

POST-DIAPAUSE DEVELOPMENT OF *DELIA RADICUM* (DIPTERA:
ANTHOMYIIDAE) AND HOST RANGE OF *ALEOCHARA BIPUSTULATA*
(COLEOPTERA: STAPHYLINIDAE) FOR CLASSICAL BIOLOGICAL CONTROL IN
CANADIAN CANOLA

By

Lars Andreassen

A thesis
submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements for the degree of

Master of Science

Department of Entomology
University of Manitoba
Winnipeg, MB

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Knut Rognes and Bernhard Merz identified the Calliphoridae species. Graham Griffiths identified the *Pegomya* species. Adrian Pont identified the Muscidae species. Russell Bonduriansky identified *Stearibia nigriceps*. Stephen Marshall identified *Spelobia luteilabris*. Iain MacGowan identified the European Lonchaeidae.

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ABSTRACT

Aleochara bipustulata, a European natural enemy of *Delia radicum*, shows promise as a biological control agent in Canadian canola. Post-diapause development of *D. radicum* and *Aleochara bilineata* was studied in the laboratory. Prairie *D. radicum* developed more slowly than from Ontario, suggesting particular source populations of *A. bipustulata* may be better suited to western Canada than others. *Aleochara bilineata* develops too slowly for effective predation of early immature *D. radicum*. *Aleochara bipustulata*'s host range was studied in the laboratory and its habitat associations studied in Europe. Beneficial Diptera species were either unsuitable hosts, or for *Lonchaea corticis* found in habitats not visited by *A. bipustulata*. Suitable laboratory host species were relatively small or closely related to *D. radicum*. Species with unusual puparia were less likely to be accepted as hosts than *D. radicum*. Species which develop quickly in the pupal stage, or with relatively heavy puparia, were unsuitable hosts.

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1. INTRODUCTION

Introducing natural enemies from one part of the world to another is a long-term and cost-effective strategy for pest control (DeBach 1964). It is however not uncommon for the introduction to fail, either because the introduced species does not establish or provides insignificant control of injury (Turnbull and Chant 1961; Beirne 1985).

Introducing a well-synchronized population is recognized as one way to improve the likelihood of success. In addition, species moved outside of their native range can cause ecological problems (Elton 1958), and this applies to biological control agents as well (Howarth 1991). We can never be certain about the ecological risk introducing a species might carry with it, but several recent papers (*e.g.* van Lenteren et al. 2003, 2006a, 2006b) outline methods which should reduce the risk of intentional introduction to a minimum.

The cabbage maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae), is an increasing problem as a pest of canola in Canada (Soroka et al. 2004). Agronomic practices can be adjusted to reduce losses due to injury caused by the cabbage maggot (Dosdall et al. 1998), but their adoption will depend on profitability, and control using these measures could be complemented with others. As *D. radicum* was introduced to North America from Europe, introducing European natural enemies is an option for its control (Biron et al. 2000; Soroka et al. 2002). *Aleochara bipustulata* L. (Coleoptera: Staphylinidae) is the most promising candidate for introduction (Hemachandra 2004). Adult *A. bipustulata* feed on immature *D. radicum*, and larvae of *A. bipustulata* parasitize *D. radicum* puparia.

This study was undertaken to improve the chance of success and determine if *A. bipustulata* can parasitize many species besides *D. radicum*. To improve the chance of

success, post-diapause development of *D. radicum* from the Canadian prairies was compared to a population from Ontario, and to a natural enemy already present in Canada, *Aleochara bilineata*, with the intention of using this information later to select an *A. bipustulata* population for introduction. The ability of *A. bipustulata* to parasitize species other than *D. radicum* was studied in the laboratory, and the likelihood of *A. bipustulata* doing so was assessed by studying what habitats it is found in where it is native, in Europe.

2. LITERATURE REVIEW

The cabbage maggot as a pest of canola

Cultural varieties, or cultivars, of *Brassica napus* L. and *B. rapa* L. (Brassicaceae) with less than two per cent erucic acid and less than 30 micromoles per gram of glucosinolates in oil-free meal from their seeds are called double low oilseed rape or canola (Gray et al. 2006). Although the term canola did not yet exist, the first cultivar to meet these specifications, Tower, was developed in 1974 at the University of Manitoba (Stefansson and Kondra 1975; Stefansson 1983). Since then, 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 200 subsequent cultivars (Carew and Smith 2006; Gray et al. 2006). In 2005, about 5.2 million hectares of canola was harvested in Canada, with the vast majority grown in Alberta, Saskatchewan and Manitoba (Statistics Canada 2005). Farmers who integrate canola in their crop rotations benefit from increased net returns and decreased variability in annual income (Zentner et al. 1996). Threats to the yield of Canadian canola crops are therefore taken seriously.

Insect pests constitute one such threat. The species involved depend upon the geographical region, but generally all parts of the canola plant are fed upon by various insects wherever it is grown (Lamb 1989; Ekbohm 1995). Furthermore, new potential pests of Canadian canola continue to appear. For example, *Contarinia nasturtii* (Kieffer) (Diptera: Cecidomyiidae) (Hallett and Heal 2001; Olfert et al. 2006) and *Meligethes viridescens* (Fabricius) (Coleoptera: Nitidulidae) (Mason et al. 2003) are both capable of spreading from eastern Canada to the prairies. In western Canada, seedlings are eaten by five species of flea beetles (Coleoptera: Chrysomelidae), the most important of which is

Phyllotreta cruciferae (Goeze) (Burgess 1977). Canola leaves are consumed by larvae of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Palaniswamy et al. 1986), *Mamestra configurata* Walker (Lepidoptera: Noctuidae) (Mason et al. 1998), and especially in drier areas by certain species of grasshoppers (Orthoptera: Acrididae) (Olfert and Weiss 2002). Flowers are eaten by adult cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae) (Doddall and Moisey 2004), *Lygus elisus* Van Duzee, *L. lineolaris* (Palisot), and *L. borealis* (Kelton) (Hemiptera: Miridae) (Butts and Lamb 1991a; Timlick et al. 1993). The fourth and fifth instars of *M. configurata* feed on pods (Mason et al. 1998), as do late instar *Lygus* spp. (Butts and Lamb 1991b), and the larvae of *C. obstrictus* develop inside the pods feeding on the seeds (Doddall and Moisey 2004). Insignificant damage to the roots is caused by flea beetle larvae (Lamb 1989); more important are the root-feeding species of *Delia* Robineau-Desvoidy (Diptera: Anthomyiidae), and contributing to their control is the focus of this thesis.

The primary pests, species that can attack undamaged plants, are the cabbage maggot *Delia radicum* (L.), turnip maggot *Delia floralis* (Fallen), and radish maggot *Delia planipalpis* (Stein) (Liu and Butts 1982; Griffiths 1991a; Vernon and Broatch 1996; Broatch et al. 2006). The seedcorn maggot, *Delia platura* (Meigen), and tobacco maggot, *Delia florilega* (Zetterstedt), typically feed on tissue already invaded by the three primary pests (Brooks 1951). The seedcorn maggot is often the most abundant species trapped as adults in canola (Vernon and Broatch 1996; Broatch and Vernon 1997; Broatch et al. 2006). The turnip maggot 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 (Griffiths 1986b). Notwithstanding, the most important root maggot pest of canola in Europe (Lamb 1984; Lerin 1995; Erichsen

and Huenmoerder 2005) and Canada (Turnock et al. 1992; Dosedall et al. 1994; Soroka et al. 2002; Broatch et al. 2006) is *D. radicum*.

The first to note root maggots infesting oilseed rape was B.R. Stefansson, who in 1958 discovered *D. radicum* damage to both *B. rapa* and *B. napus* in Manitoba (Allen 1964). Then in 1981 a survey in Alberta revealed that root maggot damage was widespread, particularly in the northern part of that province (Liu and Butts 1982). A survey in Manitoba from 1985 to 1988 again found percentage of roots infested per field to be higher in agricultural areas further north (Turnock et al. 1992). The percentage of roots infested per field and the average level of damage to plants increased in the time between the earlier studies and a survey across the three prairie provinces in 1996 and 1997 (Soroka et al. 2004). Reductions of yield due to root maggot infestation are estimated at \$100 million during years favourable to the insects (Soroka et al. 2002; 2004). The majority of this damage has been attributed to *D. radicum*.

The genus *Delia* is in the dipteran suborder Muscomorpha (=Cyclorhapha), section Schizophora, subsection Calyptratae, superfamily Muscoidea, family Anthomyiidae (Huckett 1987; McAlpine 1989). The Anthomyiidae is distinguished from other muscoid families by continuously sclerotized connections between the cerci and inner surfaces of gonostyli (Griffiths 1982). Griffiths (1991a) provides ten characters common to members of the genus *Delia*, and additional characters for placing each of the 162 described Nearctic species in one of eight sections. The greatest diversity of *Delia* species is in the subarctic and subalpine, and the larval habitats are known for only about one fifth of these species (Griffiths 1991a; 1991b). The cabbage maggot is in the *D. radicum* section and *D. radicum* subsection. Other members of the *radicum* subsection are the two other primary

invaders of canola roots, *D. floralis* and *D. planipalpis*, and two species known only from a few specimens collected in the Canadian arctic (Griffiths 1991a).

The cabbage maggot is oviparous, laying elongate, white eggs in the soil (Brooks 1951; Miles 1952a). The larvae of *D. radicum* can be distinguished from those of other Diptera found around the roots of crucifers based on characters of the anterior spiracles, relative size of the head (Miles 1952b), structure of the cephalopharyngeal skeleton, and tubercles on the eighth abdominal segment (Brooks 1951; Miles 1952b). The three larval instars of *D. radicum* can be separated on the basis of spiracles, since the first instar has only posterior spiracles, the second instar anterior spiracles and posterior spiracles with two slits, and the third instar again with both anterior and posterior spiracles, but with three slits on the posterior pair (Brooks 1951). Like all cyclorhous species, the larva pupariates, forming a hard puparium from the cuticle of the third instar (Fraenkel and Bhaskaran 1973). The larva detaches from the old cuticle and forms a larva-like cryptocephalic pupa, then a phanerocephalic pupa as the head evaginates, and finally a pharate adult before the adult fly emerges (Fraenkel and Bhaskaran 1973).

Delia radicum is distributed across the northern temperate parts of the world, from Morocco east to Irkutsk and north into Scandinavia in the Palearctic (CAB 1989). It came to North America in the 1800s (Schoene 1916; Griffiths 1991a), possibly as pupae in ship ballast (Schoene 1916). Analysis of egg micromorphology (Biron et al. 2000; Biron et al. 2003) and DNA (Biron et al. 2000) variation among different populations indicate a single introduction to eastern North America from northwestern Europe, followed by the spread of the founder population west across the rest of North America. In Canada, *D. radicum* is generally distributed where crops are cultivated, and absent in more natural

areas (Griffiths 1991a). In canola *D. radicum* can constitute all, some, or none of the root maggot community (Griffiths 1986b).

Phenology is the study of biological events which cycle (Gordh and Headrick 2001). For *D. radicum*, the events include emergence of adults, egg laying, larval and pupal development. The cycle may be interrupted by diapause, a programmed stoppage in development and growth (Danks 1987), depending on cues perceived by the insect from the environment. The cabbage maggot overwinters as a pupa inside the puparium (Schoene 1916). The environmental cues which induce diapause in *D. radicum* are temperature and photoperiod (Hughes 1960; Zabirotov 1961; McLeod and Driscoll 1967; Read 1969; Soni 1976; Whistlecraft et al. 1985b). The number of cycles or generations completed each year depends on temperature during the interval between emergence of adults in spring and the induction of diapause in the larvae (Zabirotov 1961).

In parts of North America three or four generations occur (Schoene 1916; Nair et al. 1973; Nair and McEwen 1975; Wyman et al. 1977; Jyoti et al. 2003), but the life history of *D. radicum* in the prairie provinces is most relevant to this study. In southern Alberta rutabaga, *Brassica napobrassica* Mill. (Brassicaceae), crops there are two peaks in oviposition, during the first week of June and in early September (Swales 1958). Allen (1964) reported a similar two-cycle season in Manitoba, with puparia forming in rape during July and mid-October. Just north of Edmonton at Morinville Alberta, the *D. radicum* population in canola is predominately univoltine with adults emerging at the end of May, oviposition coincident with the onset of bolting of the crop in mid-June, and formation of puparia in mid-July (Griffiths 1986a). Rutabaga and canola crops in Manitoba experience two peak periods of adult *D. radicum* activity, during early June and mid-August (Bracken 1988; Turnock et al. 1992), and in rutabaga a third peak in some

years around mid-September (Bracken 1988). At Vegreville Alberta, emergence of overwintered *D. radicum* starts in May and peaks in mid-June (Doddall et al. 1996b) and oviposition peaks in mid-June (Doddall et al. 1996a). Broatch et al. (2006) found peaks in emergence of overwintering *D. radicum* and in activity in canola crops to be coincident over three years some time in June, and in two years of their three year study in the last week of June in Lacombe Alberta. In Carman and Altamont (Manitoba) canola crops, oviposition activity peaked in the third week of June and puparia formed toward the end of July, whereas these events occurred about one week later in Shellbrook and Melfort Saskatchewan and in Vegreville Alberta in 2000 (Hemachandra 2004).

Both Griffiths (1986a) and Broatch et al. (2006) noted a slight increase in adult activity during August, and a small proportion of puparia collected in canola at two sites in Manitoba in August were not in diapause (Hemachandra 2004). Selection is expected to favour minimizing the size of this potential second generation across the Canadian prairies, for the spring-planted canola will no longer support larval development, and the emerging adults will have no place to lay their eggs.

Adult *D. radicum* disperse upwind (Hawkes 1974; Finch and Skinner 1982). The process of selecting hosts is thought to involve three stages, which together are the basis of the appropriate-inappropriate landings theory (Finch and Collier 2000). In the first stage, the female is excited and stimulated to land by volatile chemicals from host plants (Traynier 1967a). For *D. radicum*, these are the products of hydrolysis of glucosinolates such as allylthiocyanate (Nair and McEwen 1976). In the second stage the flies use visual stimuli to determine where to land. They prefer to land on green objects (Prokopy et al. 1982) and are just as likely to land on *Brassica*-shaped leaves as others (Kostal and Finch 1994; Degen and Staedler 1996). Having landed, female *D. radicum* make short

flights off the leaf and back (Kostal and Finch 1994; Morley et al. 2005). The third stage, a decision about laying an egg at the base of the plant, occurs as the female perceives chemical compounds from the leaf through her tarsi (Traynier 1967b; Roessingh et al. 1992). The chemicals are glucosinolates (Nair and McEwen 1976; Nair et al. 1976; Roessingh et al. 1992; Braven et al. 1996), phytoalexins (Baur et al. 1998), and thiazotriaza-fluorenes (Baur et al. 1996; Roessingh et al. 1997; Gouinguene and Staedler 2005). 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 (Kostal and Finch 1994; Morley et al. 2005), but if she lands on a plant without the stimuli the process of accumulation starts anew (Morley et al. 2005).

To be part of *D. radicum*'s host range, a plant must stimulate oviposition according to the process in the preceding paragraph and be suitable for larval development. Plants that will do so in confined laboratory settings are part of its fundamental host range (Klinken and Heard 2000), and those which support development in nature are its ecological host range (Onstad and McManus 1996). In addition to canola and *Brassica* vegetables (Finch 1989), *D. radicum*'s ecological host range comprises several other plant species. For instance, *D. radicum* puparia have been collected around the roots of *Hesperis matronalis* L., *Barbarea vulgaris* R. Br., *Sinapis arvensis* L., *Lepidium densiflorum* Schrad., *Sisymbrium loeselii* L. (Nair et al. 1973), *Raphanus raphanistrum* L., *Sisymbrium officinale* (L.) Scop., and *Thlaspi arvense* L. (Finch and Ackley 1977) (Brassicaceae). Stinkweed, *T. arvense*, is an important alternative host in the Canadian prairies (Griffiths 1986a; 1991a).

The cabbage maggot damages canola when the larva feeds on the roots. Once the first instar has penetrated the periderm, the larva feeds on phloem, periderm and

secondary xylem, and creates vertical furrows in the root as a second and third instar (McDonald and Sears 1991; 1992). Feeding damage reduces root weight, dry matter content and sugar content of the roots (Hopkins et al. 1999). Damaged roots are more likely to be invaded by *Fusarium* species (Griffiths 1986b; 1986a; 1991c) but not by *Rhizoctonia solani* Kuehn (Klein-Gebbinck and Woods 2002). High levels of damage cause plants to lodge (Griffiths 1991c) or die (Griffiths 1986a).

The relationship between feeding damage 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* reduce plant biomass, number of seeds per plant, number of racemes, and number of pods on axillary racemes (McDonald and Sears 1991). In field trials Griffiths (1991c) showed that root damage reduces the number of seeds and seed weight. When average damage to roots of *B. rapa* in 1 m² plots increases from zero to 50 per cent of the root surface, seed yield can be about 50 g/m² less, although the effect was only found in one year of a two year study (Dosdall 1998). Conversely, Klein-Gebbinck and Woods (2002) found plants with more damage have higher seed yield and plant biomass, and Soroka et al. (1999) found no significant effect of level of infestation on yield. However, the highest level of damage observed by Klein-Gebbinck and Woods (2002) 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 damaged (McDonald and Sears 1991; Dosdall 1998; Dosdall et al. 1998). Roots with 50-100% of the surface damaged are not uncommon across the prairies (Soroka et al. 2004), so even if economic reductions in yield were not demonstrated by Klein-Gebbinck and Woods, the large area planted to canola each year means small average losses on a farm scale combine for an expensive pest problem for western Canadian canola producers as a whole.

The categories of strategies outlined by Finch (1989) for control of *Delia* species in vegetable production can also be considered as they relate to canola in western Canada. These are chemical, cultural and biological control. Granules of cyclodienes applied in furrow at the time of seeding reduce damage to *B. rapa* by more than 90% (Allen 1964). Similar results are obtained by treating furrows with Counter, CGA 12223, and oftanol (Askew et al. 1976). Seed treatment of *B. napus* and *B. rapa* with oftanol or chlorpyrifos and terbufos granules all can protect roots and increase yield (Griffiths 1991c), and diazinon applied weekly as a soil drench reduces root damage (Ekuere et al. 2005). However, no insecticides are registered for *D. radicum* control in canola in Canada (Soroka et al. 2004), so chemical control will not be considered further.

That organisms are influenced by their environment, are tolerant of a finite range of various environmental factors, and thrive within more narrow limits is well known. Cultural control of pests involves activities which alter the environment to be outside the optimal range, or ideally outside the tolerable range, of one or more important environmental parameters. 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 cabbage maggot in canola have been proposed. 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 (Soroka et al. 2004).

The selection of what to plant influences the level of *D. radicum* infestation. *Brassica napus* receives fewer eggs and less damage than *B. rapa* (Griffiths 1991c; Dosedall et al. 1994) and certain cultivars of both species are both more attractive for oviposition and more prone to damage (Dosedall et al. 1994; Dosedall et al. 2003). *Sinapis*

alba L. (Brassicaceae) plants are less preferred for oviposition (Dosdall et al. 1994) and less damaged than canola species (Dosdall et al. 1994; Dosdall et al. 2000). Certain hybrid accessions of *B. napus* and *S. alba* are also resistant (Dosdall et al. 2000; Ekuere et al. 2005) and the quantitative trait loci associated with this resistance have been identified with the intention of developing resistant cultivars (Ekuere et al. 2005).

Deciding when to plant is also important. Seeding canola in early June instead of mid-May will reduce damage by *D. radicum*, but negatively influences yield to the extent that it cannot be recommended (Dosdall et al. 1996a). Dormant seeding in the fall and seeding earlier in the spring sometimes (Dosdall et al. 2003) but not always (Clayton et al. 2004; Dosdall et al. 2006) influences the level of damage by root maggots, and since early spring seeding results in increased yield it is recommended (Clayton et al. 2004).

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 level of damage to roots relative to lower seeding rates (Dosdall et al. 1998; Hawkins-Bowman 2006). Spacing rows 17–25 cm apart reduces oviposition by the pest relative to narrower spacing and optimizes gross returns (Dosdall et al. 1998). Although reducing tillage increases the overwintering survival of *D. radicum* (Dosdall et al. 1996a) and may result in more damage to roots (Dosdall et al. 1998), this is not always the case (Hawkins-Bowman 2006) and reducing tillage increases gross margins of canola crops (Dosdall et al. 1998), reduces soil erosion, and uses less energy without affecting yield (Bortslap and Entz 1994). 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 (Dosdall et al. 2003). Planting larger seeds (Soroka and Elliott 2006) and applying fertilizer at recommended rates (Dosdall et al. 2002;

Clayton et al. 2004) are advocated in spite of neutral or even positive effects on root maggots due to other agronomic benefits.

The third category of control strategies listed by Finch (1989) is biological control. Biological control occurs when a pest population is regulated by its natural enemies (DeBach and Rosen 1991). 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.

Natural biological control is the reduction in the pest's population size by natural enemies without human intervention (DeBach and Rosen 1991). The natural enemies of *D. radicum* include parasitoids, predators and pathogens. Insect species whose larvae feed on and kill a single host, which typically is another insect, are parasitoids (Godfray 1994). Parasitoids of minor significance in the prairies are *Aleochara verna* Say (Coleoptera: Staphylinidae), *Phygadeuon* spp. (Hymenoptera: Ichneumonidae), *Aphaereta minuta* (Nees) (Hymenoptera: Braconidae) and *Trichopria* sp. (Hymenoptera: Proctotrupidae) (Hemachandra 2004). More important are *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae) and *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae) (Turnock et al. 1995; Hemachandra 2004).

In addition to the cabbage maggot, the ecological host range of *A. bilineata* includes *D. platura*, *D. floralis*, *D. florilega*, *D. planipalpis*, *D. antiqua* Meigen, and *Pegomya betae* Curtis (Maus et al. 1998). Eggs are laid in the soil near host puparia (Wadsworth 1915). The mobile, campodeiform larva that ecloses moves away from light (Wadsworth 1915) and locates a prospective host by randomly searching (Fuldner 1960). The larva attaches to a host using its pygopodium, an adhesive structure that telescopes from the tenth abdominal segment (Fuldner 1960), to secure itself as it chews an entrance