a significant generation effect ($F = 35.29$; $df = 1, 45$; $P < 0.0001$) suggests that both beetles caused more damage in August than May, examination of sources of the significant species by generation interaction ($F = 20.07$; $df = 1, 45$; $P < 0.0001$) indicated that *P. striolata* caused significantly more damage to seedlings in the summer generation than in the overwintered generation ($t = 7.37$; $df = 1, 45$; $P < 0.0001$), but damage ratings were similar for *P. cruciferae* for both generations ($t = 1.03$; $df = 1, 45$; $P = 0.3073$) (Fig. 1). *P. striolata* damage ratings were significantly higher than those of *P. cruciferae* in both overwintered populations in May and in the summer generation in August ($t = 5.03$; $df = 1, 45$; $P < 0.0001$, and $t = 11.37$; $df = 1, 45$; $P < 0.0001$, respectively). Although feeding

damage associated with both *P. cruciferae* and *P. striolata* of both generations was significantly reduced by all seed treatments, they did not affect feeding of both beetle species similarly. *P. cruciferae* feeding damage ratings were similar among all treatments both for the overwintered (May) and summer generations (August) (Fig. 1). However, seedlings treated with both Prosper 400 and Helix XTra were more severely damaged by *P. striolata* in August than May ($t = 4.49$; $df = 1, 45$; $P < 0.0001$ and $t = 4.31$; $df = 1, 45$; $P < 0.0001$, respectively). Damage by *P. striolata* to Helix-treated seedlings was similar ($t = 1.35$; $df = 1, 45$; $P = 0.1826$) for both generations, although these seedlings experienced much more damage than those treated with either Helix XTra or Prosper 400 in May ($t = 3.87$; $df = 1, 45$; $P < 0.0001$ and $t = 3.06$; $df = 1, 45$; $P = 0.0038$, respectively). Damage to control plants by *P. cruciferae* was similar for both generations ($t = 0.17$; $df = 1, 45$; $P = 0.8678$). Damage was similar for both generations of *P. cruciferae* and spring generation *P. striolata* ($t = 0.84$; $df = 1, 45$; $P = 0.4068$ and $t = 1.00$; $df = 1, 45$; $P = 0.3204$, respectively).

Seed Treatment Effects on Spring and Summer Generation Mortality. Treatment-associated mortality of *P. cruciferae* was significantly higher than that of *P. striolata* ($F = 31.36$; $df = 1, 45$; $P < 0.0001$) (Fig. 2). Treatment associated mortalities of *P. striolata* were similar in May and August ($t = 0.62$; $df = 1, 45$; $P = 0.5405$), and *P. striolata* mortality was similar to that of *P. cruciferae* in August ($t = 0.50$; $df = 1, 45$; $P = 0.6195$). Treatment-associated *P. cruciferae* mortality was much higher in May than in August ($t = 6.30$; $df = 1, 45$; $P < 0.0001$) and much higher in May than *P. striolata* mortality in either May or August ($t = 7.42$; $df = 1, 45$; $P < 0.0001$ and $t = 6.80$; $df = 1, 45$; $P < 0.0001$, respectively), which resulted in significant generation ($F = 16.16$; $df = 1, 45$; $P = 0.0002$) and beetle species by generation ($F = 23.93$; $df = 1, 45$; $P < 0.0001$) inter-

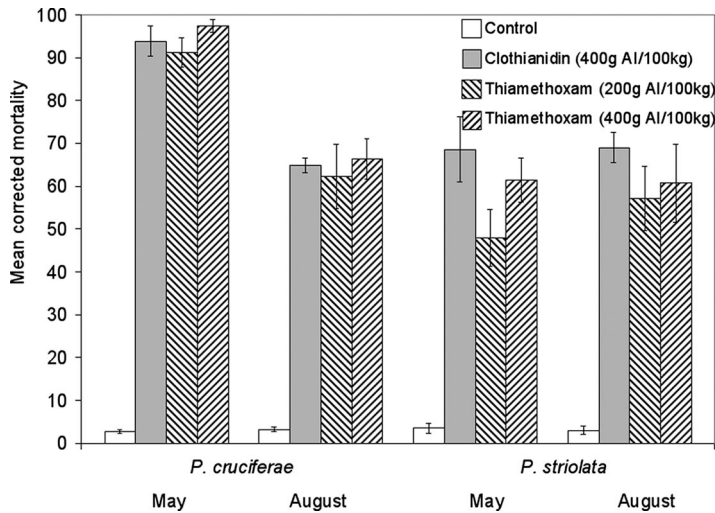


Fig. 2. Mean corrected mortality (%) mean \pm SEM for *P. cruciferae* and *P. striolata* after 72 h on treated (Prosper 400, Helix, and Helix XTra) seedlings at densities of two beetles per plant, May and August 2006.

actions. *P. striolata* mortality in May was significantly higher on Prosper 400 than Helix-treated seedlings ($t = 2.94$; $df = 1, 45$; $P = 0.0051$), resulting in a significant species by generation by seed treatment interaction ($F = 3.04$; $df = 3, 45$; $P = 0.0386$). Mortalities of both beetles were similar and very low (least squares mean 3.13%) on control plants.

Seed Treatment Effects on Intraspecific Competition. *P. striolata* caused significantly more damage to treated seedlings than *P. cruciferae* ($F = 198.55$; $df = 1, 45$; $P < 0.0001$) (least squares means 4.2319 and 2.0522, respectively). A significant density effect ($F = 29.33$; $df = 1, 45$; $P < 0.0001$) suggested that densities of four beetles per plant caused significantly more damage than two per plant (Fig. 3). However, feeding damage to treated seedlings was similar for both den-

sities of *P. cruciferae*. *P. striolata* caused significantly more damage at four beetles per plant than at two per plant ($t = 4.49$; $df = 1, 45$; $P < 0.0001$). Differences in *P. striolata* damage at the two densities were particularly apparent on seedlings treated with Helix ($t = 3.95$; $df = 1, 45$; $P = 0.0003$) (Fig. 3), contributing to a significant species by density by seed treatment interaction ($F = 4.48$; $df = 3, 45$; $P < 0.0078$).

A two-fold increase in beetle numbers per seedling did not result in twice the damage to control plants. Mean (\pm SE) damage ratings associated with groups of four and two *P. striolata* per plant were 7.24 ± 0.21 and 5.63 ± 0.36 , respectively. Increasing *P. cruciferae* numbers more closely approximated the anticipated two-fold increase in damage: mean ratings of 7.26 ± 0.23 and 4.35 ± 0.22 were observed for groups of four

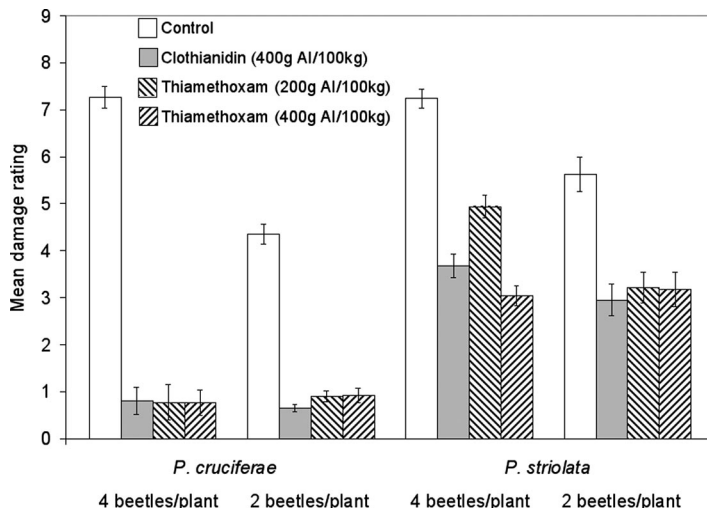


Fig. 3. Mean feeding damage ratings mean \pm SEM for *P. cruciferae* and *P. striolata* after 72 h on treated (Prosper 400, Helix and Helix XTra) seedlings at densities of two and four beetles per seedling, August 2006.

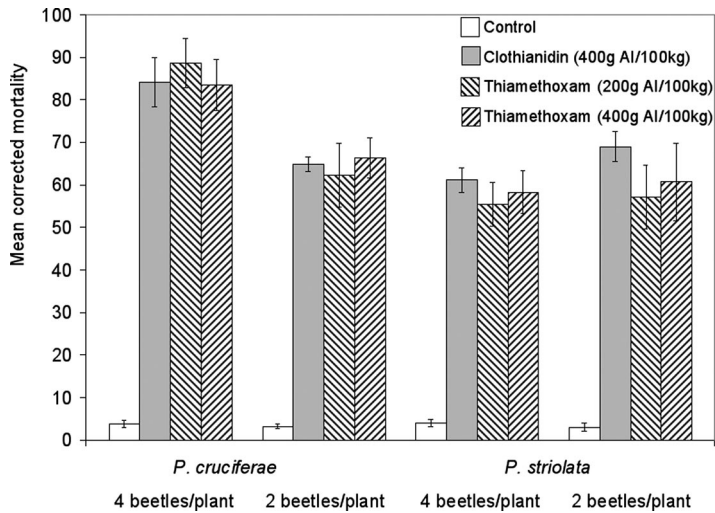


Fig. 4. Mean corrected mortality (%) mean \pm SEM for *P. cruciferae* and *P. striolata* after 72 h on treated (Prosper 400, Helix, and Helix XTra) seedlings at densities of two and four beetles per seedling, August 2006.

and two per plant. An apparent decrease in feeding damage to control plants with increasing density was more pronounced for *P. cruciferae* (Fig. 3).

Seed Treatment and Intraspecific Competition Effects on Mortality. Treatment-associated *P. cruciferae* mortality was significantly higher than that of *P. striolata* ($F = 24.78$; $df = 1, 45$; $P < 0.0001$) an effect resulting from higher mortality at four beetles per plant (Fig. 4). A significant species by density interaction ($F = 17.64$; $df = 1, 45$; $P = 0.0001$) resulted from greatly increased mortality levels for *P. cruciferae* at four beetles per plant relative to conspecifics at two beetles per plant ($t = 4.98$; $df = 1, 45$; $P < 0.0001$) and *P. striolata* at four beetles per plant ($t = 6.49$; $df = 1, 45$; $P < 0.0001$). The significant species by seed treatment interaction ($F = 3.66$; $df = 3, 45$; $P = 0.0191$) resulted from greater treatment-associated *P. cruciferae* mortality at higher densities without increase in control plant-associated mortality. Mortality was significantly higher on treated seedlings than controls for *P. cruciferae* at both densities (Fig. 4), although no significant differences among control plant-associated mortality were detected at high or low densities ($t = 0.08$; $df = 1, 45$; $P = 0.9378$). Mortality of both beetles was similar and very low (least squares mean 3.50%) when exposed to control plants at these densities.

Interspecific Competition Effects on Mortality. *P. cruciferae* mortality was significantly higher overall than that of *P. striolata* ($F = 28.60$; $df = 1, 45$; $P < 0.0001$) and highest when in interspecific groups, contributing to a significant composition effect ($F = 46.51$; $df = 1, 45$; $P < 0.0001$) (Fig. 5). Significant composition by beetle species ($F = 20.84$; $df = 1, 45$; $P < 0.0001$) and composition by seed treatment ($F = 4.96$; $df = 3, 45$; $P = 0.0046$) interactions were also evident because greater *P. cruciferae* mortality occurred in mixed than conspecific groups ($t = 8.05$; $df = 1, 45$; $P < 0.0001$)

and greater *P. cruciferae* mortality occurred in mixed species groups than for *P. striolata* in mixed species groups ($t = 7.01$; $df = 1, 45$; $P < 0.0001$). No significant differences were observed in *P. striolata* mortality among mixed and conspecific groups ($t = 1.59$; $df = 1, 45$; $P = 0.1179$) or among *P. striolata* and *P. cruciferae* conspecific groups ($t = 0.55$; $df = 1, 45$; $P = 0.5824$).

Discussion

P. striolata demonstrated lower levels of seed treatment-associated mortality in the spring at higher densities and when in congeneric groups and caused more damage to treated seedlings; consequently, we conclude that *P. striolata* is less susceptible to these neonicotinoid seed treatments than *P. cruciferae*. This is the first study to directly compare susceptibilities of the two species to insecticides, but circumstantial evidence exists to suggest that differences in the susceptibilities of *P. cruciferae* and *P. striolata* to other insecticidal compounds also may occur. *P. striolata* was relatively tolerant to carbaryl in Taiwan (Feng et al. 2000). Weiss et al. (1991) found that carbaryl was an effective insecticide against *P. cruciferae*. Although the mode of action of carbaryl differs from that of neonicotinoids (Budavari 1996, Brown et al. 2006), apparent differences in the susceptibilities of *P. striolata* and *P. cruciferae* suggest physiological differences that may influence their tolerances to other insecticidal compounds. The broader diet breadth of *P. striolata* (Feeny et al. 1970, Hicks and Tahvanainen 1974) supports this possibility. Although both *P. cruciferae* and *P. striolata* feed primarily on Brassicaceae, differences in host preferences suggest differences in physiology that have the potential to influence responses to insecticides.

Survival of *P. cruciferae* on treated canola seedlings was affected by generation. Spring-planted canola is generally not exposed to summer generation *Phyllot-*

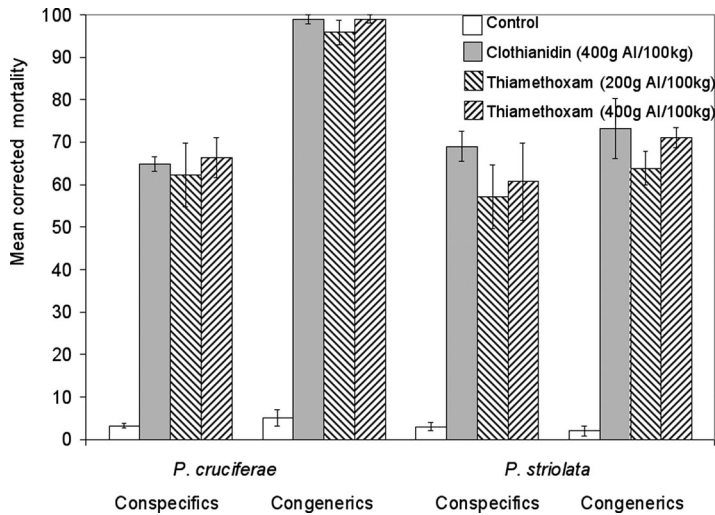


Fig. 5. Mean corrected mortality (%) mean \pm SEM for *P. cruciferae* and *P. striolata* after 72 h on treated (Prosper 400, Helix, and Helix XTra) and seedlings in single species (conspecifics) and mixed species (congenerics) groups at densities of two beetles per seedling, August 2006.

reta spp. However, as examinations of the efficacies of neonicotinoid compounds for overwintering generation beetles are lacking, these tests are warranted. Differences in the responses of pre- and postdiapause beetles also reflect the influence of overwintering stresses on insecticide efficacies. Treatment-associated mortality was significantly higher for specimens collected in May from populations that recently emerged from overwintering than for beetles of the summer generation collected in August; however, survival of beetles of the different generations did not vary on control plants. To our knowledge, this is the first report of seasonal differences in neonicotinoid susceptibilities of *P. cruciferae*. Results suggest that stresses associated with overwintering interacted with seed treatment effects and contributed to greater *P. cruciferae* mortality in May. In temperate regions of North America, adult beetles diapause during winter in soil and under leaf litter in fields, wooded areas, and shelterbelts (Ulmer and Dossall 2006). Diapause encompasses several hazards and stresses, including depletion of lipid and glycogen reserves (Danks 1987). Overwintering survival in temperate areas is generally $\approx 70\%$ in the absence of insecticidal treatments (Turnock et al. 1987). Adult *P. cruciferae* and *P. striolata* that emerge in August are not subjected to such stresses, and this may explain the survival differences observed in our study.

Mortality of *P. cruciferae* increased significantly when densities were doubled from two to four beetles per plant. Crowding at these densities had no apparent effect on *P. striolata* mortality, and given the congregative behavior of these *Phyllotreta* species (e.g., Peng et al. 1999), it is likely that crowding itself is not especially stressful to either species. However, lowered survival of *P. cruciferae* under crowded conditions after ingestion of leaf tissue containing seed treatment insecticides suggests that the beetles were

sufficiently challenged by these toxins to allow otherwise relatively innocuous environmental conditions to contribute significantly to their mortality. Negative effects of intraspecific competition due to crowding have been documented in many other organisms (Gause 1934, Bush and Lotz 2000), but not previously to our knowledge in situations involving interaction with insecticidal stress.

Interspecific competition also significantly increased mortality of *P. cruciferae* but not *P. striolata*. This experiment was conducted at densities of two beetles per plant from the August generation and consequently isolated the effects of competition in the absence of other stressors such as those putatively associated with overwintering and intraspecific competition. These results suggest that interspecific competition is another stressor with a greater antagonistic effect on *P. cruciferae* than *P. striolata* when coupled with neonicotinoid seed treatment effects.

Thiamethoxam and clothianidin have the same mode of action and thiamethoxam is converted to clothianidin in *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) (Nauen et al. 2003). Significant differences in mortality associated with these compounds were not observed among *P. striolata* or *P. cruciferae* cohorts in the absence of other stresses. However, *P. striolata* damage was consistently higher than *P. cruciferae* on treated seedlings. Imidacloprid has an antifeedant effect on *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (Nauen et al. 1998) and thiamethoxam inhibits plum curculio, *Conotrachelus nenuphar* (Herbst) (Coleoptera: Curculionidae), feeding when applied to apples (*Malus* spp.) (Wise et al. 2006). Our research suggests that clothianidin and thiamethoxam also exhibit antifeedant effects on *P. cruciferae* because of its reduced feeding relative to *P. striolata* on treated seedlings.

Variable effects of different neonicotinoid compounds and application rates have been described for some other insect species. For example, only clothianidin adequately controlled *Lygus hesperus* (Knight) (Hemiptera: Miridae) in cotton (*Gossypium hirsutum* L.) in Arizona compared with other neonicotinoids, including thiamethoxam (Ellsworth and Barkley 2005). *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) was controlled by imidacloprid applied at recommended application rates, but it was more likely to survive and reproduce at lower rates (Foster et al. 2003). In our study, similarities in *P. striolata* mortality and feeding damage between Prosper 400 and Helix Xtra treatments and greater mortality and reduced feeding associated with these treatments than with Helix suggest that application rate is more important than compound differences in these neonicotinoids.

Because *P. cruciferae* is the dominant canola pest in most production regions in northwestern North America, it has been the target of control strategy evaluations including insecticidal seed treatment efficacy tests (e.g., Knodel and Olson 2002). Most seed treatment evaluations occur in regions where *P. cruciferae* is the dominant pest. Researchers generally acknowledge the presence of both species but tend to group them as a homogeneous complex (e.g., Andersen et al. 2006). With very few exceptions (e.g., Pivnick et al. 1992), efforts to distinguish effects of control strategies on different flea beetle species are not undertaken in regions with sympatric populations. Our research has demonstrated the risks associated with the assumption that both species respond similarly, and emphasizes the need for controlled experimentation with different species. Another likely and as yet untested study organism for neonicotinoid efficacy tests is *Psylliodes punctulata* Melsheimer. This beetle occurs sympatrically with *P. cruciferae* and can be economically important for canola production in western Canada. Its diet breadth differs from those of *P. cruciferae* and *P. striolata* (Hicks and Tahvanainen 1974) suggesting physiological differences between it and *P. cruciferae* that may be relevant to its control.

P. cruciferae is likely a more effective competitor than *P. striolata* under most field conditions; however, these neonicotinoids favor *P. striolata* when sublethal insecticide effects are coupled with overwintering and interspecific and intraspecific competition. Such differential pressures have important agronomic and ecological implications primarily because these beetles usually exist sympatrically in western Canada.

In agronomic terms, differences in tolerances to these treatments have the potential to influence crop protection. In the Peace Lowland Ecoregion of Alberta, neonicotinoid seed treatments have been periodically ineffective for controlling damage to seedling canola from attack by *P. striolata* (Western Committee on Crop Pests 2004). Because no other families of insecticidal seed dressing are currently registered, the use of neonicotinoids has been adopted over a vast geographical area encompassing Alberta, Saskatche-

wan, Manitoba, British Columbia, Ontario, North Dakota, and Minnesota. Continued extensive use of these compounds, particularly at low application rates, may not offer sufficient protection for seedling canola from *P. striolata*.

In ecological terms, differences in susceptibilities to neonicotinoid seed treatments have the potential to influence interactions between *P. cruciferae* and *P. striolata*. Because *P. striolata* benefits from competitive release when *P. cruciferae* is removed (Kareiva 1982), its populations are likely limited by *P. cruciferae* where they co-occur. Price and Stanley (1982) suggested that different susceptibilities of *Liriomyza trifolii* Burgess (Diptera: Agromyzidae) and *Liriomyza sativae* Blanchard to insecticides was a dominant factor contributing to displacement of *L. sativae* where the two species occurred sympatrically. No other described differences in the biology of these species could account for the documented shift (Reitz and Trumble 2002). With continued extensive use of these neonicotinoid compounds for flea beetle control in canola, population displacement of *P. cruciferae* by *P. striolata* also may occur. Annual surveys of the distribution and abundance of these species should be undertaken to document a potential shift in flea beetle species dominance.

Because excessive reliance upon neonicotinoid seed treatments over vast geographical areas could eventually lead to reduced levels of population control, crop production in areas infested annually by damaging populations of these pests also should use cultural strategies to minimize the need for insecticidal intervention. In canola cropping systems, dormant seeding in fall can enable seedlings to escape severe flea beetle injury without insecticidal applications because plants develop to the true-leaf stages by the time that most flea beetle invasions occur in spring (Dosdall and Stevenson 2005). Increasing plant density (Dosdall et al. 1999, Dosdall and Stevenson 2005), growing canola in a zero tillage regime rather than with conventional tillage (Dosdall et al. 1999), and planting large rather than small seeds (Bodnaryk and Lamb 1991, Elliott et al. 2007), at wide row spacings (Dosdall et al. 1999) also have been shown to reduce damage from these pests. Results of the current study emphasize the importance of combining such cultural strategies in an integrated flea beetle management strategy to enable growers to reduce insecticide reliance in canola production systems.

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