Review

Classical biological control of the cabbage root fly, *Delia radicum*, in Canadian canola: an analysis of research needs

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Abstract

The cabbage root fly (=cabbage maggot), *Delia radicum*, has increased in importance over the past two decades as a pest of canola (oilseed rape) in Canada. Although *D. radicum* has been a part of the North American insect fauna for some time, it is not native, so the introduction of natural enemy species from Europe is being considered for integration with existing management strategies. The biology of *D. radicum*, the injuries it causes to the crop, and strategies already available for its control are briefly reviewed, followed by the process by which *Aleochara bipustulata*, a predator and parasitoid of *D. radicum*, was identified as the most promising candidate for introduction in a classical biological control programme. The literature on *A. bipustulata* and other species in the same genus is then brought together to illustrate the importance of studies to evaluate the potential of *A. bipustulata* to provide control, and its effects on non-target species.

Introduction

Agricultural commodities, including oilseeds, are a mainstay of the Canadian economy and support a vital rural society. Cultural varieties of oilseed rape (*Brassica napus* L. and *Brassica. rapa* L. [Brassicaceae]) with <2% erucic acid and <30 μmoles/gm of glucosinolates in oil-free meal from their seeds are called double low oilseed rape or canola [1]. Coordination by the Canola Council of Canada, research by university and government scientists, and increased involvement of the private sector have contributed to the development of more than 200 canola cultivars [1, 2]. Farmers who integrate canola in their crop rotations benefit from increased net returns and decreased variability in annual income [3]. Between 2000 and 2005, 3.6–5.3 million hectares of canola were harvested in Canada, with the vast majority grown in the prairie provinces of Alberta, Saskatchewan and Manitoba [4]. The area planted on the prairies will have to increase substantially over the next decade to provide a stable supply for the burgeoning biodiesel industry [5]. The abundance of herbivorous insects depends on the abundance of their host plants [6, 7], so as more canola is grown on the prairies, insect pests will likely become more numerous and damaging. To meet the challenge of this evolving pest community will require that production and pest management techniques be constantly re-evaluated and integrated.

This review is about research requirements for improving integrated management of an exotic canola pest

in Canada by the introduction of natural enemies from Europe. The biology of the pest, the damage it causes to canola and existing control strategies are described. This is followed by a description of how a candidate for introduction was identified, and an outline of what is known about the biology and ecology of this candidate. The final section addresses areas where research could be focused to improve the probability of the natural enemy's establishment, and to ensure it is introduced only if it is effective and does not negatively affect non-target species.

Biology of *Delia radicum*

All parts of canola plants are eaten by various insect herbivores [8]; roots are fed upon by larvae of *Delia* Robineau-Desvoidy (Diptera: Anthomyiidae). The primary pests, species which can attack uninjured plants, are *D. radicum* (L.), *Delia floralis* (Fallen), and *Delia planipalpis* (Stein) [9–11]. *Delia platura* (Meigen) and *Delia florilega* (Zetterstedt) typically feed on tissue already invaded by the three primary pests [11]. *D. platura* is often the most abundant species trapped as an adult in canola [12–14]. *D. floralis* is the predominant primary pest in northeastern Alberta and the agricultural region around the Peace River, where relatively high summer moisture deficits and low summer precipitation are typical [15]. These facts notwithstanding, the most important *Delia* pest of canola in Europe [16] and Canada [17–19] is *D. radicum*. Larvae of *D. radicum* were first noticed feeding on roots of oil-seed rape, in Manitoba in 1958 [20]. Later, in 1981, a survey in Alberta revealed that root maggot injury was widespread, particularly in the northern part of that province [9]. A survey in Manitoba from 1985 to 1988 again found the percentage of roots infested per field to be higher in agricultural areas further north [17]. The percentage of roots infested per field and the average level of injury to plants increased in the time between the earlier studies and a survey across the three prairie provinces in 1996 and 1997 [21]. Reductions in yield caused by root maggot infestations are estimated to cost CAN$100 million during years favourable to the insects [19, 21].

The elongate, white eggs of *D. radicum* are laid at the base of host plants, on or just below the soil surface [11, 22]. Larvae develop through three larval instars while feeding on the root tissue [11]. The pupa is formed inside a puparium, the hardened cuticle of the third larval instar [23]. Diapause is induced if developing larvae are exposed to a combination of low temperature and short photoperiod [24–27], in which case the pupa overwinters inside the puparium [28]. In many parts of the world, several generations occur each year before diapause is induced [10]. On the Canadian prairies, however, most of the population in canola is induced to diapause during the first generation [29]. Selection is expected to favour a minimal second generation on the prairies because the most abundant host, spring-planted canola, is normally harvested before the second generation can develop to the overwintering stage.

Eggs are laid in a process that is thought to involve three stages, which together are the basis of the 'appropriate–inappropriate landings' theory [30]. In the first stage, the female is excited and stimulated to land by volatile chemicals from host plants [31], specifically products of hydrolysis of glucosinolates [32]. In the second stage, the flies use visual stimuli to find a plant on which to land. Having landed, female *D. radicum* make short flights off the plant and back [33, 34]. The third stage, a decision about laying an egg at the base of the plant, occurs as the female perceives chemical compounds from the plant through her tarsi. If sufficient stimuli are accumulated in a series of successive landings, the female will lay an egg in soil at the base of the plant [33, 34], but if she lands on a plant without the stimuli the process of stimulus accumulation starts anew [34]. Numerous non-crop plant species stimulate *D. radicum* oviposition and are suitable for complete development of the larvae [35, 36]. On the Canadian prairies, the most important of these is stinkweed, *Thlaspi arvense* L. (Brassicaceae) [10, 29].

Injury to Canola Caused by *D. radicum*

Injury to canola occurs when the *D. radicum* larva feeds on the roots. Once the first instar has penetrated the periderm, the larva feeds on phloem, periderm and secondary xylem, and creates a vertical furrow in the root as a second and third instar [37, 38]. Feeding injury reduces root weight, dry matter content and sugar content of the roots [39]. Injured roots are more likely to be invaded by *Fusarium* species [15, 29, 40] but not by *Rhizoctonia solani* Kuehn [41]. High levels of injury cause plants to lodge [40] or die [29].

The relationship between feeding injury to roots and reduction in yield is still ambiguous despite several attempts at characterization. In the laboratory, *D. radicum* feeding on roots of *B. rapa* reduces overall plant biomass, number of seeds per plant, number of racemes and number of pods on axillary racemes [37]. In field trials the situation is complicated by the presence of other *Brassica*-feeding *Delia* spp. In field trials Griffiths [40] showed that root injury reduces the number of seeds and seed weight. When average root injury to *B. rapa* in 1 m^2 plots increases from zero to 50% of the root surface, seed yield can be about 50 g/m^2 less, although this effect was found only in one year of a two-year study [42]. Conversely, field studies by Klein-Gebbinck and Woods [41] found that injury to roots did not affect seed size or the relationship between plant size and seed yield. Likewise, Soroka *et al.* [43] found no significant effect of level of infestation on yield of canola in field cages. However, the highest level of injury observed by

Klein-Gebbinck and Woods was 32% of the root surface, and the greatest reduction in number of seeds per plant occurs when at least 25% of the surface is injured [37, 42, 44]. Also, determining whether a canola pest influences the relationship between plant size and yield may not be the best way to assess the pest's impact [41]. In any event, roots with 50–100% of the surface injured are not uncommon across the prairies [21], so aggregated over the large area planted to canola each year the small average losses at the farm scale constitute an expensive pest problem in western Canadian canola production as a whole. Significant progress has already been made in developing strategies to control *D. radicum* in canola.

Existing Control Strategies for *D. radicum*

The chemical, cultural and biological control strategies outlined by Finch [45] for control of *Delia* species in vegetable production can also be considered as they relate to canola in western Canada. Granules of cyclodienes applied in furrow at the time of seeding reduce injury to *B. rapa* by more than 90% [20]. Diazinon applied weekly as a soil drench reduces root injury in small experimental plots [46]. However, no insecticides are registered for *D. radicum* control in canola in Canada [21], so chemical control will not be considered further.

Cultural control involves activities that alter the pest's environment to be outside its optimal range, or ideally outside its tolerable range, for one or more important environmental factors [47]. The options for cultural control are restricted by their influence on the crop and net return to the producer. Several strategies for cultural control of the cabbage root fly in canola have been identified. Decisions about implementing cultural controls in prairie canola based on the expected level of root maggot infestation are supported by a predictive model based on ecozone, canola species and the previous season's rainfall and temperature [21].

One cultural control practice is the selection of what species or cultivar to plant. *B. napus* receives fewer eggs and less injury than *B. rapa* [40, 48] and certain cultivars of both species are both more attractive for oviposition and more prone to injury [48, 49]. *Sinapis alba* L. (Brassicaceae) plants are less preferred for oviposition [48] and less injured than canola species [48, 50]. Certain hybrid accessions derived from crosses between *B. napus* and *S. alba* are also resistant [46, 50] and quantitative trait loci associated with this resistance have been identified with the intention of developing resistant cultivars [50].

Deciding when to plant is also important. Seeding canola in early June instead of mid-May reduces injury by *D. radicum*, but negatively influences yield to the extent that it cannot be recommended [51]. Dormant seeding in the fall and seeding earlier in the spring sometimes [49] but not always [52, 53] reduces the level of injury

by root maggots. As early spring seeding also results in increased yield it is recommended [52].

Decisions made about how to plant and manage the canola crop influence root maggot infestation further still. Seeding at a rate of 7–11 kg/ha reduces the level of injury to roots relative to lower seeding rates [44, 54]. Spacing rows 17–25 cm apart reduces oviposition by the pest relative to narrower spacing and optimizes gross returns [44]. Although reducing tillage increases the overwintering survival of *D. radicum* [55] and may result in more injury to roots [44]; this is not always the case [54] and reducing tillage increases the gross margins for canola crops [55]; reduces soil erosion and uses less energy without affecting yield [56]. Delaying weed removal from when the crop has reached the two-leaf stage to the four-leaf stage reduces the severity of root maggot infestation and maintains yield as high as or higher than earlier weed removal [49]. Planting larger seeds [57] and applying fertilizer and recommended rates [52, 58, 59] are advocated in spite of neutral or even positive effects on root maggots, because of other agronomic benefits.

The third category of control strategies listed by Finch [45] is biological control. In biological control, a pest population is regulated by its natural enemies [60]. There are several different types of biological control, and placement of a particular option into a category requires a geographical frame of reference. The frame of reference used here is the Canadian prairies.

The natural enemies of *D. radicum* include parasitoids, predators and pathogens. Parasitoids of minor significance on the Canadian prairies are *Aleochara verna* Say (Coleoptera: Staphylinidae), *Phygadeuon* spp. (Hymenoptera: Ichneumonidae), *Aphaereta minuta* (Nees) (Hymenoptera: Braconidae), and *Trichopria* sp. (Hymenoptera: Proctotrupidae) [61]. More important are *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae) and *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae) [61, 62]. Adult *A. bilineata* feed on *D. radicum* eggs and larvae, and *A. bilineata* larvae chew a hole in *D. radicum* puparia, enter, and develop inside while feeding on the *D. radicum* pupa [63–65]. Female *T. rapae* oviposit into *D. radicum* larvae, and the *T. rapae* larvae develop as endoparasitoids until *D. radicum* pupates, and then as ectoparasitoids on the pupae still within the puparia [66]. Carabid and staphylinid beetles feed on immature *D. radicum* [67–69]. Outbreaks among adult *D. radicum* of the fungi *Entomophthora muscae* (Cohn) Fresenius [70] and *Strongwellsea castrans* Batko and Weiser (Zygomycota:Entomophthoraceae) [71] have been reported. Finally, larvae are somewhat susceptible to entomopathogenic nematodes, particularly *Steinernema* sp. (Rhabdita: Steinernematidae) [72–74].

Conservation biological control is based on the idea that agricultural activities have disrupted a pest's natural enemies, and amendments can be made to make the environment more favourable for these natural enemies and thereby improve control [60]. No conservation

biological control strategies have been devised explicitly for control of *D. radicum* in canola on the prairies, although conventionally tilled plots have significantly more *Agonum placidum* Say (Coleoptera: Carabidae) than untilled plots [54] so the relative proportion of *D. radicum* eggs eaten may be higher. Insecticides used against *D. radicum* in *Brassica* vegetables negatively affect predators [69], and may do so when these are applied against other pests in canola crops as well, so reducing insecticide applications in canola could be a worthwhile conservation biological control opportunity. However, modifications that increase the abundance of *D. radicum* predators will not necessarily result in improved control, as the predators can compete with and feed on one another [75, 76].

Augmentation biological control is the release of particular natural enemy species in large numbers in places where they are missing, arrive too late in the growing season, or occur naturally in numbers insufficient for the desired level of control [60]. Rearing and releasing carabids for *D. radicum* control does not work well because many *D. radicum* eggs are slightly below the soil surface and not eaten [77]. *A. bilineata* can be mass-produced [78, 79], and releasing two beetles per cabbage plant significantly reduces the proportion of *D. radicum* that complete development [80], but production of sufficient *A. bilineata* to control *D. radicum* on even a portion of the five million hectares of canola in Canada is unrealistic.

Any new strategies to manage *D. radicum* should be compatible with the above-mentioned methods. One such strategy is the classical biological control, where a natural enemy of an exotic pest is imported from the area where both species originated to the region the pest has invaded. Introduction of species of natural enemies to Canada may help to reduce the annual variations in *D. radicum* density and levels of parasitism, which are less stable than in Europe [62]; introduced natural enemies may reduce *D. radicum* densities in canola crops [19]. The most promising place to search for natural enemy species to introduce is north Western Europe, where the *D. radicum* now in North America most likely originated [81].

Selecting a Candidate Classical Biological Control Agent for Further Study

Classical biological control of *D. radicum* in Canada has already been attempted. A survey of the parasitoids of *D. radicum* in Europe was conducted from 1949 to 1954 [82, 83]. The species present in Europe were compared with those already in Canada [84] and five 'missing' species were introduced. Two of these species, *A. bilineata* and *T. rapae*, were subsequently determined to be already part of the Canadian fauna but known by different names [85]. *Phygadeuon trichops* Thomson (Hymenoptera: Ichneumonidae) and *Aphaereta* sp. (Hymenoptera: Braconidae) were also introduced but seem not to have

established [85]. The fifth species supposed to have been introduced was *Aleochara bipustulata* (L.) [85], a species similar in many ecological respects to *A. bilineata*. However, it was not possible before 1986 to distinguish *A. bipustulata* from at least three structurally-similar species of *Aleochara* [86], so another species may in fact have been released. Whether or not *A. bipustulata* was introduced in the 1950s, there is no evidence that it is currently found in North America [87].

The first attempt at classical biological control of *D. radicum* in Canada is illustrative of avoidable mistakes in several respects. First and foremost, Wishart *et al.* cannot be held responsible if taxonomic concepts for the *Aphaereta* and *Aleochara* species they introduced were not yet well refined, but if voucher specimens had been deposited it would be possible now to re-examine which species were involved. A related problem is that information on the origin and number of individuals released is now lost, so it is impossible to determine whether establishment failed because too few were released, the populations introduced were an inappropriate match with the Canadian climate, or for some other reason.

Work is now well underway to revive a classical biological control programme for *D. radicum* in Canada, with a focus on reducing damage to canola. To choose a natural enemy for further study, the community of parasitoids attacking *D. radicum* was compared between the areas of origin and introduction to identify and subsequently fill vacant niches in Canada [88, 89]. In 2000, samples of all immature stages of *D. radicum* were collected in canola fields at six locations in western Canada and reared for parasitoids [61]. No egg parasitoids were found. The seven species of larval and pupal parasitoids collected were *A. bilineata*, *A. verna*, *T. rapae*, two *Phygadeuon* species, *A. minuta* and a *Trichopria* species. In 2001 and 2002, similar collections and parasitoid identifications were made in canola and *Brassica* vegetable crops at 12 locations in Switzerland and Germany [61]. Again, seven parasitoid species were found: *T. rapae*, *A. bilineata*, *A. bipustulata*, *P. trichops* and another *Phygadeuon* species, a *Trichopria* species and *A. brevipennis* Gravenhorst, of which only the first three were common. On numerous occasions *A. bipustulata* has been reported to occur in North America, but two staphylinid systematists agree that the North American beetles that resemble *A. bipustulata* in external structure differ in critical respects in the structure of their genitalia [90, 91]. Entomological museums across North America were therefore contacted so that specimens previously identified as *A. bipustulata* could be re-examined. All these specimens that were collected in North America and previously identified as *A. bipustulata* were determined to be *A. verna* [87]. As the only parasitoid present in appreciable numbers that was not already in Canada, *A. bipustulata* became the candidate for introduction [61].

Whenever a natural enemy is considered for introduction to another part of the world, it is critical to have

a good understanding of its biology and ecology. Basic information can be gained from the literature, and the gaps subsequently filled with focused research. To succeed in Canada, *A. bipustulata* must be able to establish, complement existing natural enemy species that reduce *D. radicum* problems for canola producers, and pose insignificant risk to North American species other than the target pest. Information about *A. bipustulata* and other species in the genus relevant to the problems of establishment, effectiveness and non-target effects is provided below, followed by the opportunities for research.

The Biology of *A. bipustulata*

Adults of *Aleochara* species are found together with dipteran eggs and larvae, on which the adults feed, often in or around decaying vegetation, dung and carrion [90]. The larvae of all *Aleochara* species are ectoparasitoids of Cyclorrapha (Diptera) species [86, 90] except the phylogenetically ancient *Aleochara clavicornis* Redtenbacher [92], whose larvae can complete development on meat, dipteran larvae or puparia [86]. The subgenus *Coprochara* Mulsant and Rey, one of the seven *Aleochara* subgenera [90], contains *A. bipustulata* and 29 other species [91]; hosts are known for only 12 of these [86]. The subgenus is clearly monophyletic in both morphological [90] and molecular [92] aspects.

The most complete information about the seasonal activity of adult *A. bipustulata* is contained in a paper by Jonasson [93], who collected *A. bipustulata* in pitfall traps weekly from mid-May to September in *Brassica* vegetable plots in Sweden. The beetles were already abundant by the first week of sampling, indicating that *A. bipustulata* are active before the middle of May. There are four progressively smaller peaks in adult activity in southern Sweden: late May, mid-June to early July, late July, and early September. Oviposition by *D. radicum* on the Canadian prairies is often in mid-June [15, 29, 51, 94, 95], although it is sometimes slightly later [13]. In southern Sweden, oviposition by the first generation of *D. radicum* is also in mid-June, and it is at this time in particular when *A. bipustulata* adults are more abundant than *A. bilineata* [93]. As *A. bilineata* adults in Canada may emerge later than the time of *D. radicum* oviposition [96], and there is predominately only one generation of *D. radicum* on the Canadian prairies, control could probably be improved by introducing a species like *A. bipustulata* to feed on eggs and early instar larvae. Parasitism of *D. radicum* puparia by larvae of *A. bipustulata* and *A. bilineata*, in addition to predation by adults, is what makes these two species particularly intriguing agents for biological control.

The Prospects for Establishment

A. bipustulata is distributed in the Oriental and Palaearctic regions [91]. Specimens of *A. bipustulata* have been collected as far north as Fredrickstad in Norway, and as far south as Berguent, Algeria and from maritime climates to severe continental climates of mountainous central Asia [91]. Since *A. bipustulata* is so widely distributed in the Palaearctic, the probability of its survival in Canada is high. Its distribution could also indicate that certain source populations are more appropriate for introduction. *Aleochara bipustulata* from central Asia are expected to survive winter on the prairies better than a population collected in Algeria.

The Prospects for Effectiveness

As a predator, *A. bipustulata* is one of several Coleoptera species that destroy *D. radicum* eggs and larvae in Europe [97]. In Canada, *A. bipustulata* may either add to the level of predation, or replace predation that would have occurred anyway by another species. As a parasitoid, *A. bipustulata* often is prevalent in a smaller percentage of puparia than *A. bilineata* or *T. rapae* in Europe [83]. However, in northwestern France [98] and southern Sweden [93] *A. bipustulata* adults are more abundant than those of *A. bilineata*. In vegetable *Brassica* crops in France, parasitism of *D. radicum* puparia by *A. bipustulata* reaches 44%, and 98% of puparia can be parasitized by either *A. bipustulata* or *A. bilineata* [98]. In Europe, spring-seeded canola is a favourable habitat for *A. bipustulata* [61]. Ultimately, the effectiveness of *A. bipustulata* in Canada will depend on how it interacts with those species already present, and its adaptability to *D. radicum* in spring-seeded canola crops in Canadian climatic conditions.

The Prospects for Non-Target Effects

Canadian Diptera species could be at risk of parasitism by *A. bipustulata* if they match its ecological host range, and understanding how hosts are selected will help to guide research about non-target effects. The ecological host range of an insect parasitoid is dictated by which hosts fulfil the requirements of each of five sequential steps: host habitat location, host location within the habitat, host acceptance, host regulation and host suitability [99, 100]. The first three steps are typically activities of a searching adult female and the last two usually involve an immature parasitoid. For *Aleochara*, however, the female lays eggs in the soil and the first instar larva must actively locate and accept hosts itself. Our knowledge about the processes of habitat and host location, host acceptance, host regulation and host suitability in *Aleochara*, and when information is available for *A. bipustulata* in particular, are summarized below. Then, the habitats from which *A. bipustulata* are recorded in the literature and, when applicable, information about what hosts were parasitized are discussed.

The attraction of adult *Aleochara* to host habitat and hosts is known to involve volatile chemicals. In an olfactometer, adult *A. bilineata* prefer to move toward *D. radicum* larvae, frass, or host plants over clean air, and prefer infested host plants to uninfested ones [101]. Airborne volatiles from defatted mustard seed meal attract *A. bipustulata* but not *A. bilineata* [102]. Adults are also involved in the acceptance of hosts by deciding to lay an egg or not. In laboratory arenas, female *A. bilineata* lay more eggs in the vicinity of a host plant infested with eggs or artificially buried *D. radicum* puparia than in sand [103]. The adults can detect presence and parasitism status of host puparia, and lay more eggs close to an injured plant with puparia than an injured plant alone, and more close to an injured plant with unparasitized puparia than one with parasitized puparia [103]. Based on these studies, one expects female *A. bipustulata* are similarly involved in the location of hosts by laying eggs preferentially in certain areas, but no work has yet been published about oviposition site selection by *A. bipustulata*.

Once the egg hatches, the larva needs to locate and accept a host. In one study, the probability of larvae of both *A. bilineata* and *A. bipustulata* locating hosts decreases with increasing distance the larvae are placed from puparia in Petri dish arenas [65], suggesting chemical cues from puparia do not guide them. However, the experimental design did not investigate the possibility that parasitoid larvae follow a trail left by the migrating host larva, a phenomenon that occurs with the congener *Aleochara bisolata* [104] (as *Aleochara* sp., see [86]). Wingo *et al.* [105] suggest searching may be random until the larva enters the threshold zone of some olfactory stimulus. After hosts are located, their acceptance by the parasitoid larva must involve at least two steps: the acceptance of the puparium for chewing an entrance hole, and acceptance of the pupa within for feeding. The location of the entrance hole in *D. radicum* made by *A. bilineata* larvae is most often on the puparium's dorsal side, in the abdominal region where the ridges on the puparium surface are lowest [106]. Larvae of both *A. bilineata* and *A. bipustulata* prefer to parasitize puparia with a pupa inside to one with a pharate adult fly [107], and avoid puparia already occupied by another *Aleochara* larva [108]. Given a choice, *A. bipustulata* larvae prefer smaller *D. radicum* puparia in laboratory arenas [109], and may also do so in nature [93], but as sample size increases, this tendency is no longer apparent [110]. Having successfully entered a puparium, *A. bisolata* larvae may not feed, suggesting that in at least some *Aleochara* spp. the final step in host acceptance requires a feeding stimulus or that an antifeedant stimulus be absent [111].

Acceptance of a puparium by an *Aleochara* larva depends on the host species. In laboratory arenas, *A. bipustulata* larvae are equally likely to accept *Delia antiqua* Meigen or *D. platura* as *D. radicum* puparia, but do prefer *D. radicum* to a species of *Lonchaea* Fallén [109].

Wright *et al.* [111] determined that *Aleochara bisolata* larvae typically prefer one species to another when given a choice, and sometimes first attack one species, then reject it and attack another. The preference of *A. bisolata* larvae for particular species is related to puparial mass [111]. Clearly, the acceptance of a host by an *Aleochara* larva is an intricate process, and involves puparium mass, ridge size, the presence of antifeedants or feeding stimuli, and possibly other factors associated with host species or condition. It is difficult to design experiments that isolate or combine these factors so that a general model of host acceptance for *A. bipustulata* could be constructed. Such a model would be useful for assessing risk to non-target species.

The suitability of accepted hosts for complete development is the next consideration in the host range of *Aleochara*. Fuldner [65] noted two important characteristics of the host in determining suitability. Firstly, *Aleochara* larvae feed on the liquid haemolymph of the developing dipteran pupa, so species that develop from pupa to adult more quickly provide less temporal availability of liquid food, and an adult fly emerges unharmed if the *A. bipustulata* larva enters the puparium too late. That puparia entered too late are less suitable has been demonstrated for *A. bipustulata*, *A. bilineata* [107], *A. bisolata* [104], *Aleochara tristis* Gravenhorst [112, 113] and *Aleochara taeniata* Erichson [114]. Secondly, the cessation of feeding by the third instar *Aleochara* larva is based on some physiological clock, rather than how much of the pupa remains uneaten; decay of uneaten host material can result in the death of the immature parasitoid [65].

North American Diptera species for which the five sequential steps (host habitat location, host location within the habitat, host acceptance, host regulation and host suitability) can be completed by *A. bipustulata* could suffer non-target effects if *A. bipustulata* is introduced to Canada. The literature about the hosts and habitats of *A. bipustulata* in its native range will help to identify which North American species these could be. In this context, it is worth remembering Maus *et al.* [86] caveat that records prior to Lohse [115] cannot possibly have distinguished *A. verna* from *A. bipustulata*. Several *Aleochara* species are quite similar in external anatomy, with reddish spots on the elytra, and species such as *A. bipustulata*, *A. verna* and *A. binotata* Kraatz may be misidentified as one another [86]. However, the records may have been correct and it is worthwhile to assemble them in the context of assessing *A. bipustulata*'s host range.

The target habitat, broadly defined as cruciferous crops, has the greatest number of literature records about the presence of *A. bipustulata* and parasitism of Diptera species. Besides *D. radicum*, species that reportedly hosted *A. bipustulata* in cruciferous crops are *D. platura*, *D. floralis* and *D. florilega* [86]. These are all pests in cruciferous crops [11], and parasitism by *A. bipustulata* of these species in Canadian canola fields can only be

considered beneficial. Negative evidence, where parasitism was looked for but not found, can also be useful [116]. For example, Jonasson [93] collected an unspecified number of puparia of species in the dipteran families Agromyzidae, Drosophilidae, Fanniidae and Muscidae around cabbage and cauliflower roots in southern Sweden, reared them out, and found no *A. bipustulata*.

The second largest number of records about the habitat associations of *A. bipustulata* concerns its occurrence in dung. In France, *A. bipustulata* were collected in dung-baited pitfall traps and emerged from *Adia cinerella* (Fallen) (Diptera: Anthomyiidae) puparia that developed in cow dung, but not from puparia of Muscidae, Sepsidae and Sphaeroceridae species collected in the same pats [117]. Other reliable records [118, 119] confirm that cow dung is a habitat of *A. bipustulata* at least occasionally. The reports of *A. bipustulata* adults in horse [120, 121], yak and marmot dung [120] are less certain. Three species, *Ravinia pernix* Harris, *Sarcophaga* (*Helicophagella*) *gorodkovi* (Grunin) and *Sarcophaga* (*Helicophagella*) *altitudinis* (Grunin) (Diptera: Sarcophagidae) ([122] for synonyms) reportedly host *A. bipustulata* in these sorts of dung [120]. *Physiphora demandata* F. (Diptera: Otitidae), *Lonchaea* sp. (Diptera: Lonchaeidae) and *Musca domestica* L. (Diptera: Muscidae) puparia collected from nature reportedly host *A. bipustulata* [123, 124], but it is not clear whether the puparia were collected in cow dung or supralittoral algae, and *A. verna* is listed as a possible synonym of *A. bipustulata* [124], so the identity of the beetles is uncertain. Finally, reliably identified *A. bipustulata* adults emerged from puparia of unidentified Diptera collected in manure piles in Kazakhstan (Roger Moon, personal communication, 2006).

Parasitism of the wheat bulb fly, *Delia coarctata* (Fallen) (Diptera: Anthomyiidae), by *A. bipustulata* has been reported several times. Like *D. radicum*, *D. coarctata* is a European species now in North America [125]. Eggs are laid on bare soil, and *D. coarctata* is a pest of winter wheat, potato and sugar beets. In Europe, Dobson [126] found 2 and 8% of *D. coarctata* puparia in two wheat fields supported development of *A. bipustulata*. Puparia of *D. coarctata* only hosted *A. bipustulata* occasionally in two German studies [127, 128], where the habitat could have been sugar beets, potatoes, or both. All three records of development in *D. coarctata* puparia may have been misidentifications. Another host record from the sugar beet habitat concerns one or more species of *Pegomya* Robineau-Desvoidy, but since the species concepts in this genus were recently revisited [129], it is difficult to know which species was hosting the *Aleochara*. *Pegomya betae* Curtis and *Pegomya hyoscyami* (Panzer) are not synonyms as suggested by Maus *et al.* [86], so the reported development of *A. bipustulata* [130] may have been in puparia of either or both species. Of course, the '*A. bipustulata*' may have been another *Aleochara* species as well. A Polish survey of parasitoids of *P. betae* found *A. bilineata* but not *A. bipustulata* [131].

There is a single record of *A. bipustulata* in carrion in Europe. Puparia of *Lucilia sericata* (Meigen) (Diptera: Calliphoridae) were parasitized by *A. bipustulata* in an open area but not in forest, and puparia of *Calliphora vicina* Robineau-Desvoidy (Diptera: Calliphoridae) were parasitized only by *A. curtula* in both habitats [132].

In bean fields, *A. bipustulata* has been recorded as a parasitoid of *D. platura* and *D. florilega*. These records are suspect, though, as Dinther [133] apparently assumed puparia with *Aleochara*-like exit holes had been parasitized by *A. bipustulata*, and Miles [134] did not specify if the parasitized puparia had been collected in cabbage or bean fields. Finally, up to 26% of *D. platura* puparia were parasitized by *A. bipustulata* in a Hungarian study [135], and beans are mentioned along with several other crops, but it is not clear what crop was sampled to assess the level of parasitism.

In addition to these reported natural hosts, two other species are within *A. bipustulata*'s fundamental host range. *Piophila casei* (L.) (Diptera: Piophilidae) [123] and *D. antiqua* [109] support complete development in the laboratory.

Adult *A. bipustulata* have also been reported in diverse habitats without any indication about whether the beetles were foraging for hosts. One beetle was collected in a *Formica rufa* L. (Hymenoptera: Formicidae) nest [136], and *A. bipustulata* is reportedly common in pea fields [137]. One adult was found under bark of a *Betula* stump, and another under the bark of a dead, standing *Betula* (Oscar Vorst, personal communication, 2006). On nine occasions small collections have been made from shoreline debris [119]. Pitfall traps in carrot fields [138] and apple and pear orchards [139] catch *A. bipustulata*. Emergence traps in oat fields [140] and sticky traps in onion fields [65] do likewise. Along rivers in Scotland *A. bipustulata* occurs most frequently in dry open sites and disturbed sites, and less frequently in areas with trees and dense vegetation [141]. On Scottish moors, *A. bipustulata* is found most frequently in grassy areas without *Calluna vulgaris* L. (Ericaceae) [142]. Along coastal salt marshes, *A. bipustulata* is found associated with *Juncus gerardii* Loisel (Juncaceae) [143].

At first glance, *A. bipustulata* seems neither narrowly specific to *D. radicum*, nor to the habitats of cruciferous crops. However, in addition to the possibility that many of the records are about other species of *Aleochara*, several inconsistencies are apparent. For example, *A. bipustulata* adults are reportedly common in onion crops in Europe [65], but field-collected onion fly, *D. antiqua*, have not been parasitized by *A. bipustulata* even though it is a suitable laboratory host [86]. Likewise, *A. bipustulata* may be associated with dung and carrion in Europe, but it is not part of many inventories of species involved in succession during the break down of dung, nor species of importance to forensic entomology. Whether *A. bipustulata* is specific to *D. radicum* and cruciferous crops requires further study.

Research Needs

Many natural enemy species introduced for biological control fail to reduce problems caused by the pest [144, 145]. Failure can result if the individuals introduced do not find mates [146]. The probability that *A. bipustulata*, if introduced to Canada, will not establish because of inability to find mates is not high, however, since adults can be attracted to canola plots where defatted mulch of white mustard seeds has been spread around the roots [102]. Another cause of past failure in classical biological control has been poor synchronization between the pest in the area of introduction and the population of natural enemy introduced [145]. The *D. radicum* on the Canadian prairies develop slowly in the spring after diapause, before adult flies emerge, relative to populations from eastern North America and Europe [110, 147]. If *A. bipustulata* adapted to rapidly developing *D. radicum* from Europe are introduced to Canada, they may be poorly synchronized with *D. radicum* on the prairies and therefore ineffective. Research is required to characterize post-diapause development of *D. radicum* on the Canadian prairies, relative to other parts of the world, and to use this information in the identification of a well-suited population of *A. bipustulata* for introduction to western Canada.

The interaction of *A. bipustulata* with parasitoids of *D. radicum* already in Canada also requires further study. Competition between *A. bipustulata* and *A. bilineata* or *T. rapae* could be considered as a non-target effect of biological control, and reduced mortality of *D. radicum* could also result. In small laboratory arenas, larval *A. bilineata* prefer to parasitize *D. radicum* puparia that have not already been parasitized by *T. rapae* [148] and *A. bipustulata* [108]. Larval *A. bipustulata* similarly prefer to parasitize *D. radicum* not already parasitized by *A. bilineata* [108], and are expected to show disinclination to attack puparia already parasitized by *T. rapae*. As the parasitoids may not be always be given a choice between parasitized and unparasitized puparia in nature, information should be gathered about whether the parasitoids complement one another and increase mortality of *D. radicum* in more natural settings. Predicting how effective *A. bipustulata* will be in Canada will require life table or similar studies to determine the importance of predation and parasitism by *A. bipustulata* relative to other sources of *D. radicum* mortality.

It is necessary to assess the risks to non-target species of *A. bipustulata* larvae developing as parasitoids within their puparia. Exposure of a representative group of non-target species to the parasitoid in a series of experiments that increasingly mimic nature is recommended [149]. A preliminary list of species to test could be compiled based on the reported hosts and habitats of *A. bipustulata*, and focusing on dipteran species from the seven families of recorded hosts which also have larvae in habitats from which *A. bipustulata* has been reported.

In doing so, the non-target species to test will be identified based on ecological and taxonomic relatedness to *D. radicum* and other reported hosts [150]. Several beneficial Diptera, perhaps members of the Syrphidae or Tachinidae, should be tested as well, to ensure that the introduction of *A. bipustulata* will not disrupt natural control of other pests [150]. The results of these tests will provide a picture of how specific *A. bipustulata* is to *D. radicum* as a parasitoid.

Adult *A. bipustulata* are predators, but the range of prey the adults consume is not yet understood. If the adults do not feed exclusively on immature *D. radicum*, the potential exists for further non-target effects. Extensive studies will be required about the range of prey eaten before a decision can be made about whether introducing *A. bipustulata* to Canada is environmentally responsible or not.

Conclusions

D. radicum is an important pest of spring-seeded canola, and its management in the future will require an integrated approach. Canadian canola farmers already can reduce damage with prudent decisions about what varieties to plant, and how these varieties are planted. As a non-native species, *D. radicum* is also a promising target for classical biological control by the introduction of *A. bipustulata*. It is envisaged that, if introduced, *A. bipustulata* would complement the existing agronomic strategies. On the basis of its distribution, *A. bipustulata* seems likely to establish. Selecting appropriate *A. bipustulata* populations will further increase the probability of establishment. Research is required to determine whether it will also complement the natural enemies of *D. radicum* already in Canada. Impacts to non-target species are also an important concern, and one that must be addressed by determining the range of hosts that can support *A. bipustulata* larval development, the range of prey eaten by *A. bipustulata* adults, and the habitats used by *A. bipustulata*. A final decision about importing *A. bipustulata* awaits the outcome of risk assessment, but the prospects for reviving classical biological control of *D. radicum* are encouraging.

Acknowledgements

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