PARASITOIDS OF *Delia radicum* (Diptera: Anthomyiidae) IN CANOLA: ASSESSMENT OF POTENTIAL AGENTS FOR CLASSICAL BIOLOGICAL CONTROL

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Submitted to the

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by

Kennantudawage Siril Hemachandra

In Partial Fulfillment of the Requirements

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ABSTRACT

Kennantudawage Siril Hemachandra. University of Manitoba, 2004. **Parasitoids of *Delia radicum* (Diptera: Anthomyiidae) in canola: assessment of potential agents for classical biological control.**

Major supervisor: Dr. N.J. Holliday

Delia radicum L. is an important insect in canola on the Canadian Prairies and there is no single effective method of control. Hence, classical biological control has been proposed. The main objective of this study was to assess the parasitoid community of *D. radicum* in canola on the Canadian Prairies and Europe. Immature stages of *D. radicum* were sampled in six canola fields on the Canadian Prairie Provinces and in 11 canola fields and one brassica vegetable field in Switzerland and Germany. Immatures were individually reared in the laboratory until emergence of parasitoids and adult *D. radicum*. Parasitoid species found in canola on the Canadian Prairies and in canola and brassica vegetables in Europe included *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae) and *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae). *Aleochara verna* Say (Coleoptera: Staphylinidae) was found only in Canadian canola while *A. bipustulata* L. (Coleoptera: Staphylinidae) was found only in European canola and brassica vegetables. Minor parasitoids found in canola included *Phygadeuon trichops* (Thomson) (Hymenoptera: Ichneumonidae), three undescribed *Phygadeuon* species, *Aphaereta minuta* (Nees) (Hymenoptera: Braconidae), *Aleochara brevipennis* Gravenhörst (Coleoptera: Staphylinidae) and *Trichopria* sp. (Hymenoptera: Proctotrupidae). Specimens collected by other workers in North America and labeled as *A. bipustulata* were examined and found to be *A. verna*. The previous reports of

occurrence of *A. bipustulata* in North America were erroneous. Hence, *A. bipustulata* is the most promising candidate for introduction to canola on the Canadian Prairies. In addition, some aspects of the biology of *D. radicum, A. bilineata,* and *T. rapae* were studied.

Dedication

To my wife Sandhya and daughter Shashika

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CHAPTER 1

Introduction

Delia radicum (L.) (Anthomyiidae: Diptera) is an introduced insect now present in many regions of North America (Griffiths, 1991). The insect is of European origin (Biron *et al.,* 2000) and it is assumed that it was introduced to North America in the mid 19th century (Schoene, 1916; Griffiths, 1991). The presence of *D. radicum* in North America, with a positive identification, was confirmed with the report of an outbreak of *D. radicum* in New York State in 1856 (Riley, 1885). The species was reported to be in Canada at about the same time and it had been reported from Nova Scotia to Ontario by 1885 (Fletcher, 1886). In Manitoba, *D. radicum* was probably present in the valleys of the Red and Assiniboine Rivers by the 1930s (Turnock *et al.*, 1995), but its presence with definite identification was not confirmed until 1958 (Allen, 1964). Moreover, it was present in Saskatchewan by 1949 (Brooks, 1949) and in British Columbia by 1913 (Wilson, 1913). *Delia radicum* now occupies the Nearctic and Palaearctic regions from 35 to 60°N and is associated with agriculture and horticulture (Griffiths, 1991).

Delia radicum infests brassica vegetables in the Atlantic Provinces causing economic damage (Read, 1960) and it infests canola (*Brassica napus* L., and *Brassica rapa oleifera* (DeCandolle) Metger) on the Canadian Prairies (Griffiths, 1986a, 1986b; Turnock *et al.*, 1992; Soroka *et al.*, 2002). *Delia radicum* larvae feed on canola roots and feeding injuries interfere with nutrient and water uptake (McDonald and Sears, 1991). In addition, root injuries predispose the root to attack by pathogenic microbes (Griffiths, 1986a). *Delia radicum* causes economic damage to canola in the northwestern agricultural region of Alberta (Griffiths, 1986a, 1986b), but its damage on canola in other

parts of the Canadian Prairies has yet to be quantified. In a year when *D. radicum* infestation is high and canola is under poor growing conditions, the estimated yield loss could be high as $100 million (Soroka *et al.,* 2002). Even though the relationship between yield loss and root damage of canola is yet to be defined, a yield loss of a few dollars per hectare due to root injuries would amount to millions of dollars because canola is grown so extensively. From 1994–2003, on average 4.6 million ha of canola was grown on the Canadian Prairies (Canola Council of Canada, 2004). Therefore, *D. radicum* damage in canola, even though it may not result in economic damage for a farmer, leads to significant losses in foreign income to Canada.

Canola growers on the Canadian Prairies do not apply any particular management practices for *D. radicum* (Canola council of Canada, 2004). However, manipulation of cultural operations such as tillage regime (Dosdall *et al.*, 1996b) and seed density (Dosdall *et al.*, 1996a) can have a significant effect on population suppression of *D. radicum.* Insecticides applied as seed-dressings do not provide effective control of *D. radicum*. This is because *D. radicum* generally infests canola more than a month after seeding, when canola is in the bolting stage (Griffiths, 1986a). Even though management of *D. radicum* in brassica vegetables is well established (Finch, 1987, 1989, 1993; Gehringer and Goldstein, 1988; Finch and Collier, 2000b), those management practices are not technically feasible in canola on the Canadian Prairies (Soroka *et al.*, 2002). Therefore, additional control strategies for *D. radicum* in canola are required and classical biological control has been suggested (Turnock *et al.*, 1995).

Classical biological control of *D. radicum* in brassica vegetables in eastern Canada was attempted in 1949. In that attempt, *Aleochara bilineata* Gyllenhal,

Aleochara verna Say, *Trybliographa rapae* (Westwood), *Phygadeuon trichops* (Thomson), and *Aphaereta* sp. were introduced (McLeod, 1962; Soroka *et al.*, 2002). However, the programme was suspended when it was found that the main parasitoid species that were introduced were already present in Canada (Soroka *et al.*, 2002). Introduction of *A. bilineata* to Canada was partly associated with misidentification of Canadian specimens of *A. bilineata* as *Baryodma ontarionis* Casey (Colhoun, 1953). This signifies the need for precise identifications of parasitoid species, including agreement on parasitoid identities by taxonomists in Europe and North America.

Biological control of *D. radicum* in canola is a viable option and technically feasible. Crops that can tolerate a reasonable level of pest injury with no economic damage are suitable target crops for biological control (Turnbull and Chant, 1961). Canola plants can tolerate a reasonable level of *D. radicum* larval injury (McDonald and Sears, 1991); therefore, it is not necessary to suppress larval populations to a very low level. In addition, *D. radicum* injury does not directly affect market standard of the product or economic value of the crop. Moreover, shortage of hosts for parasitoids is unlikely because canola is grown every year on a large scale (Canola Council of Canada, 2004). *Delia radicum* larvae remain on roots for about 2–3 weeks and then overwinter as pupae in soil until next spring (Brooks, 1949, 1951). Consequently, the immature stages of *D. radicum* are available to parasitoids and predators for an extended period of time.

In developing classical biological control of *D. radicum* in canola on the Canadian Prairies, it is absolutely essential to characterize the parasitoid community of *D. radicum* in canola in Canada to avoid the introduction of parasitoid species that are already present. Comparing the Canadian parasitoid community with the European

parasitoid community facilitates the selection of potential biocontrol agents for introduction to Canada. Here and throughout this thesis, parasitoid community refers to all "parasitoid species that exploit the population of" *D. radicum* "in a given locality" (Mills 1994, p 399). Therefore, the objectives of this study were to assess the parasitoid community of *D. radicum* in canola in Canada and in canola in Europe to choose potential biocontrol agents for introduction, and to study the tritrophic interaction among canola, *D. radicum* and its parasitoids to understand the biological control system in canola.

This thesis is organized in paper style, comprising four chapters. Chapter one is devoted to a general introduction, and is followed by a literature review in chapter two. Chapter three consists of eight sections, each section detailing a facet of the research in the general format of a research paper. Chapter four is a general discussion.

CHAPTER 2

Literature Review

Economically important *Delia* species in Canada

In Canada, there are seven species of *Delia* that are economically important pests in agriculture. *Delia coarctata* (Fallén), the wheat bulb fly, infests wheat, barley, and rye, and the larvae damage the plant by feeding on the crown below the ground. As a result, the central shoot dies or becomes stunted (Griffiths, 1992). *Delia platura* (Meigen) and *Delia florilega* (Zetterstedt), seed maggots, attack a wide range of crops, which includes brassica root crops, solanaceous crops, legume crops and corn. Legumes are attacked at the time of seed germination (Griffiths, 1993). *Delia antiqua* (Meigen), the onion maggot, infests cultivated species of *Alium* such as onion, shallot, garlic and leeks (Ellis and Eckenrode, 1979). *Delia floralis* (Fallén) and *Delia planipalpis* (Stein) infest a wide range of brassica crops such as cabbage, cauliflower, broccoli, Brussels sprouts, mustard, rapeseed, turnip and rutabaga (Griffiths, 1991). *Delia radicum,* cabbage root maggot, also infests a wide range of brassica crops in common with *D. floralis* and *D. planipalpis.* Of these species, *D. radicum* is the most important pest in brassicas, particularly in canola in Canada (Griffiths, 1986a, 1986b, 1991).

Taxonomic status of *Delia radicum*

The taxonomic status of *Delia* species has been reviewed by Griffiths (1991). The genus *Delia* is classified under the order Diptera, and family Anthomyiidae (Borror *et al.*, 1992). The genus *Delia* has been included in the *Delia* group with a series of other genera based on the characteristics of the hypandrium, gonostyli, and the sclerotization of the distal section of aedeagus and processes of the 5th sternite (Griffiths, 1991). The

Delia species that occur in the Nearctic region have been divided into the nine sections *discalis, radicum, longicauda, bracata, interflua, elongata, frontella, coarctata* and *albula* (Griffiths, 1991). The division of sections is based on the characteristics of the 5th sternite process, prealar bristle, the lower surface of the costa, the 3rd abdominal sternite and twenty other characteristics (Griffiths, 1991). The species of the *radicum* section are further divided into two subsections based on their host range. The larvae of the species in the *D. radicum* subsection feed on roots of brassicas whereas the species of the *D. cardui* subsection are borers or leaf miners on Chenopodiaceae and Caryophyllacaeae (Griffiths, 1991). Griffiths (1991) included *D. radicum* in the *D. radicum* subsection together with two other economic pests, *Delia planipalpis* and *Delia floralis*, and two new species, *Delia notobata* and *Delia banksiana.*

There are many synonyms for *D. radicum* depending on the countries (Finch, 1989), time period, and research group (Griffiths, 1991). *Delia radicum* was first described by Linneaus as *Musca radicum* L. in 1758 (Pont, 1981). Subsequently, many different names have been used for *D. radicum.* According to Griffiths (1991) those synonyms were: *Anthomyia brassicae* Hoffmannsegg, *Anthomyia brassicae* Bouché, *Chortophila floccosa* Macquart, *Aricia villipes* Zetterstedt, *Phorbia brassicae* (Bouché), *Anthomyia raphani* Harris, *Anthomyia radicum* (L.), *Anthomyia ruficeps* Meigen, *Pegomya brassicae* (Bouché), *Chortophila brassicae* (Bouché), *Chortophila brassicae* (Wiedemann), *Hylemyia brassicae* (Bouché), *Erioischia brassicae* (Bouché), *Delia brassicae* (Bouché), *Delia brassicae* (Hoffmannsegg and Wiedemann), and *Hylemya brassicae* (Wiedemann). The currently accepted name is *Delia radicum* (L.) (Pont, 1981).

External anatomy and developmental biology of *Delia radicum*

Adults

External anatomy and identification characteristics of adult *D. radicum* are well documented (Schoene, 1916; Brooks, 1949, 1951; Huckett, 1987; Griffiths, 1991). The adult male is very bristly, and dark and has gray markings on thorax and abdomen (Schoene, 1916); the compound eyes are holoptic; the thorax is ash gray with three distinct longitudinal lines on the dorsum (Schoene, 1916; Brooks, 1951). Females are lighter in colour than males; the body and legs are gray with a tinge of brown, and the compound eyes are dichoptic (Schoene, 1916; Brooks, 1951; Griffiths, 1991); the longitudinal lines on the thorax are less distinct than in males (Schoene, 1916).

Several other characteristics of adults are useful in identification to the species level. The bristle arrangement on the hind femur and the thoracic chaetotaxy, particularly the length of the prealar bristle, may be used to separate *D. radicum* from other closely related brassica-feeding *Delia* species (Brooks, 1949, 1951; Griffiths, 1991).

Eggs

Eggs of *D. radicum* are white, elongate, 0.9–1.1 mm long and 0.3–0.4 mm broad (Schoene, 1916; Hughes and Salter, 1959); the anterior end has a broad circular depression (Schoene, 1916; Hinton and Cole, 1965). The chorion has a sculptured surface, which consists of coarse longitudinal ribbing (Brooks, 1951; Miles, 1952b). Generally, eggs hatch within 3–4 days of oviposition and the first-instar larvae emerge (Schoene, 1916; Harris and Svec, 1966; Whistlecraft *et al.*, 1985b). Viability of eggs is usually very high, 90–100% (Harris and Svec, 1966).

Larvae

The larva is a typical, legless maggot; the head is reduced and the posterior end of the body is somewhat triangular in profile. The head is deeply retracted into a broad prothorax (Miles, 1952b). First-instar larvae are 1.5 mm long, cylindrical and tapers anteriorly (Schoene, 1916). They do not have exterior anterior spiracles (Schoene, 1916), but developing anterior spiracles can be seen through the integument. Posterior spiracles are knob-like with a circular opening, and project horizontally from the dorsal oblique area (Brooks, 1949; Miles, 1952b). The duration of development of the first-instar larva is about 4 days (Hughes and Salter, 1959; Swailes, 1963; McDonald, 1985). Second-instar larvae are about 3.8 mm long, and have both anterior and posterior spiracles (Schoene, 1916). The anterior spiracles have densely-sclerotized 11–13 finger-like processes, and the number of processes is useful in identification of *Delia* species (Miles, 1952b). Each posterior spiracle has two slits (Brooks, 1949). The duration of development of the second-instar larva is about 6 days (Hughes and Salter, 1959; Swailes, 1963; McDonald, 1985). The body length of third-instar larvae is highly variable, 2.5–8 mm. The body is white, fleshy, and cylindrical and tapers anteriorly (Schoene, 1916). Third-instar larvae have three slits on each posterior spiracle (Schoene, 1916; Brooks, 1949) and the anterior tubercles are very conspicuous (Brooks, 1949). Duration of development of the third-instar larvae is 8–12 days (Schoene, 1916).

The differences in structures of the mouthparts are also useful for distinguishing the larval instars (Brooks, 1949; Miles, 1952b), particularly the distance between the tip of the mandible and the ventral process of the pharyngeal sclerites (Hughes and Salter, 1959). Tubercle number and arrangement on the 8th abdominal segment are used to determine the identity of *Delia* species. When the third larval instar is about to pupate, it

moves away from its feeding place and pupates in the soil (Jones, 1986). The distance that the larva moves depends on soil moisture (Hughes and Salter, 1959). Seventy-five per cent of larvae pupate within 0–5 cm of their feeding place and 61% of larvae pupate within the top 5 cm of the soil surface (Jones, 1986). There is a prepupal stage, which lasts about 3 days (Harris and Svec, 1966). Total duration of larval development is 18–22 days at 19°C (Brooks, 1949, 1951; Whistlecraft *et al.*, 1985b). Premature pupation can occur when food is scarce (Harris and Svec, 1966).

Puparia

Puparia are sub-elliptical, smoothly rounded, and brownish (Miles, 1952b). Protuberances of the puparium are the remains of tubercles of the 8th abdominal segment of larvae (Brooks, 1951; Miles, 1952b). The average weight of puparia is 16.6 mg when larvae feed on rutabaga (Harris and Svec, 1966). Here and throughout this thesis, the term "puparium" refers to the puparium including the pupa within it. The weight of diapausing puparia is greater than of non-diapausing puparia (Johnsen and Gutierrez, 1997). The length of the puparium varies from 3.5 to 6.5 mm and averages about 5.5 mm (Schoene, 1916). Adult flies emerge from non-diapausing puparia within two weeks in the field (Jones, 1986). Success of emergence of the fly is not associated with the depth of pupation up to 15 cm from the soil surface, but 80% puparia at ≥30 cm deep failed to reach the soil surface (Finch and Skinner, 1980).

Host plant associations of *Delia radicum*

Host range

Delia radicum larvae attack a wide range of wild and cultivated brassica plants. Common brassica crops that serve as hosts are cabbage (*Brassica oleracea* var capitata

(L.)), cauliflower (*Brassica oleracea* var botrytis (L.)), broccoli (*Brassica oleracea* var cymosa (L.)), Brussels sprouts (*Brassica oleracea* var gemmifera (Zenker)), turnip (*Brassica rapa* (L.)), rutabaga (*Brassica napus* var. napobrassica (L.)), mustard (*Synapis alba* (L.)), radish (*Raphanus sativus* L.), Chinese cabbage (*Brassica rapa* var. pekinensis) and rapeseed (*Brassica napus* L. and *Brassica rapa oleifera* (DeCandolle) Metzger) (Griffiths, 1991). Weed plants that support the development of *Delia* maggots in the field are *Barbarea vulgaris* R.Br., *Sysymbrium officinale* (L.), *Brassica nigra* (L.), *Synapis arvensis* L., *Sisymbrium altissimum* L., *Raphanus raphaistrum* L. and *Conringia orientalis* (L.) (Griffiths, 1991). Many other wild brassica plants can support the development of *D. radicum* (Finch and Ackley, 1977).

Host plant location

Delia radicum females respond to the chemical profile of a plant when choosing the plant for oviposition (Finch, 1978; Nottingham, 1988; Roessingh and Stadler, 1990; Baur *et al.*, 1996a, 1996b; Finch and Collier, 2000a). Females respond to glucosinolates, one of the chemical groups present in brassicas (Traynier, 1967a, 1967b; Finch, 1978). One of these glucosinolates, allyl isothiocyanate (mustard oil), attracts gravid female *D. radicum* (Nair *et al.*, 1973; Nair and McEwen, 1976; Hawkes and Coaker, 1979; Finch and Skinner, 1982a, 1982b; Tuttle *et al.*, 1988). In addition, *D. radicum* females respond to chemicals that are not glucosinolates (Nair *et al.*, 1976; Birch *et al.*, 1993); these chemicals have not been identified but are commonly called cabbage identification factor "CIF" (Birch *et al.*, 1993). In contrast, *D. radicum* flies avoid plants that have some chemicals. For instance, carboxylic acid (Cole *et al.*, 1989), monoterpenes (Ntiamoah and Borden, 1996), naphthalene (Ouden, 1988), and cynaptic acid (Jones and Finch,

1987) function as deterrents. *Delia radicum* also responds positively to odours emanating from damaged tissues of brassica plants as a result of larval feeding. The odour is associated with damaged roots, soil or associated microbes (Baur *et al.*,1996c, 1996d).

Delia radicum flies respond to visual cues, including colour and shape, in host plant selection (Prokopy *et al.*, 1983; Vernon and Broatch, 1996; Kostal, 1991; Finch and Collier, 2000a). Yellow attracts *D. radicum* flies (Tuttle *et al.*, 1988; Kostal and Finch, 1996; Liburd *et al.*, 1998). Adult *D. radicum* responds to the level of reflection of host compared with the background, and land more frequently on brassica plants surrounded by bare soil than on brassica plants surrounded by green clover (Gehringer and Goldstein, 1988; Kostal and Finch, 1994a, 1994b, 1996). *Delia radicum* flies respond to shape of the leaves (Prokopy *et al.*, 1983), but conspicuousness of the object is more important than the shape (Kostal, 1993b). In addition, they respond to the texture of the leaf surface (Roessingh and Stadler, 1990).

Plant varieties within the subspecies of *Brassica oleracea* are chosen over other brassicas when there is a choice (Matthewman and Lyall, 1966; Mukerji, 1969; Hardman and Ellis, 1978; Ellis and Hardman, 1988; McKinlay and Birch, 1992; Freuler *et al.*, 1996). *Delia radicum* flies prefer certain subspecies of *Brassica oleracea* to other subspecies when they have a choice (Matthewman and Lyall, 1966; Radcliffe and Chapman, 1966; Hardman and Ellis, 1978; Doane and Chapman, 1962; Ellis, 1992; Dosdall *et al.*, 1994). Chinese cabbage is preferred to Brussels sprouts, broccoli, cabbage and cauliflower (Mukerji, 1969).

Delia radicum responds to the physiological age of the plant, which may be associated with both its chemical and physical characteristics (Ellis *et al.*, 1979; McDonald and Sears, 1992). In addition, *D. radicum* flies are not attracted to plants infested by aphids, *Brevicoryne brassicae* (L.) or *Myzus persicae* (Sulz.) (Finch and Jones, 1989). *Delia radicum* also responds to plant density (Finch and Skinner, 1976) and crop diversity (McKinlay *et al.*, 1996).

Feeding behaviour of *Delia radicum* larvae

Delia radicum is a primary phytophagous insect; larvae do not need a previously damaged place to start feeding (Brooks, 1949). Upon emerging from an egg, the first-instar crawls through the soil to locate roots. Generally it enters the root about 1 cm below the soil surface (Read, 1958). In canola, first-instar larvae mine into the roots and enter the periderm where they start to feed on the parenchyma tissues of the secondary phloem. The second- and third-instars aggregate on the root surface and continue to feed, making tunnels along the taproot. Larvae can attack the conductive and storage cells within a narrow band of tissues between the secondary xylem near the root stele and the secondary phloem within the periderm (McDonald and Sears, 1991, 1992).

Impact of larval feeding on the plant

Feeding injury caused by *Delia* species negatively influences the growth of brassica crops depending on the type of crop and the growing stage (Hopkins *et al.*, 1996). Root feeding injury is critical in the early stages of cabbage and cauliflower, and causes heavy plant mortality. Early root feeding causes distortion of roots in early crop stages of rutabaga and radish (Forbes and King, 1957; Read, 1960). Feeding damage causes stunting and yield loss in late stages of cabbage and cauliflower, and maggot

feeding on the swollen tap-root of late stages of rutabaga causes severe loss of economic yield (Read, 1960). *Delia radicum* does not oviposit in canola when the plants are at the seedling or rosette stages (Griffiths, 1986a). Females oviposit when the plants are at the bolting stage (Griffiths, 1986a). Hence, seedling mortality due to root damage does not occur in canola. Canola plants can withstand considerable larval feeding on roots without significant yield loss (Liu and Butts, 1982). However, plants with 50% of root surface area injured produced fewer racemes and seed pods (McDonald and Sears, 1991).

Behavioral biology of *Delia radicum*

Oviposition

Delia radicum females start to lay eggs 4–6 days after emergence (Read, 1965b; Hawkes, 1972), and continue to lay for two to five weeks (Hughes and Salter, 1959; Whistlecraft *et al.*, 1985b; Griffiths, 1991). Females generally live about 25–39 days (Swailes, 1961; Read, 1965b; Nair and McEwen, 1976). The number of eggs laid varies and averages 78 eggs per female (Swailes, 1961; Finch, 1971; Nair and McEwen, 1976). Generally, about 50% of the egg load is laid within the first five days of oviposition (Swailes, 1961). Eggs are laid singly or in batches of two to five on soil near the root collar of brassica plants (Miles, 1952a; Hughes and Salter, 1959; Mukerji, 1971; McDonald and Sears, 1991). More than one female may choose the same plant for oviposition, and up to 40 eggs per plant have been observed during the peak oviposition period (Miles, 1953, 1954). Weather conditions, especially warm temperature (18–20°C), low precipitation, low wind (0.2–0.4 m / s), and long hours of sunshine result in increased fly activity and oviposition (Carlson *et al.*, 1947; Miles, 1953, 1954; Bligaard, 1996; Nair and McEwen, 1974).

Winter diapause

Delia radicum is restricted to the Holarctic region, and winter diapause is an essential element of its life cycle (Johnsen and Gutierrez, 1997). Diapause of *D. radicum* is facultative, and the insect overwinters as a pupa (Hughes, 1960; McLeod and Driscoll, 1967). Abiotic factors affect diapause induction, diapause development, diapause termination and post-diapause development. Temperature and photoperiod are the main cues for induction of winter diapause (Hughes, 1960; Read, 1965a, 1968, 1969; Soni, 1976; Collier and Finch, 1983a, 1983b; Collier *et al.*, 1988). In addition, light intensity also affects diapause induction (Read, 1969). In addition to a direct photoperiodic effect, photoperiod affects larvae through chemical changes in the host plant (Hughes, 1960). Diapause induction can also be triggered in the adult stage (Read, 1965a, 1969; McLeod and Driscoll, 1967), egg stage (Johnsen and Gutierrez, 1997) and larval stage, particularly the second- and third-instars (Hughes, 1960; McLeod and Driscoll, 1967; Soni, 1976; Johnsen and Gutierrez, 1997). In fact, the proportion of puparia entering diapause is the result of the interaction among temperature, photoperiod, and *D. radicum* instar; exposure of immature *D. radicum* to different combinations of temperature and photoperiod results in different proportions of diapausing pupae (Soni, 1976). Geographical location of the population also affects diapause induction. For example, critical day length, the day length when 50% of population enter diapause, for a population in Finland at 60.5°N was >19 h, much longer than the 14–16 h observed at 46.2°N in Switzerland (Collier *et al.*, 1988). Generally, when the third larval instar is exposed to <15°C together with a short photoperiod, ≤12 h, subsequent pupae enter diapause (Read, 1969).

Diapause development of *D. radicum* puparia depends on the temperature. Generally, rate of diapause development at 0–8°C is more or less similar but above 10°C

the development rate declines (Collier and Finch, 1983b). The minimum time period required for diapause development varies with population in relation to geographical location. For example, members of a *D. radicum* population at Wellesbourne in the United Kingdom require a minimum of 19 weeks at <10°C for the completion of diapause development (Collier and Finch, 1983a). In contrast, members of a population of *D. radicum* in Denmark require 17 weeks to complete diapause development at <10°C in the field (Johnsen *et al.*, 1997). When the duration of the diapause period is short, few flies emerge. For example, following warming, only 30% of flies emerged when puparia had been exposed to 5°C for 12 weeks (Coaker and Wright, 1963). After completion of diapause development, pupae remain dormant until they experience warm temperatures that allow post-diapause development (Collier and Finch, 1983a).

The time required for post-diapause development of *D. radicum* depends on temperature and varies among populations. The lower threshold for post-diapause development is 4–5°C (Collier and Finch, 1983b; Collier *et al.*, 1989; Johnsen *et al.*, 1997). Generally 50% of flies emerge in the field when they receive 230 ± 10 air degree-days Celsius (DDC) or 179 ± 8 soil DDC above 4°C (Collier and Finch, 1985). These values have been estimated using a *D. radicum* population at Wellesbourne in the United Kingdom. Thermal accumulations based on air temperature needed for fly emergence in brassica vegetables fields are in: Arlington, Wisconsin, 343–680 DDC (base 5.5°C) (Eckenrode and Chapman, 1972) or 300–608 DDC (base 6.1°C) (Wyman *et al.*, 1977), Cambridge, Ontario, 374–567 DDC (base 6°C) (Nair and McEwen, 1975) and Winnipeg and Portage la Prairie, Manitoba, 387 ± 69 DDC (base 5°C) (Bracken, 1988). The variation in the required degree-days for peak fly emergence is partly associated with

differences among populations (Finch *et al.*, 1986) and the methods used to estimate fly emergence (Collier and Finch, 1985). *Delia radicum* populations can be divided into early, intermediate and late emerging subpopulations on the basis for time required for post-diapause development; this emergence pattern is heritable (Hawkes *et al.*, 1988; Finch and Collier, 1983). Emergence patterns are associated with geographic locations of populations (Finch *et al.*, 1986; Taksdal, 1992) and with cropping pattern (Hawkes *et al.*, 1988).

Aestivation

Delia radicum undergoes aestivation in warm weather in mid summer. Only the early pupae can be induced to aestivate in the laboratory, but not eggs or larvae (Finch and Collier, 1985). An increasing proportion of *D. radicum* aestivate with increasing temperature. In a Wellesbourne population, 50% aestivate at 23.5°C whereas 100% aestivates at 27.4°C (Finch and Collier, 1985). Based on emergence of *D. radicum* adults, Nair and McEwen (1975) suggested that the second generation *D. radicum* aestivate in rutabaga fields in southwestern Ontario. When aestivating puparia are exposed to comparatively low temperatures, they resume development with subsequent adult emergence (Finch and Collier, 1985).

Population biology of *Delia radicum*

The number of generations that *D. radicum* completes per year depends on geographical location, weather and host plant availability. *Delia radicum* is univoltine in northern parts of Alberta in canola (Griffiths, 1986a, 1986b), but completes two generations in southwestern parts of Alberta in rutabaga (Swailes, 1958). In southern Manitoba, *D. radicum* completes one or two generations per year on rutabaga (Bracken,

1988). Spring weather, particularly temperature, affects emergence of flies (Bracken, 1988), and warm spring weather allows the flies to complete two generations per year provided that host plants are available. In southern Manitoba, successive plantings of rutabaga are available in the field for four to six months depending on the frost-free period of the year. When rutabaga plants are available, *D. radicum* completes two or three generations per year (Dr. N.J. Holliday, personal communication).

Precipitation and soil moisture affect the activity of *D. radicum*. Rainy weather reduces activity of ovipositing females (Miles, 1952a; Finch and Skinner, 1975). Low soil moisture delays the establishment of the first-instar larvae on roots, and so affects the number of generations per year (Nair and McEwen, 1975; Griffiths, 1991).

Several cultural practices carried out by farmers affect *D. radicum* mortality. Fall and spring tillage reduce the emergence of flies as a result of mortality of puparia (Dosdall *et al.*, 1996b; Finch and Skinner, 1980). Increased plant density of canola appears to reduce the level of infestation (Dosdall *et al.*, 1996a). Meanwhile, soil moisture affects establishment of the first-instar larvae on roots (Mukerji, 1971; Nair and McEwen, 1975), and mortality of first-instar larvae is associated with the difficulty of finding a host plant (Hughes and Salter, 1959; Mukerji, 1971). Mortality of the first-instar larva is also associated with rainfall, soil temperature and root texture (Mukerji, 1971). Low temperature in winter months is not a mortality factor for *D. radicum* pupae (Turnock *et al.*, 1983, 1985; Kostal, 1993a)

Biotic mortality factors greatly affect the population biology of *D. radicum*. Egg predation by staphylinids and carabids is important (Wishart *et al.*, 1956; Hughes, 1959; Hughes and Salter, 1959; Coaker and Williams, 1963; Coaker, 1965; Mukerji, 1971;

Mowat and Humphreys, 1994). Estimate of *D. radicum* egg predation varies from 80–90%, depending on composition and abundance of the predator fauna and estimation methods. For example, egg loss in the field has been estimated at 90% (Coaker and Williams, 1963) and 86% (Hughes and Salter, 1959) at Wellesbourne in rutabaga fields and 81% in Belleville, Ontario and 88% in Prince Edward Island in cabbage fields (Wishart *et al.*, 1956). In addition, *Scatophaga stercoraria* (L.) is scatophagid fly that preys upon *D. radicum* adults (Read, 1958). Microbial diseases cause mortality of *D. radicum; Strongwellsea castrans* Batko and Weiser (Nair and McEwen, 1973, 1975; Humber, 1976; Griffiths, 1991; Lamb and Foster, 1986; Finch, 1989) *Entomophthora muscae* (Cohn) (Griffiths, 1986a,1991), *E. virulenta* Hall and Dunn, *Conidiobolus coronatus* (Costantin) (Matanmi *et al.*, 1974), *Metarrhizium anisopliae* (Metschnikow) and *Paecilomyces fumosoroseus* (Wize) (Vanninen *et al.*, 1992) cause pathogenic infections in *D. radicum.* Among nematodes that attack *D. radicum* larvae are *Heterorhabditis bacteriophora* (Oswego) (Finch, 1989), *Heterorhabditis* sp. (Nair and McEwen, 1975), *Steinernema carpocapsae* All (Royer *et al.*, 1996) and *Steinernema feltiae* Filipjev (Schroeder *et al.*, 1996; Vanninen *et al.*, 1992).

Parasitoid-related mortality is a major factor in the population biology of *D. radicum* (Miles, 1956; Hughes, 1959; Finch and Skinner, 1980; Finch and Collier, 1984). Among the parasitoids of *D. radicum, Aleochara bilineata* Gyllenhal is the major coleopteran parasitoid that occurs in both North America and Europe. *Aleochara bipustulata* L. is the second major coleopteran parasitoid of *D. radicum* and occurs only in Europe (Maus *et al.*, 1998). Among the hymenopteran parasitoids, *Trybliographa rapae* (Westwood) is the most important parasitoid in both North America and Europe

(Wishart and Monteith, 1954; Wishart, 1957). These parasitoids considerably affect population biology of *D. radicum;* hence, their life histories are considered in detail below.

Life histories of major parasitoids of *Delia radicum*

Aleochara bilineata Gyllenhal

Aleochara bilineata is an important natural enemy of *D. radicum* because it functions as a predator as well as a parasitoid (Fuldner, 1960). The adult beetle is a general predator and feeds on dipteran eggs among other foods (Colhoun, 1953; Klimaszewski, 1984; Fournet *et al.*, 2000). First-instar larvae of *A. bilineata* parasitize dipteran puparia, mainly puparia of *D. radicum, D. platura, D. antiqua, D. floralis, D. planipalpis, Pegomyia hyoscyami* Curtis (Anthomyiidae), *P. cepetorum* Maede, *Musca domestica* L. (Muscidae) and *Calliphora erythrocephala* Meigen (Calliphoridae) (Klimaszewski, 1984; Maus *et al.*, 1998).

External anatomical characteristics of adults are important to distinguish *A. bilineata* from related species, but precise identification requires microscopic examination of genitalia. The external anatomy of *A. bilineata* has been well characterized by both North American and European researchers (Casey, 1916; Colhoun, 1953; Fuldner, 1960; Read, 1962; Klimaszewski, 1984; Whistlecraft *et al.*, 1985a; Maus, 1996). The adult beetle is 2–6 mm long (Klimaszewski, 1984) and there is no size difference between males and females (Fuldner, 1960). The size of the beetle is associated with the size of the host puparium in which it developed (Wadsworth, 1915b; Langlet *et al.*, 1998). The body is black and the elytra are uniformly coloured (Fuldner,

1960; Klimaszewski, 1984). Precise identification of *A. bilineata* relies on structure of the aedeagus and spermatheca (Klimaszewski, 1984; Maus, 1996, 1998).

The biological characteristics of adult and immature stages influence the value of *A. bilineata* as a natural enemy of *D. radicum.* Adult beetles readily copulate after emergence, and in the laboratory no courtship period or mating play has been observed (Wadsworth, 1915b; Colhoun, 1953; Fuldner, 1960). The preoviposition period is 2 days (Colhoun, 1953). *Aleochara bilineata* lays eggs in the soil around the host's habitat throughout its life, and average total fecundity is 500–640 eggs (Read, 1960; Bromand, 1980; Fournet *et al.*, 2000). On average, females lay 8–15 eggs per day and the average adult life span is about two months (Read, 1962; Bromand, 1990; Langlet *et al.*, 1998). Eggs are milky white and shiny, oval, and 0.45 x 0.36 mm (Fuldner, 1960). The incubation period varies from 3–7 days depending on temperature and on average is 5 days at 22°C (Bromand, 1980; Ahlström-Olsson, 1994b).

The external anatomy of the campodeiform first-instar larva is well documented (Colhoun, 1953; Fuldner, 1960). The first-instar larva actively seeks and enters a *Delia* puparium, where it spends the rest of its immature life (Fuldner, 1960). The first-instar larvae of *A. bilineata* search for host puparia in soil. In laboratory experiments, first-instar larvae burrow up to 9.5 cm in sand to parasitize a puparium (Bromand, 1980) and in the field there is hardly any parasitism of puparia that lie below 20 cm in soil (Bromand, 1980). Generally, only one larva enters a puparium; two or three larvae per puparium are possible, but only one larva survives (Wadsworth, 1915b; Fuldner, 1960; Read, 1962). Temperature and humidity affect the entry of the first-instar larva into the puparium (Brunel and Langlet, 1994). Humidity softens the puparium wall, which

affects ease of parasitoid penetration (Brunel and Langlet, 1994). Upon entering the puparium, the larva closes the entry hole within 6–12 h using a white anal secretion, which later turns brown or black (Fuldner, 1960). *Aleochara bilineata* overwinters as a first-instar larva (Wadsworth, 1915b; Fuldner, 1960).

The second larval instar is eruciform and 2.8 mm long; the third-instar larva is similar to the second-instar, but 7–7.6 mm long (Wadsworth, 1915b; Fuldner, 1960). *Aleochara bilineata* pupates within the host puparium. The pupa is milky white and all appendages are clearly visible. Durations of the second-instar, third-instar and pupa at 15.5°C are 5, 10, and 34 days respectively (Fuldner, 1960). Total duration from egg to adult at 15.5°C is 67 days (Fuldner, 1960).

The importance of adult *A. bilineata* as predators has been assessed. Adults have been found in brassica crops feeding on *D. radicum* eggs and larvae (Colhoun, 1953; Wilkes and Wishart, 1953; Wishart *et al.,* 1956; Read, 1962; Coaker and Williams, 1963; Bromand, 1980). In laboratory conditions, a pair of beetles, male and female, has the potential to eat 2400 eggs or young larva, or 350 third-instar larvae in their lifetime (Read, 1962).

Behaviour of adults and first-instar larvae evidently influences the value of *A. bilineata* as a parasitoid. *Aleochara bilineata* adults respond to semiochemicals originating from brassica host plants and from *D. radicum* larvae and frass (Royer and Boivin, 1999; Fournet *et al.*, 2000). They also respond to host density (Langer, 1996), probably as a result of their response to the semiochemicals of hosts. Risk of parasitization of *D. radicum* puparia, which involves the behavioral responses of both

adults and the first-instar larvae, increases with host density in the root (Langer, 1996) and is lower in a mixed crop than in a monoculture (Langer, 1996).

The first-instar larvae respond to physical characteristics of the host puparium. First-instar larvae avoid the area of puparia with transverse ridges when making entry holes (Royer *et al.*, 1998). When *D. radicum* puparia, ranging from 4 to 19 mg, are available for parasitism, the first-instar *A. bilineata* larvae parasitize a significantly higher percentage of small puparia, 4–8 mg (Ahlström-Olsson, 1994b; Jonasson, 1994). However, preference for small puparia for parasitism is not evident when 9–25 mm puparia are available for parasitism (Ahlström-Olsson, 1994b). First-instar larvae also respond to semiochemicals emanating from host puparia (Royer *et al.*, 1999). Density dependent parasitism by *A. bilineata* (Mukerji, 1971) might be one of the results of response to semiochemicals. First-instar larvae are also capable of discriminating host puparia parasitized by conspecifics by responding to semiochemicals (Royer *et al.*, 1999). Host discrimination decreases with increasing age (after 2 days) of attacking larvae and decreasing host density (Royer *et al.*, 1999). In addition, the ability of a first-instar larva to enter a host puparium decreases with increasing age of the larva (Royer *et al.*, 1999). Life expectancy of the first-instar larva is 5–6 days, which includes the duration of both free living and parasitic forms (Fuldner, 1960; Royer *et al.*, 1999).

When the first-instar *A. bilineata* larva parasitizes the host puparia, it appears that there is some degree of selection of healthy *D. radicum* puparia rather than puparia parasitized by *T. rapae* (Bromand, 1980). This phenomenon was most conclusively shown in experiments conducted by Jones (1986) and Reader and Jones (1990). When host puparia containing first- and second-instar endoparasitic larvae or third or fourth

instar ectoparasitic larvae of *T. rapae* are presented to *A. bilineata* larvae, they parasitize more puparia with endoparasitic *T. rapae* than puparia with ectoparasitic larvae (Reader and Jones, 1990). When *A. bilineata* parasitizes puparia containing an endoparasitic *T. rapae,* it is common for both parasitoids to die; those that do survive are mainly *A. bilineata.* The first-instar larva of *A. bilineata* is capable of discriminating to some degree between unparasitized and *T. rapae*-parasitized puparia when the *T. rapae* is an ectoparasitic larva (Jones, 1986; Reader and Jones, 1990). If *A. bilineata* parasitizes such puparia, *T. rapae* is more likely to survive to adulthood than *A. bilineata* (Reader and Jones, 1990).

***Aleochara bipustulata* L.**

The biology of *A. bipustulata* is generally similar to that of *A. bilineata* except for the external anatomy of the adult, its host preference, and the overwintering stage (Fuldner, 1960; Ahlström-Olsson, 1994a; Fournet *et al.*, 2000). General external anatomy of the beetle is similar to that of *A. bilineata*, but the base of each elytron has a brownish red spot. This spot can extend up to one quarter of the length of the elytron (Fuldner, 1960). The posterior margin of the 6th abdominal tergite has 10 strong spines in males and 14 such spines in females (Fuldner, 1960). Precise identification of species relies on characteristics of aedeagus and spermatheca (Maus, 1996, 1998).

The first-instar larva of *A. bipustulata* parasitizes a wider host range than the host range of *A. bilineata* (Maus *et al.*, 1998). It does not show a preference for host species among *D. radicum, D. platura* and *D. antiqua,* but does show a preference for small puparia when it has a choice (Ahlström-Olsson, 1994b). The first-instar larva parasitizes host puparia regardless of their age (Fuldner, 1960; Ahlström-Olsson, 1994b). In

Sweden, *A. bipustulata* coexists with *A. bilineata* in brassica vegetable fields (Ahlström-Olsson and Jonasson, 1992). Unlike *A. bilineata, A. bipustulata* overwinters as an adult and becomes active early in the season (Fuldner, 1960). Application of mustard meal in cabbage attracts *A. bipustulata* adults (Ahlström-Olsson and Jonasson, 1992).

***Trybliographa rapae* (Westwood)**

The external anatomy of the adult *T. rapae* has been well documented and can be used in identification (Kerrich and Quinlan, 1960; Hertveldt, 1970; Nordlander, 1981). Generally, *T. rapae* is 2.3 mm long, with a shiny black body (Wadsworth, 1915a; Wishart and Monteith, 1954; Hertveldt, 1970) and 13-segmented antennae, each with an 11-segmented flagellum (Butterfield and Anderson, 1994). Males have longer antennae (James, 1928) with more elongated segments than those of females (Kerrich and Quinlan, 1960). Female antennae are moniliform, moderately hairy, and segment three is distinctly longer than segment four (Kerrich and Quinlan, 1960).

This parasitoid is found almost everywhere in Europe, North America and Asia wherever host insects are available (Wishart and Monteith, 1954). It parasitizes a wide range of hosts that includes *D. radicum, D. floralis, D. antiqua,* and *D. platura* (Wishart and Monteith, 1954).

Trybliographa rapae is pro-ovigenic; oviposition starts within 2 days of emergence, and continues for 10 days (James, 1928). Total fecundity averages 37.7 eggs per female (Jones, 1986). *Trybliographa rapae* adults are not active fliers (Wishart and Monteith, 1954). The adult female parasitoid crawls through soil along the root (James, 1928) and can parasitize all three larval instars of *D. radicum* (Neveu *et al.,* 2000). When searching for hosts for oviposition, *T. rapae* responds to volatiles emanating from hosts,

host plants and host tissues damaged by *D. radicum* (Jones, 1986; Brown and Anderson, 1999), and also responds to physical stimuli arising from larval movement (Vet and Alphen, 1985). Visual cues are less important for host finding (Jones, 1986). The probability of hosts on a plant being attacked by *T. rapae* increases with the host density per plant (Langer, 1996) and, once an infested plant is found females spend more time there if host density is high (Jones and Hassell, 1988). The level of ground cover, monoculture or mixed culture, does not significantly affect parasitism of hosts (Langer, 1996). *Delia radicum* puparia parasitized by *T. rapae* were found at depths upto 10 cm in the soil; 63% of parasitized puparia were found at depths of 0–5 cm in a rutabaga field in England (Block *et al.,* 1987).

Trybliographa rapae eggs are 0.50 x 0.16 mm, with a 0.35 mm long pedicel (Kacem *et al.*, 1996). Eggs are deposited in the haemocoel of the host larva, a location where there is no encapsulation of eggs (Neveu *et al.*, 2000). First-instar parasitoid larvae are eucoiliform, sub-cylindrical, 0.7 mm long and have a distinct head. The presence of a caudal appendage, 0.24 mm long, is a specific character (Wishart and Monteith, 1954; Kacem *et al.*, 1996). The first-instar parasitoid larva remains dormant until the host larva matures (Neveu *et al.*, 2000). The second-instar *T. rapae* is polypodous, 2.3 mm long when full grown, with a reduced caudal appendage; the integument is thin and soft (Wishart and Monteith, 1954; Kacem *et al.*, 1996). The third and fourth instar larvae are ectoparasitic, in contrast to the endoparasitic first- and second-instars (Wishart and Monteith, 1954). The third-instar larva is about 3.5 mm long when fully grown, with an integument that is thin and adapted to apneustic respiration. The third-instar larva takes up an external feeding position on the host pupa. The fourth

instar is a grub-like hymenopteran larva and varies in size (2.66–4.40 mm) depending on the host size. Parts of the head and spiracles are sclerotized (James, 1928; Wishart and Monteith, 1954). *Trybliographa rapae* overwinters as a fourth instar larva within the host puparium (Wishart and Monteith, 1954; Block *et al.,* 1987). Hence, duration of the fourth instar larva could vary from two weeks to several months depending on temperature and diapause state (Wishart and Monteith, 1954). A pupal stage follows after the fourth instar larva, and the adult gnaws an irregular exit hole in the puparium (Wishart and Monteith, 1954). On average, females live three weeks and males live 10 days (Jones, 1986).

The duration of the life cycle of *T. rapae* varies depending on the stage of host attacked. The total development time is 54–61 days when the eggs are laid in first-instar larvae, the time is 5–6 days for incubation of eggs, 15 days for the first-instar, 5 days for the second-instar, 3 days for the third-instar, 13 days for the fourth instar and 25 days for the pupa at 20°C and 60% RH (Kacem *et al.,* 1996). The duration of the life cycle when the eggs are laid in the second-and third-instar of *D. radicum* is 54 and 50 days at 20°C, respectively (Neveu *et al.,* 2000).

Classical biological control of *Delia radicum* in canola on the Canadian Prairies

Incorporation of additional mortality factors is required to further suppress the population level of *D. radicum* in canola on the Canadian Prairies because current mortality factors are not adequate. *Delia radicum* populations in canola are related to farm operations and biotic and abiotic mortalities. Fall and spring tillage and seeding rate affect *D. radicum* populations (Dosdall *et al.*, 1996a, 1996b). Insecticide application as a seed dressing (Canola Council of Canada, 2004) may have little effect on the *D. radicum*

populations because *D. radicum* infest canola at the bolting stage (Griffiths, 1986a). Precipitation and temperature in June and July affect *D. radicum* populations (Turnock *et al.*, 1992). Cool and wet weather in spring favours higher *D. radicum* populations (Soroka *et al.*, 2002). Soil moisture affects desiccation of eggs (Mukerji, 1971; Nair and McEwen, 1975). Predation of immature *D. radicum* by carabids and staphylinids accounts for a considerable mortality of *D. radicum* (Wishart *et al.*, 1956; Hughes, 1959; Hughes and Salter, 1959; Coaker and Williams, 1963; Coaker, 1965; Mukerji, 1971; Mowat and Humphreys, 1994). *Aleochara bilineata* has only limited value as an egg predator of *D. radicum* because the occurrence of adult beetles and *D. radicum* eggs is not synchronized in the spring (Read, 1962; Finch, 1989). *Aleochara bilineata* and *T. rapae* parasitize a variable proportion of *D. radicum* populations (Finch, 1989). Mortality of *D. radicum* through all the above factors does not provide sufficient and consistent suppression of *D. radicum* population in canola; hence, there is a requirement for additional mortality factors (Turnock *et al.*, 1995). Addition of exotic parasitoids might provide the additional mortality of *D. radicum* required to lower the population level of *D. radicum.*

Assessment of the parasitoid community of the target host in the release areas and in the areas of origin is a prerequisite for classical biological control (Waage, 1990). This avoids the introduction of an already existing biocontrol agent, which has been a reason for failure for several biological control projects (McLeod, 1962). Confirmation of the identity of the parasitoid species, including agreement on identities by taxonomists in source and target areas, avoids the potential introduction of already existing parasitoid species. In addition, study of the biology of the host insect and its parasitoids provides a

better understanding of the host and parasitoid system in the target crop. Therefore, this study initially focused on comparative assessments of the parasitoid community of *D. radicum* on the Canadian Prairies and Europe, followed by studies of the biology of the host and its parasitoids.

CHAPTER 3 SECTION 1

Assessment of the parasitoids of *Delia radicum* in canola on the Canadian Prairies

Introduction

Delia radicum is one of several injurious insects in canola (Alford *et al.,* 2003) on the Canadian Prairies (Soroka *et al.*, 2002; Canola Council of Canada, 2004). Larvae of *D. radicum* feed on conductive and storage cells within a narrow band of tissues on canola roots, and severe feeding damage disrupts water and nutrient uptake (McDonald and Sears, 1992). In addition, larval feeding predisposes the root to infection by pathogenic microbes e.g. *Fusarium* spp. (Griffiths, 1986a). Severe root damage causes plant wilting, stunting, lodging, reduced flowering and plant death (Liu and Butts, 1982; Soroka *et al.,* 2002). Infestations of *D. radicum* have been found in Alberta, Saskatchewan and Manitoba (Turnock *et al.,* 1992; Soroka *et al.,* 2002) and economic damage to canola has been documented in some parts of Alberta (Liu and Butts, 1982; Griffiths, 1986a; Soroka *et al.,* 2002).

Current control methods for *D. radicum* in canola do not provide adequate plant protection. Manipulation of tillage regime and seeding rate has an effect on *D. radicum* damage to canola (Dosdall *et al.,* 1996a, 1996b), and also applying granular insecticides at seeding provides some suppression of *D. radicum* (Canola Council of Canada, 2004). However, these methods do not provide adequate control of *D. radicum*. Furthermore, the control methods used in brassica vegetables, such as inter-cropping, mulching, manipulation of planting date and insecticide drenches (Finch, 1987, 1989), are not technically feasible in canola on the Canadian Prairies. One of the options available is classical biological control (Turnock *et al.,* 1995; Soroka *et al.,* 2002).

Classical biological control of *D. radicum* in brassica vegetables was attempted in eastern Canada (McLeod, 1962). Several parasitoid species were introduced into Canada in the1950s, but the biocontrol program was discontinued after a few years, because it

was found that the introduced species had already been present in Canada (Soroka *et al.*, 2002).

The parasitoid community of *D. radicum* in brassica vegetables has been characterized in Canada. *Aleochara bilineata* Gyllenhal and *Trybliographa rapae* (Westwood) are present in brassica vegetable growing areas of all Canadian provinces (Wishart, 1957). *Aleochara verna* Say, *Aphaereta* spp. and *Phygadeuon trichops* Thomson are present, but not highly abundant in Canada (Turnock *et al.*, 1992).

The biology of *D. radicum* in canola differs in several respects from that in brassica vegetables. Canola is mainly grown in Western Canada in geographically different areas to brassica vegetable growing areas; therefore, the number of generations of *D. radicum* per year is different (Griffiths, 1991). Moreover, the canola habitat is different from the brassica vegetable habitat, and the difference may affect the *D. radicum* parasitoid community. In addition, the different agronomic operations in brassica vegetable farming and canola production may influence the host-parasitoid system. Some characteristics of canola render the crop more suitable than brassica vegetables for biological control. Canola can tolerate a low level of *D. radicum* population with little or no effect on yield (McDonald, 1985) and the insect does not attack economically valuable parts of the canola plant. Suppression of such insects to a very low population level is not generally required (Munroe, 1971). Canola is grown over large areas in every year (Canola Council of Canada, 2004), hence there is no shortage of host plants or hosts for parasitoids. Therefore, revisiting the topic of classical biological control of *D. radicum* is not a repetition of the previous attempt.

Among the desirable characteristics of a biocontrol agent, synchronization of the parasitoid's and host's life histories is important and may affect the level of suppression of the host population (Huffaker *et al.,* 1976). Imperfect synchronization of host-seeking stages of parasitoids and susceptible stages of hosts results in some hosts being at low or no risk of parasitism (Godfray *et al.,* 1994). The level of host-parasitoid asynchrony affects the stability of both populations (Godfray, 1994; Godfray *et al.,* 1994). Data on dynamics of the parasitism of host can be used to assess the synchronization of host and parasitoids (Macdonald and Cheng, 1970).

The objectives of this study were to define the parasitoid community of *D. radicum* in canola on the Canadian Prairies and to obtain information on times of parasitoid attack and emergence in relation to host phenology.

Methods

In summer 2000, immature *D. radicum* were collected from selected locations on the Canadian Prairies, and individually reared to assess the parasitoid community. There were six major sampling sites, two fields in each of Manitoba, Saskatchewan and Alberta. Canola fields for sampling were selected based on infestation levels of *D. radicum* in the area in 1999, infestation level of *D. radicum* in canola in 2000, the history of crop rotation, usage of insecticide in 2000 and ease of access to fields. The sampled fields in Manitoba were at the University of Manitoba Carman Field Research Station, (49°30'N; 98°0'W), and at Altamont (49°24'N; 98°30'W). The field at Carman was a 1.4 ha research plot, bordered by barley, canola, wheat and uncultivated land to the south, west, east and north, respectively. There were farm roads between the research plot and the adjacent fields in all directions except to the south. The field was sown with LG 3235 Roundup-

Ready canola and no insecticides were applied. Canola had been grown in an adjacent plot on the west side in 1999. The canola field at Altamont was a 256 ha commercial canola field of cv "Express". Canola had been grown in the same field in the previous year and root damage had been observed. No insecticide was used in the sampling year.

Sampling sites in Saskatchewan were at Melfort (52°52'N; 104°35'W) and Shellbrook (53°15'15"N; 106°20'41.9"W). At Melfort, a 0.4 ha research plot at the Crop Research Station, Agriculture and Agri-Food Canada was used. It had spring seeded *B. rapa oleifera* (DeCandolle) Metzger, cv "Horizon" and the field borders had abundant volunteer "Quest" *B. napus* L. and wild mustard, *Sinapsis arvensis* L.. There was no insecticide use in the previous year or the sampling year. The field at Shellbrook was a commercial canola field of about 41 ha. The field was bordered by a forest, pastureland, forest and a wheat field to the east, north, west and south respectively.

The sampling sites in Alberta were at Vegreville and are called Vegreville-1 (53°30'N; 112°2'W) and Vegreville-2 (53°30'N; 112°6'W). Both were commercial canola fields, cv "Conquest". Each field was about 100 ha. Oat was grown in both fields in 1999. No insecticides were applied to the canola in the sampling year. In 2000, the Vegreville-1 field was bordered by wheat fields to the east and north and by woods to the west and south. The Vegreville-2 field was bordered by wheat fields to the east, west and north and by woods to the south. Small patches of uncultivated land were scattered in both fields.

Sampling was carried out for different durations depending on the abundance of immature *D. radicum* in the field (Table 1.1). At each location except Shellbrook, sampling started with the appearance of *D. radicum* eggs in the field. Each field was

sampled weekly for eggs, larvae, and puparia of *D. radicum.* The target sample size each week was at least 100 immatures (eggs plus larvae plus puparia) from each sample site. Sampling in each field was confined to a 3 m wide strip along the field margin. The plants were taken from several areas of field margin; sampling areas of field margin were about 100 m apart. Within each sampling area, sampling places were at least 3 m from each other. One to three randomly chosen plants were taken from each sampling place and 15–20 plants were collected in each sampling area. The total number of plants collected per site (=location) varied depending on the level of *D. radicum* infestation and the stage of *D. radicum.* Generally, a higher number of plants was collected when *D. radicum* was at first-instar larva and puparial stages.

Eggs of *D. radicum* were sampled by examining the soil at the base of canola plants and collecting eggs with soil into a 500 ml plastic cup. Sampling was continued until an adequate number of eggs was collected. Eggs were separated from soil under the microscope (60 x) in the laboratory, or by adding the egg and soil mixture to water and collecting the floating eggs with a paintbrush (Hughes, 1959). Collected eggs were examined under the microscope to separate eggshells from unhatched eggs. Larvae of *D. radicum* were sampled from randomly chosen infested canola roots. Collection of plants was continued until adequate numbers of larvae were obtained. Thus, the number of plants per sample depended on the level of infestation. Larvae were extracted in the laboratory by dissecting plant roots under the microscope (16 x). Puparia of *D. radicum* were sampled by collecting canola roots and the soil around the root (10 cm diameter and 6 cm deep). The soil was sorted in the field on a 30 x 15 cm white plastic tray and the puparia were collected into a plastic cup.

In addition to regular weekly sampling, one sample of canola roots with larvae was collected in a research field at Beaverlodge Research Farm, Agriculture and Agri-Food Canada, Alberta (55°12'N; 119°27'W). Also, a mass collection of puparia was made in October 2000, from the margins of both sample fields at Vegreville and from the field at Shellbrook.

Immature *D. radicum* collected from Carman and Altamont and the mass collection of puparia were transported in a picnic cooler by truck to the University of Manitoba. Immatures collected during weekly sampling from Saskatchewan and Alberta were shipped to the University of Manitoba by courier. For courier shipment, eggs were placed on moist filter paper in a 10 cm Petri dish. Larvae were placed on 1 cm thick slices of rutabaga and allowed to burrow into them for 48 hours before shipping. The rutabaga slices with larvae were packed in Petri dishes before transport. Puparia were packed in sand-filled Petri dishes. Petri dishes with immature *D. radicum* were packed in polystyrene boxes padded with packing sponge for shipping.

Rearing

Immature *D. radicum* from sampling sites were reared individually until the emergence of a host or parasitoid adult. Immatures were processed immediately upon receipt at the University of Manitoba. Eggs were separated from the filter paper and placed individually on a 1 cm^3 rutabaga cube in a plastic vial (5 cm height and 2.3 cm diameter). If eggs hatched during transport, each first-instar larva was individually placed on a rutabaga cube in a vial. Eggshells and dead larvae were discarded. Each living larva was placed on a rutabaga cube in a vial, and a small amount of fine, moist sand was added to support the establishment of the larva on the rutabaga. Each puparium

was placed in a vial with fine, moist sand only. All stages were incubated at 20°C, at 16:8 L:D photoperiod, and 60% RH. Rearing vials that contained larvae were checked regularly until pupation, and food was replaced as required. Upon pupation, each puparium was placed in a fresh vial with fine moist sand. Vials with puparia were examined biweekly for adult emergence until 15 October 2000, when those in which there was no emergence were placed at 1°C for 22 weeks. In early April, 2001, temperature for the rearing vials was raised to 20°C over a two week period and held at 20°C. If emergence did not occur within five weeks, the puparia were dissected under a microscope (60 x) and the contents examined to determine whether they were parasitized.

All the adults that emerged were examined under a microscope (60 x) and grouped based on external anatomy. Subsequently, the groups were identified using taxonomic keys and comparing with museum specimens from the J.B. Wallis Museum of Entomology, Department of Entomology, University of Manitoba. *Trybliographa rapae* specimens, received from Dr. Liliane Krespi-Bailhache, Université de Rennes, France, were also used for comparison. Representative samples of *Aleochara* specimens were dissected and genitalia were mounted on plastic slides, and the structure of the aedeagus and spermatheca was compared with the drawings of Klimaszewski (1984) and Maus (1996, 1998). Most of the specimens were stored in 70% ethanol in 5 ml plastic vials and some specimens were mounted on paper points. Voucher specimens of parasitoids and host insects were deposited in the J.B. Wallis Museum of Entomology, University of Manitoba.

Representative samples of *Aleochara* were sent to J. Klimaszewski, Laurentian Forestry Centre, Canadian Forestry Service, Sainte-Foy (Québec), Canada, and C. Maus,

Institut für Biologie I, Freiburg, Germany for confirmation of identity. *Phygadeuon* specimens were sent to K. Horstmann, Theodor-Boveri-Institut für Biowissenschaften, Universität, Würzburg, Germany and *Trybliographa rapae* specimens were sent to G. Melika, Systematic Parasitoid Laboratory, Ministry of Agriculture of Hungary, Kszeg, Hungary. Specimens of *Aphaereta* species were sent to K. van Achterberg, National Natuurhistorisch Museum, Leiden, Netherlands. Specimens of *Trichopria* were sent to L. Masner, Eastern Cereal and Oilseed Research Centre, Ottawa, Canada. A representative sample of *D. radicum* from each sample site was sent to G.C.D. Griffiths, Alberta, Canada for the confirmation of identity.

Data analysis

Percentage parasitism of host by a parasitoid was estimated as the number of parasitoid adults divided by the total number of hosts collected in susceptible stages for parasitization and surviving to adults, and multiplied by 100. Parasitism among sites was compared using log linear modeling. Here and throughout this thesis, parasitism refers to the ratio of number of parasitized hosts to total number of hosts in the sample susceptible to parasitism and developed to adulthood (Driesche, 1983, Mills, 1997). Synchronization of hosts and parasitoids was examined using the method of Macdonald and Cheng (1970), in which cumulative fractions of parasitized and unparasitized hosts were calculated for each sampling time. The proportions of parasitized and unparasitized hosts among samples were compared using contingency table analysis. Preliminary analysis revealed that contingency table analysis was more appropriate than Kolmogorov-Smirnov two-sample test to detect the synchronization in host and parasitoids in my data.

Diapause of unparasitized larval and pupal *D. radicum* in relation to time of collection was examined using logistic regressions. Logistic regression was also used to compare induction of diapause of *T. rapae* and *A. bilineata* with that of *D. radicum.* Proportions of diapaused-unparasitized puparia and diapaused-parasitized puparia by *T. rapae* and *A. bilineata* were compared using logistic regression in which the independent variable was time of collection. Only the samples in which parasitism was found were included in this analysis. In one method, the number in diapause was estimated as the number of adults that emerged in the spring, 2001. Adults that emerged in spring 2001 had diapaused, but emergence in spring was poor and the numbers available for analysis were low. Therefore, a second method of estimation was also used, in which the puparia from which adults did not emerge by 15 October 2000 were considered to be in diapause. The second method assumes that all the individuals that developed to adulthood but did not emerge had died after overwintering. This method tends to over estimate numbers diapausing. However, preliminary analysis showed that the general trend of diapause time of *D. radicum* and parasitoids remained the same regardless of which method of estimation was used. Therefore only results of the second analysis, in which diapause were estimated from numbers that did not emerge by fall, are presented.

Results

Phenology of *Delia radicum*

Phenology of *D. radicum* was slightly different among geographical locations. Data were more comprehensive for Altamont and Carman than other sites because *D. radicum* samples were taken at the two sites for over 100 days. *Delia radicum* eggs

were present from early June to the end of June in canola fields at Altamont and Carman (Fig. 1.1–1.2). Peak abundance of eggs was in the third week of June, and on that date, canola plants were bolting. In general, the eggs were found in bare soil near canola stems, and 3–4 eggs were found in one place. First-instar larvae were in the field for a short period in late June followed by the second- and the third-instar larvae. The greatest number of third-instar larvae was on 10 July at Carman and on 17 July at Altamont. Puparia were first found in mid July. *Delia radicum* completed only one generation in canola at Altamont and Carman in 2000.

Canola fields in Saskatchewan were sampled for 30–35 days (Table 1.1). At Melfort, only eggs and larvae of *D. radicum* were sampled. Relative abundance of eggs of *D. radicum* had diminished by the second week of July at Melfort. Third-instar larvae were found in five samples and peaked on 24 July (Fig. 1.3). At Shellbrook, the greatest number of third-instar larvae was also on 24 July, and puparia were present in the first sample on 10 July (Fig. 1.4). In both Saskatchewan sites, phenology was about one week later than in Manitoba sites.

At Vegreville, eggs were found until late June, and then again in the second week of July. First- and second-instar larvae were at Vegreville fields for a more extended time period than in other sites and third-instars were present as late as or later than in Saskatchewan sites (Fig. 1.5–1.6).

Diapause of *Delia radicum*

A proportion of *D. radicum* collected on any sampling date entered diapause, and this proportion was greater in samples collected later in the season. The logistic regression relationship between the proportions entering diapause and the time of

sampling (Julian date), based on data from all the sites, was significant (Likelihood Ratio (L.R.) $\chi^2 = 1012$, df = 1, $P < 0.001$), and the location effect (L.R.$\chi^2 = 177$, df = 5, $P < 0.001$) and the location x time interaction (L.R.$\chi^2 = 11.7$, df = 5, $P = 0.04$) were also significant. The relationship was significant for four individual locations (Fig. 1.7): Carman (L.R.$\chi^2 = 438$, df = 1, $P < 0.001$), Altamont (L.R.$\chi^2 = 584$, df = 1, $P < 0.001$), Vegreville-1 (L.R.$\chi^2 = 14.3$, df = 1, $P < 0.001$) and Vegreville-2 (L.R.$\chi^2 = 23.4$, df = 1, $P < 0.001$). Among these four sites, location effect was significant (L.R.$\chi^2 = 41.8$, df = 3, $P < 0.001$), but location x time interaction was not significant (L.R.$\chi^2 = 4.4$, df = 3, $P = 0.226$). The Julian dates at which 50% diapaused were (with 95% confidence limits): Carman 190 (187–192), Altamont 197 (195–200), Vegreville-1 184 (171–190) and Vegreville-2 184 (177–188). Thus Vegreville sites were different from the Manitoba sites and within Manitoba sites, Carman differed from Altamont. The probability of immatures collected at Vegreville entering diapause was greater than that in the other sites (Fig. 1.7). At Carman and Altamont, more than 80% of *D. radicum* diapaused when they were collected after the first week of August. Logistic regressions were not individually significant for the Saskatchewan locations, where smaller series of samples (Table 1.1) were available.

Parasitoid community of *Delia radicum*

Individuals of seven parasitoid species emerged from *Delia* samples. *Trybliographa rapae* (Hymenoptera: Eucoilidae) emerged from samples collected as larvae or puparia. The other six species were pupal parasitoids, four species of Hymenoptera and two species of Coleoptera. The hymenopteran species were two *Phygadeuon* species (Ichneumonidae), *Aphaereta minuta* (Nees) (Braconidae) and

Trichopria sp. (Proctotrupidae). The coleopteran species were *Aleochara bilineata* and *Aleochara verna* (Staphylinidae). No egg parasitoids emerged from the eggs sampled.

Total parasitism of *D. radicum* by all parasitoid species, based on puparia collected in fall, varied significantly among the five sampling sites where collections were made (L.R.χ^2 = 54.9, df = 4, $P < 0.001$) and also among the provinces (L.R.χ^2 = 20.6, df = 2, $P < 0.001$). Variability of parasitism between sites within provinces was also significant (L.R.χ^2 = 34.3, df = 2, $P < 0.001$). Hence, parasitism was variable on a local scale (Table 1.2).

Trybliographa rapae

Trybliographa rapae was present in samples collected at all sites, and was present in larval and pupal samples. Adult *T. rapae* emerged from the host puparium. Levels of parasitism of *D. radicum* larvae differed among sampling sites when assessed on the basis of a single sample of puparia per site collected in the later part of the season (Table 1.2). Parasitism varied significantly among sampling locations (L.R.χ^2 = 110.8, df = 4, $P < 0.001$) and between locations within provinces (L.R.χ^2 = 14.6, df = 2, $P < 0.001$). Generally, levels of parasitism of *D. radicum* fluctuated with sampling dates (Fig. 1.8–1.13), with a tendency to increase through larval instars until the third-instar larvae were rare (<10%) in the field (Fig. 1.8–1.9). However, this pattern of increasing parasitism with increasing instars of host larva was not universal (Table 1.3). There was a trend of diminishing levels of parasitism over time in pupal samples.

Parasitism of *D. radicum* larvae was not significantly different among the sampling sites (L.R.χ^2 = 0.6, df = 5, P = 0.988), when it was estimated based on a single

sample of larvae per site that was taken when the third-instar larvae population was at its peak (Table 1.4). The unweighted average parasitism was 11.2%.

Synchronization of *T. rapae* and *D. radicum* larvae appeared to be related to locality. Four of the sampling sites had sufficient numbers of *T. rapae* adults (Table 1.3) for analysis. Of these four sites, *T. rapae* was synchronized with *D. radicum* in two sites, Carman (L.R.$\chi^2 = 0.9$, df = 3, $P = 0.837$) (Fig. 1.14) and Shellbrook (L.R.$\chi^2 = 0.03$, df = 2, $P = 0.983$) (Fig. 1.15). Lack of synchronization was significant at Altamont (L.R.$\chi^2 = 6.9$, df = 2, $P = 0.032$) (Fig. 1.14) and Melfort (L.R.$\chi^2 = 7.6$, df = 2, $P = 0.023$) (Fig. 1.15): in both locations, the occurrence of parasitoids was delayed relative to the occurrence of hosts. At Altamont, there was a difference of 7 days between the occurrence of 50% host population and 50% of parasitized hosts (Fig. 1.14), and at Melfort that difference was 3 days (Fig. 1.15). Vegreville sites did not have sufficient numbers of parasitoids (Table 1.3) for synchronization to be assessed adequately (Fig. 1.16).

Of the parasitized puparia collected in regular samples at all sampling sites (412), 49.5% emerged in the summer, whereas 7.5% naturally emerged in spring, 2001. The rest, 43%, had developed to adults but did not emerge naturally. Generally, there was a tendency for the frequency of diapausing puparia (parasitized and unparasitized) to increase towards the later part of the season, when diapause was determined as number that did not emerge by fall, 2000. The relationship of proportion diapausing with time followed a logistic regression (L.R.$\chi^2 = 385.1$, df = 1, $P < 0.001$), but the effect of species (*D. radicum* or *T. rapae*) (L.R.$\chi^2 = 204.2$, df = 1, $P < 0.001$) and of location (L.R.$\chi^2 = 94.5$, df = 4, $P < 0.001$) were significant. In addition, the species x time

interaction (L.R.χ^2 = 82.3, df = 1, P < 0.001), and location x time interaction (L.R.χ^2 = 14.3, df = 4, P = 0.006) were significant. Furthermore, the location x species x time interaction was significant (L.R.χ^2 = 10.5, df = 4, P = 0.033). When data were examined based on site, only the Altamont data had a significant logistic relationship between *T. rapae* diapause and time (L.R.χ^2 = 14.2, df = 1, P < 0.001) (Fig. 1.17). Species effect was significant (L.R.χ^2 = 91.4, df = 1, P < 0.001), and species x time interaction was not significant (L.R.χ^2 = 1.6, df = 1, P = 0.202). There was a 50 day delay between 50% diapause of *D. radicum* and *T. rapae* (Fig. 1.17).

Aleochara bilineata

Aleochara bilineata was the most abundant coleopteran parasitoid of *D. radicum* and was present in all sampling sites where puparia were collected (Table 1.2–1.3). Regular sampling of puparia in sufficient numbers was done only at Altamont and Carman. Parasitism of *D. radicum* by *A. bilineata* fluctuated with sampling time reaching a peak in early August and declining towards the end of August (Fig. 1.8–1.9). Variation of parasitism among sampling sites was significant (L.R.χ^2 = 117.5, df = 4, P < 0.001) but variation between sites within provinces was not significant (L.R.χ^2 = 5.4, df = 2, P = 0.067) and variation among provinces was significant (L.R.χ^2 = 112.1, df = 2, P < 0.001) (Table 1.2) when estimation was based on a single collection of puparia per site. The highest parasitism was found at Vegreville-2 (Table 1.2).

In the regular sampling at Carman and Altamont, *D. radicum* puparia parasitized by *A. bilineata* were found beginning in the samples collected in mid July, and there was significant lack of synchronization between *A. bilineata* and *D. radicum* host puparia at Carman (L.R.χ^2 = 42.4, df = 8, P < 0.001) and at Altamont (L.R.χ^2 = 197, df = 7,

$P < 0.001$) (Fig. 1.18). In both locations, phenology of parasitoids in hosts was early relative to that of unparasitized hosts. At Carman, there was a difference of 3 days between the occurrence of 50% unparasitized hosts and of 50% parasitized hosts, and at Altamont the difference was 9 days (Fig. 1.18).

Adult *A. bilineata* emerged in summer or they diapaused within puparia and emerged in the following spring. Of the 481 parasitized puparia collected in regular sampling at Carman and Altamont, 78.8% emerged in summer 2000, and 1.0% emerged in spring, 2001. The rest did not emerge naturally in the spring. When diapause was determined as the number that did not emerge by fall, 2000, the proportion diapausing of parasitized and unparasitized puparia followed a logistic regression (L.R.$\chi^2 = 231.4$, df = 1, $P < 0.001$). The effect of species (*D. radicum* or *A. bilineata*) (L.R.$\chi^2 = 828.9$, df = 1, $P < 0.001$), and effect of location (L.R.$\chi^2 = 42.6$, df = 1, $P < 0.001$) were significant. In addition, neither the species x time interaction (L.R.$\chi^2 = 1.5$, df = 1, $P = 0.218$), nor the location x time interaction (L.R.$\chi^2 = 1.6$, df = 1, $P = 0.212$) was significant. The location x species x time interaction was not significant (L.R.$\chi^2 = 0.7$, df = 1, $P = 0.413$). When data were examined based on location, at Altamont, the species effect was significant (L.R.$\chi^2 = 362.7$, df = 1, $P < 0.001$), but the species x time interaction was not significant (L.R.$\chi^2 = 1.0$, df = 1, $P = 0.321$). At Carman, the species effect was significant (L.R.$\chi^2 = 427.3$, df = 1, $P < 0.001$), and species x time interaction was not significant (L.R.$\chi^2 = 1.8$, df = 1, $P = 0.176$) (Fig. 1.19). There was a 38 and 45 day difference between 50% diapause of *D. radicum* and *A. bilineata* at Carman and Altamont, respectively (Fig. 1.19).

Aleochara verna

Aleochara verna was present in all the sampling sites where puparia were collected. The levels of parasitism were lower than those of *A. bilineata* (Table 1.2–1 .3). Both *Aleochara* spp. occurred over a similar time period (Fig. 1.8–1.9). At Carman, four samples collected from 24 July to 9 September had 0.7–1.8% parasitism with an average of 1.4% (Fig. 1.8). One sample of 23 puparia collected on 11 October had 17.4% parasitism. At Altamont, levels of parasitism varied from 0.6–5.9% in four puparial samples collected from 24 July to 30 August, and the average parasitism was 3.3% (Fig. 1.9). Host synchronization and diapause relationships were not examined due to the small numbers of *A. verna* present in the samples (Table 1.3).

Phygadeuon species

Phygadeuon species that parasitize *D. radicum* puparia were found only at Carman (49 insects) and Altamont (1 insect). The *Phygadeuon* found at Carman were probably of two undescribed species (Dr. Horstmann, personal communication). The levels of parasitism varied from 0.7–8.8% in seven puparial samples collected at Carman with an average of 3.5% (Fig. 1.8). The population of *Phygadeuon* was not synchronized with the population of *D. radicum* puparia (L.R.$\chi^2 = 27.4$, df = 3, $P < 0.001$) (Fig. 1.20). There was a difference of 3 days between the occurrence of 50% host population and 50% of parasitized hosts. Parasitism of *D. radicum* puparia by *Phygadeuon* spp. was at a peak in the last week of August (Fig. 1.8). All the collected puparia that had been parasitized by *Phygadeuon* spp. emerged by 15 October in the laboratory, which indicates that there was no tendency to diapause as immatures within the host puparia.

Aphaereta minuta and *Trichopria* sp.

Aphaereta minuta (Nees) was reared from an extra collection of puparia taken from the middle of the regularly sampled canola field at Carman; regular sampling was done in the peripheral area of the field. These puparia were collected in July and August, 2000. Eleven individuals of *A. minuta* emerged from 961 puparia reared from this collection. One puparium collected in fall at Shellbrook had been parasitized by *Trichopria* sp., and about 30 adults emerged from this puparium.

Discussion

Implication of methods

In this study, the target number of immature *D. radicum* was 100 per site per sampling day. In Manitoba sites, the number of immatures collected in each sampling date was higher than 100 (Fig. 1.1–1 .2). The number of plants collected to reach the target number of immatures was highly variable depending on population levels of *D. radicum* in different sites and developmental stage of *D. radicum.* For example, when *D. radicum* was at the first-instar larva, a higher number of plants was required to obtain the target number than they were at the third-instar because the first-instar is less detectable than the third-instar. In addition, only the larvae on roots were collected.

The focus of this study was to assess the parasitoid community; therefore, sampling was limited to the edges of fields, where *D. radicum* are easily found. Sampling at edge of the field reduces potential effects of field size on assessments of parasitism. However, it is possible that the parasitoids at edge of the field are not identical to those at the center of the field. Therefore, assessments of parasitism of this

study should be considered as the parasitism in canola where *D. radicum* is available. No attempt was made to compare the parasitism at edge and center of the field.

Sampling on the Canadian Prairies was limited to one year. One year sampling is sufficient to characterize the general structure of the parasitoid community. Parasitism would be better assessed if sampling occurred over several years, but this was not compatible with the constraints of this study. Sampling in sites that were relatively close to each other took place in Alberta and Manitoba, and comparison within these pairs of sites provides a measure of local variability of parasitism.

Exploration of synchronization of hosts and parasitoids, and diapause induction of hosts and parasitoids was the by-product of the main study. The sampling protocol was not particularly designed to study the host-parasitoid synchronization, and laboratory-rearing conditions were not designed to study the diapause, and are not ideal for this purpose. However, exploration of host parasitoid synchronization and diapause with the available numbers of samples and insects provides useful indications on host-parasitoid ecology.

Delia radicum

The record of phenology of *D. radicum* at Altamont and Carman was more comprehensive than at other sites because of the longer sampling period. Although in these two sites sampling started by the end of May, no eggs were found in the field until 8 June 2000. Therefore, oviposition activity of *D. radicum* probably started a few days before June 8, 2000. In Alberta, peak oviposition of *D. radicum* extends for 1–2 weeks and is synchronized with the rosette and bolting stages of canola (Dosdall *et al.,* 1994), a pattern which was observed in the Manitoba sites in this study.

Relative to third-instars, first- and second-instar larvae were not numerous in the samples collected. This may be because first-instar larvae live only 4 days on average in the field (McDonald, 1985), and during this period they have to find a host root and start feeding. Therefore, a proportion of first-instar larvae may be in the soil at the time of sampling; only the larvae settled on roots were sampled. In addition, sample size was reduced because survival of first-instar larvae was low during transportation especially when there were delays in courier service. Hence, the number of first-instar larvae in samples probably did not represent the field population of first-instar larvae. Four weeks elapsed between peaks of eggs and third-instar larvae at Carman and Altamont; this is in agreement with the findings of Griffiths (1986a).

The entry of *D. radicum* into diapause is a result of interaction between diapause induction cues and stage of development of *D. radicum* (Soni, 1976). Temperature and photoperiod are the main cues for induction of winter diapause (Hughes, 1960; Read, 1965a, 1968, 1969; Soni, 1976; Collier and Finch, 1983a, 1983b; Collier *et al.*, 1988). In addition, light intensity affects diapause induction (Read, 1969). Diapause induction can be triggered in the adult stage (Read, 1965a, 1969; McLeod and Driscoll, 1967), egg stage (Johnsen and Gutierrez, 1997) and larval stages, particularly the second- and third-instars (Hughes, 1960; McLeod and Driscoll, 1967; Soni, 1976; Johnsen and Gutierrez, 1997). The number of generations that *D. radicum* completes depends on the geographical location (Griffiths, 1991), host plant availability and weather (Leather *et al.*, 1993). At Morinville, Alberta, *D. radicum* completes only one generation in canola (Griffiths, 1986a). In canola at Carman, Manitoba, *D. radicum* completes one or two generations (Hawkins-Bowman, personal communication) depending on weather. In

southern Manitoba, *D. radicum* completes one or two generations in rutabaga (Bracken, 1988). In addition, seeding date of canola affects the seasonality of *D. radicum.* For example, the canola field at Altamont was seeded about a week later than the field at Carman. Consequently, seasonality of *D. radicum* was also late at Altamont compared to Carman. Generally, *D. radicum* that complete larval development early emerge in the same season whereas *D. radicum* that complete larval development later enter diapause at the pupal stage (Fig. 1.7).

Difference of seasonal pattern of *D. radicum* among sites may be partly explained by weather. Seasonal pattern in *D. radicum* population is generally related to rainfall and degree-day accumulation (Turnock and Boivin, 1997). Relation between weather data and seasonal pattern of *D. radicum* is related to several other factors such as seeding date, availability of host plants at a suitable stage for oviposition, and availability of food resources for female adults (Turnock and Boivin, 1997). Therefore, seasonal pattern was not examined in relation to climatic data.

The *D. radicum* populations at Vegreville had a greater tendency to enter diapause than the population at Carman and Altamont. This may be associated with the geographical origin of the population. Generally, critical day length at which 50% of the population enters diapause is positively related to latitude (Collier *et al.*, 1988). A higher proportion of a high-latitude population enters diapause than a low-latitude population when both populations are exposed to 16 h day length at 17°C. For example, 95% of the *D. radicum* population from Finland (60.5°N) enters diapause at 16 h day length at 17°C compared with 20% of the population from England (52.1°N) (Collier *et al.*, 1988).

Parasitoids of *Delia radicum*

The two major parasitoid species of *D. radicum* in canola were the same as reported in brassica vegetable fields in Canada (Table 1.5). *Aleochara bilineata* and *T. rapae* were the major parasitoids found in both crops. They are both present in brassica vegetables in all the provinces of Canada (Wishart, 1957). Both of these parasitoids respond to semiochemicals of brassica plants (Royer and Boivin, 1999; Brown and Anderson, 1999), so they can exploit both crop habitats to find the hosts. Even though the microclimates of canola and brassica vegetables are probably different, the two parasitoid species can survive in them both, and both crops appear to provide enough resources to retain adult parasitoids. *Aleochara bilineata* functions as a predator of *D. radicum* eggs and larvae (Wishart *et al.,* 1956; Bromand, 1980) and a parasitoid of puparia of *Delia* species (Wadsworth, 1915b; Colhoun, 1953; Fuldner, 1960). It parasitizes economically important *Delia* species that include *D. radicum, D. floralis, D. antiqua, D. platura, D. florilega* and *D. planipalpis* (Klimaszewski, 1984; Maus *et al.*, 1998). Adult beetles lay eggs on soil and emerging first-instar larvae search for and enter host puparia (Wadsworth, 1915b; Colhoun, 1953; Fuldner, 1960). Parasitoid larvae feed externally on host pupae and emerge from the puparia as adults (Fuldner, 1960).

Trybliographa rapae parasitizes all three larval instars of *D. radicum* (Neveu *et al.*, 2000). Female *T. rapae* lays eggs in larvae, and first-instar parasitoid larvae remain dormant until the host larvae mature or pupate (Neveu *et al.*, 2000). First- and second-instar parasitoid larvae feed internally within host larvae and pupae and third and fourth instar parasitoid larvae feed externally on the host pupae (Wishart and Monteith, 1954). Nondiapausing adult parasitoids emerge from host puparia after 54–61 days at 20°C, 60±10% RH (Kacem *et al.*, 1996). *Trybliographa rapae* parasitizes *Delia* species

including *D. radicum, D. floralis, D. platura* (Wishart and Monteith, 1954). In addition, *T. rapae* parasitizes many other dipteran species.

Aleochara verna (as *A. bipustulata*) has been found in brassica vegetables in several provinces of Canada (Wishart, 1957; Nair and McEwen, 1975). Small numbers have been found in brassica vegetables and it may prefer other hosts (Monteith, 1956). It parasitizes economically important *Delia* species which includes *D. radicum, D. platura, D. floralis, D. florilega, D. antiqua* and *D. planipalpis* (Maus *et al.*, 1998). In addition, it parasitizes *Paregle cinerella* (Fallén), an anthomyiid associated with cow manure (Blume, 1986).

There are several other species of parasitoids that parasitize *D. radicum* in brassica vegetables. *Phygadeuon* spp. have been reported parasitizing *D. radicum* in Newfoundland (Wishart, 1957). *Phygadeuon trichops* and *P. fumator* Gravenhörst are also minor parasitoids of *D. radicum* in Europe (Monteith, 1956). *Phygadeuon* species are generally polyphagous and opportunistic; hence, their value as potential biocontrol agents is limited (Horstmann, personal communication). *Phygadeuon* spp. parasitize *D. radicum* (Monteith, 1956), *D. floralis, D. antiqua* (Plattner, 1975), *Musca domestica* L., *Stomoxys calcitrans* L., *Fannia* sp., *Muscina* sp. and *Ophyra* sp. (Legner and Olton, 1968). *Phygadeuon* spp. were not found in the samples collected at Vegreville and Shellbrook and this may be related to the time of sampling. If a *Phygadeuon* sp. emerges before fall, and diapauses as an adult or as a larva in another host, it is unlikely that parasitized *D. radicum* puparia would be collected in the fall samples. No samples were collected in mid summer at those two sites.

Aphaereta pallipes (Prov.) is another minor parasitoid of *D. radicum* found in Québec (Wishart, 1957), Ontario and Manitoba (Turnock *et al.,* 1995). *Aphaereta minuta* is a minor parasitoid of *D. radicum* in brassica vegetables in Russia (Adashkevich, 1983). In this study, *A. minuta* was not found in regular samples but only in the middle of the same field in July and August. Therefore, it can be speculated that *A. minuta* is limited to the middle of the field but reasons for this are obscure. Further examination of spatial distribution of *A. minuta* is necessary to assess it as a biocontrol agent.

Trichopria cilipes Kieff is a minor parasitoid of *D. radicum* in brassica vegetables in Russia (Adashkevich, 1983). Further study of the *Trichopria* sp. from Shellbrook is required, and it must be compared with *T. cilipes.* However, the *Trichopria* species was extremely rare at Shellbrook, so its value as a potential biocontrol agent is probably also limited.

Assessment of parasitism

The method of assessment of parasitism in this study was based on collection of puparia in late summer or fall and is comparable with studies of parasitism of *D. radicum* in brassica vegetables (Wishart and Monteith, 1954; Wishart, 1957; Nair and McEwen, 1975; Turnock *et al.,* 1995). Puparial collection has been considered adequate because all the parasitoids that attack *D. radicum* emerge from puparia (Wishart, 1957). However, assessment of parasitism based on puparia collected in fall has several weaknesses. Parasitoid species such as *Phygadeuon* that emerge shortly after host pupation and overwinter in different hosts or host habitats are not adequately assessed. If the host and parasitoids respond to different cues for diapause induction, estimation of parasitism based on fall samples could be biased. In this study, both *T. rapae* and

A. bilineata exhibited less propensity to diapause than hosts collected on the same day (Fig. 1.17, 1.19). Thus fall samples could underestimate levels of these parasitoids. In addition, the interactions among parasitoids could lead to under or over estimation of parasitism. *Aleochara bilineata* parasitizes *D. radicum* puparia that have been parasitized by *T. rapae.* The species that survives to adulthood depends on the degree of development of *T. rapae* at the time of multiparasitism (Jones, 1986; Reader and Jones, 1990). In this study, parasitism of *T. rapae* was also assessed based on a larval sample collected when third-instar larvae were most abundant (>75%); this estimate was free from the effect of multiparasitism.

Assessment of parasitism using larval samples may also be subject to error. Larval estimates may be biased if there is a delay of development of parasitized hosts compared with unparasitized hosts (Driesche, 1983; Hassell and Waage, 1984). Parasitoid-mediated mortality could affect estimates of parasitism (Hassell and Waage, 1984), but *T. rapae* parasitization does not influence larval mortality of *D. radicum* (Neveu *et al.*, 2000). In addition, larvae were susceptible to parasitism until pupation, and not all the larvae in the samples were at the end of the third-instar, so estimates are likely to underestimate the true parasitism experienced at the end of the vulnerable stage.

The difference of estimates of parasitism of *T. rapae* based on larval samples (Table 1.4) and pupal samples (Table 1.2) was negatively correlated with the parasitism by *A. bilineata.* Even though there were only five sampling sites (Table 1.2) the relation was almost significant (Pearson correlation $r = -0.844$ $P = 0.07$). When *A. bilineata* parasitism was low in a field, assessment of *T. rapae* parasitism based on a puparial sample was higher than that from larval estimation. In contrast, when *A. bilineata*

parasitism was high, the estimation of *T. rapae* parasitism based on puparial samples was lower than that from larval samples. Hence, it can be speculated that under estimation of puparial parasitism may be associated with the *T. rapae* and *A. bilineata* interaction through multiparasitism.

Time of sampling and the stage/s of host sampling are important on assessment of parasitism. These two parameters should be chosen appropriately with the objectives of the study and the biology of the parasitoids and hosts in the given locality and crop. For example, if the focus of study were to assess the parasitism of *D. radicum* by *T. rapae,* then sampling of pupae, soon after pupation, would be appropriate.

Methods used in determination of parasitism also affect assessment. Generally parasitism is determined by rearing of the host until adult emergence, examining signs of parasitism on hosts, or dissection of hosts for parasitoids (Driesche, 1983). Turnock *et al.* (1995) looked for entry holes made by first-instar larvae of *A. bilineata* during parasitization. However, the entry hole is not always obvious (Fuldner, 1960). In my study, some puparia had no obvious signs of larval entry but an *Aleochara* larva was found when the puparium was dissected. The presence of a *T. rapae* egg in a *D. radicum* larva is a reliable indication of parasitism, but it is easy to overlook *T. rapae* eggs during examination (Jones, 1986). In rearing of hosts to determine parasitism, there is unavoidable mortality, which results in reduced numbers of hosts and parasitoids. When this mortality is not related to parasitism, it does not bias the estimates of parasitism.

Parasitism

Parasitism of *D. radicum* by *T. rapae* and *A. bilineata* is highly variable in vegetable brassica crops (Table 1.5). Variability of parasitism is associated with crop,

soil type, geographical location (Wishart, 1957), weather, host density (Jones, 1986; Turnock *et al.*, 1995) and host generation (Nair and McEwen, 1975). Use of insecticides as a drench to control *D. radicum* in vegetables was a common practice in the 1950–60s (Forbes and King, 1957; Read, 1960), and affects populations of parasitoids and predators, and subsequent parasitism (Finlayson, 1976; Finlayson *et al.*, 1980).

In this study, parasitism by *T. rapae* varied from 4 to 21% depending on geographical location (Table 1.2). Parasitism of *D. radicum* larvae based on a single sample of larvae was less variable and on average was 11.2% (Table 1.4). Total larval parasitism is generally similar to the parasitism of third-instar larvae (Table 1.4) because larval samples were dominated by third-instars. This dominance may be related to the duration of the third-instar larvae. The lifespan of third-instar larvae is 8–12 days, which represents 50% of the total larval duration (Whistlecraft *et al.*, 1985b) available for parasitization. Furthermore, the third-instar larvae were more easily detectable than the first- and the second-instar larvae. Comparison of parasitism in larval and pupal samples suggest that parasitism by *T. rapae* was relatively consistent among the fields and variability resulted after pupation of host, probably because of different levels of adult emergence and interaction between *T. rapae* and *A. bilineata.*

Parasitism of *D. radicum* by *A. bilineata* is also variable among study sites (Table 1.5). The range of parasitism in this study (Table 1.2) lies within the range of parasitism in previous studies in brassica vegetables (Table 1.5). Variability of parasitism may relate to population levels of hosts and parasitoids, weather, crop, and geographical location (Wishart, 1957; Turnock *et al.*, 1995).

Generally the parasitism by *A. bilineata* is higher than that of *T. rapae* (Table 1.5), but this pattern was not consistent among the sites in my study (Table 1.2). Multiparasitism of *D. radicum* puparium by *A. bilineata* when *T. rapae* larva is in the first- instar larva, that is endoparasitic larva, generally leads to mortality of both species (Jones, 1986; Reader and Jones, 1990). *Aleochara bilineata* larvae are capable of avoidance of puparia parasitized by *T. rapae* if the *T. rapae* larvae are in the third and fourth larval instars, which are ectoparasitic (Jones, 1986). If *A. bilineata* parasitizes the *D. radicum* puparia containing the third or fourth instar *T. rapae, T. rapae* has a better chance of surviving to adulthood than *A. bilineata* (Reader and Jones, 1990).

In this study, the *A. bilineata* and *T. rapae* interaction was in favour of *T. rapae* based on the time of possible multiparasitism. *Aleochara bilineata* parasitized 52 and 60% of *D. radicum* puparia between 31 July and 17 August at Carman and Altamont respectively. By the 31 July, *T. rapae* might have developed to the ectoparasitic third-instar larva within puparia. Generally the third-instar *T. rapae* larvae occur in a puparium a week after host pupation (Kacem *et al.*, 1996). The first-instar *A. bilineata* larvae avoid parasitization of puparia containing ectoparasitic *T. rapae* larva and if parasitized, *T. rapae* is the species that normally survives to adulthood (Reader and Jones, 1990).

Interactions of *A. bilineata* and *T. rapae* that favour *A. bilineata* may be the reasons for higher parasitism by *A. bilineata* compared to *T. rapae* in the previous studies on brassica vegetables. This might occur through timing of occurrence of parasitoids in the field. Different levels of tolerance for insecticides in the two parasitoid species can also lead to dominance of one species (Turnock *et al.*, 1995).

Within a season, temporal variation of parasitism is common in host-parasitoid associations (Sivinski *et al.*, 1998; Lill, 1999; Corff *et al.,* 2000), and may result from changing parasitoid and host population levels during the season and imperfect synchronization of hosts and parasitoids (Macdonald and Cheng, 1970). In addition, relative proportions of adult emergence of both host and parasitoid (Driesche, 1983), and variability of sampling techniques (Macdonald and Cheng, 1970) can cause variation in assessments. In this study, there was a tendency for decreasing parasitism levels of *T. rapae* and *A. bilineata* in sites where sampling was continued through August (Fig. 1.8–1.9). This may relate to the times of emergence of nondiapausing hosts and parasitoids.

Synchronization of host and parasitoids

Synchronization of hosts and parasitoids has variable effects on their populations. If a parasitoid emerges when a susceptible stage of host is available in the field, the parasitoid has the opportunity to parasitize the maximum number of potential hosts (Godfray, 1994). However, when a parasitoid is capable of parasitizing a host for an extended period of time, high parasitism is still possible despite a lack of synchronization of hosts and parasitoid (Godfray, 1994). Temporal asynchrony of hosts and parasitoids leads to a refuge from parasitism for part of the host population (Godfray *et al.*, 1994). Such refuges contribute to the stability of host parasitoid interactions (Godfray *et al.*, 1994), but constitute major limitations to suppression of the host populations (Messenger *et al.,* 1976). For example, *Metaphycus helvolus* (Compare), a parasitoid of black scale, *Saissetia oleae* (Oliv.), effectively controls black scale on citrus in southern California

but not in northern California because of a lack of host parasitoid synchronization (Messenger and van den Bosch, 1971).

Trybliographa rapae

Assessment of synchronization of host and parasitoid was based only on larval instars (Macdonald and Cheng, 1970). There were few larvae in samples at the beginning and at the end of the larval period with a peak at the middle as a result of transition of *D. radicum* from the egg to larval stages and larval to pupal stages. The proportion of parasitized and unparasitized hosts occupied a 0–1 scale, and both ends were fixed though the sample size was small at both ends. Therefore, the time when the proportion of parasitized hosts reaches 1 compared to the time for unparasitized hosts should be interpreted with caution.

In this study, *T. rapae* was synchronized with *D. radicum* in two of the four sites with sufficient data (Fig. 1.14–1.15). It appears that sites that had host-parasitoid synchronization did not have higher levels of parasitism than sites without synchronization when the assessment was based on larval samples (Table 1.4). Therefore, it can be speculated that a few days delay of occurrence of parasitoids does not affect parasitism in the *T. rapae* and *D. radicum* system. The *D. radicum* larval stage lasts about 18–22 days (Brooks, 1949, 1951; Whistlecraft *et al.*, 1985b) and is susceptible to *T. rapae* parasitism throughout (Neveu *et al.*, 2000). Adult *T. rapae* lay eggs over 10 days starting 2 days from emergence (James, 1928). Delay of one week of the parasitoids would not lead to a large proportion of the host population being in a refuge from parasitism. However, it appears that host larvae that occur very late escape parasitism.

Both at Melfort and Altamont, the cumulative per cent of parasitized hosts reached 100% before the unparasitized host reached 100% (Fig. 1.14–1.15).

Aleochara bilineata

Aleochara bilineata was not synchronized with host puparia in either Altamont or Carman, and the *A. bilineata* larvae occurred early relatively to hosts (Fig. 1.18). The effect of the early occurrence, 3 and 9 days early at Carman and Altamont respectively, was not apparent in the parasitism (Table 1.2). However 30–38% of parasitized puparia was parasitized in the second week of August, when the host puparial population was almost at its peak. In southern Ontario, *A. bilineata* generally emerge three weeks later than *D. radicum* from overwintered puparia (Nair and McEwen, 1975). It was suggested that this delay in emergence leads to synchronization of host puparia and first-instar larvae of *A. bilineata* (Ahlström-Olsson and Jonasson, 1992). *Aleochara bilineata* lays eggs on the soil near brassica plants and emerging first-instar larvae search for host puparia and parasitize them (Fuldner, 1960). The duration of the first-instar larva is 5–6 days (Fuldner, 1960; Royer *et al.*, 1999). First-instar larvae are vulnerable to soil moisture and temperature (Brunel and Langlet, 1994). Hence, occurrence of *A. bilineata* larvae earlier than occurrence of *D. radicum* puparia would reduce the fitness of *A. bilineata.*

In this study, the first sample of puparia included *A. bilineata* parasitized puparia, indicating that a certain proportion of *A. bilineata* larvae were active in the field at the first time of occurrence of *D. radicum* puparia in the field. This may be because the emergence of *A. bilineata* is related to temperature in spring (Read, 1962) whereas occurrence of host puparia is related not only to emergence of *D. radicum* which is

temperature related, but to occurrence of suitable host plants for oviposition, which is dependent on crop type and farm operations. Delayed or early seeding of canola may have an effect on host parasitoid synchronization.

Aleochara bilineata adults respond to semiochemicals originating from brassica host plants and from *D. radicum* larvae and their frass (Royer and Boivin, 1999; Fournet *et al.*, 2000). Therefore, the probability of finding a host plant with *D. radicum* larvae on it might be higher than that of finding a host plant with puparia but no *D. radicum* larvae. Consequently, the probability of early pupating *D. radicum* being parasitized by *A. bilineata* may be high.

In the assessment of synchronization, hosts are sampled until they are no longer present or susceptible to parasitization (Macdonald and Cheng, 1970). In this study, sampling was probably stopped before the cessation of activity of the first-instar larvae of *A. bilineata* in the field. In the graphical presentation, it was assumed that the proportion of parasitized and unparasitized hosts reached 1 on the day that the last sample was collected. It should be noted that the time period in which host parasitoid synchronization is important, was included in the sampling period.

Phygadeuon species

Phygadeuon spp. was not synchronized with *D. radicum* puparia (Fig. 1.20). It appears that *Phygadeuon* was active within a narrower period than that in which hosts were available. Furthermore, occurrence of *Phygadeuon* coincided with the time all hosts were at the pupal stage (Fig. 1.1, 1.8). Since *Phygadeuon* spp. parasitize a wide range of hosts, they might shift among hosts depending on their availability. The biology of

Phygadeuon is not well known. Therefore, host use and the effect of parasitism cannot be related to the results of this study.

Diapause

Diapause induction of parasitoids is variable with species. Some parasitoid species depend entirely on host physiology (Schoonhoven, 1962) and respond to the diapause state of their host's endocrine system e.g. *Nasonia* sp. and *Pteromalus puparium* (L.) (Tauber *et al.,* 1983). Some parasitoid species use abiotic factors and physiological status of their host as cues to enter diapause (Tauber *et al.,* 1983). For example, *Aphaereta minuta* and *Alysia manducator* Panz respond primarily to photoperiod and temperature for diapause induction, and host physiology has only a secondary effect (Vinogradova and Zinovjeva, 1972). Some other parasitoid species are relatively independent of host's physiology in diapause induction. e.g. chalcidoid parasitoids of pine sawfly (Tauber *et al.,* 1983).

Diapause of parasitoids in response to the state of host diapause leads to synchronization of hosts and parasitoids in the next generation (Godfray, 1994). For example, the hyperparasitoid, *Catolaccus aeneoviridis* (Girault) (Pteromalidae) enters diapause if it attacks a diapausing host, *Cotesia congregatus* (Say) (Braconidae) (McNeil and Rabb, 1973). In the current study, *A. bilineata* and *T. rapae* exhibited a lower proportion in diapause than *D. radicum* collected on the same date (Fig. 1.17, 1.19). There are two possible explanations of these results.

First, diapause status of the host could dictate the diapause status of the parasitoids, but the diapause state of parasitoids and possibly of hosts could be reversible by rearing temperatures (20°C) and light period (16 h) in the laboratory. When the

parasitoids were in the field for a long period before collection then diapause status was less reversible by laboratory conditions. Furthermore, the diapause status of *D. radicum* was less reversible than that of parasitoids. Reversal of diapause induction can occur shortly after induction in the Colorado potato beetle, *Leptinotarsa decemlinata* (Say) (de Wilde *et al.,* 1959). Conditions of diapause induction of *T. rapae* are not well defined, but Wishart and Monteith (1954) suggested that the diapause state of *D. radicum* induces the diapause of *T. rapae.* Miles (1952a) indicated that conditions that induce diapause in *D. radicum* induce a similar diapause in *T. rapae.* Meanwhile, cues for induction of diapause in field populations of *A. bilineata* are unknown, but <14°C and 0:24 L:D induced diapause in *A. bilineata* larvae in the laboratory (Whistlecraft *et al.*, 1985a).

The second explanation is that the diapause state of *D. radicum* did not dictate the diapause state of parasitoids. Host and parasitoids responded differently to diapause induction cues, and the laboratory rearing temperature did not affect the diapause state of host or parasitoids. Under these circumstances, there would have been a second generation of parasitoids in the field. *Trybliographa rapae* takes an average of 58 days at 20°C to develop from egg to adult at 20°C (Kacem *et al.*, 1996). In the current study, *D. radicum* larvae started to appear in the field in the last week of June. Hence, non-diapausing *T. rapae* may emerge in the third week of August or later. *Trybliographa rapae* parasitize mainly *Delia* species (Wishart and Monteith, 1954), and the probability of finding a larval host for oviposition at the end of August or later was low (Fig. 1.1–1.6). Consequently, progeny contribution by summer emerging female *T. rapae* to the next generation would be low. Even though late emergence could be disastrous for parasitoid populations it may be that *T. rapae* adapted to associate with *D. radicum* in

brassica vegetables, and has not yet adapted to its host's phenology on canola. *Aleochara bilineata* takes an average of 67 days at 15.5°C, 46 days at 20°C (Fuldner, 1960) and 30 days at 22°C (Bromand, 1980; Whistlecraft *et al.*, 1985a) to develop from egg to adult (Fuldner, 1960). In this study, *D. radicum* puparia started to appear from 10 July onwards. Hence, nondiapausing *A. bilineata* may emerge in mid August or later. Since *A. bilineata* larvae parasitize *Delia* puparia at any stage, they may attack diapausing puparia in the field in late August and successfully emerge the following spring.

There are parasitoid species in which summer-emerging females do not contribute a progeny to next generation. They are multivoltine in Europe and univoltine in northern North America (Turnock, 1973). For example, *Bessa harveyi* (Townsend), a parasitoid of larch sawfly, *Pristiphora erichsonii* (Hartig) does not respond to host physiology in induction of diapause, and a proportion of the parasitoid emerges in the same summer (Turnock, 1973). These bivoltine parasitoids do not contribute progeny to the next generation (Turnock, 1973). In this study, there was not enough data to exclude either explanation of the differences in diapause state of *D. radicum* and its two principal parasitoids. It is however clear that parasitoid diapause is not slavishly dependent upon, or identical to that, of the host.

Conclusions

Delia radicum started oviposition in canola in June in Manitoba, passed through its three larval instars and was mostly in the pupal stage by the first week of August. Some flies emerged by mid July. However, there was no second generation of *D. radicum* in canola in 2000 at Carman or at Altamont. *Delia radicum* appeared to have

a slightly different phenology in Alberta, and tended to diapause earlier in Alberta than in Manitoba.

The major parasitoid species of *D. radicum* in canola were similar in Manitoba, Saskatchewan and Alberta, and were *T. rapae, A. bilineata* and *A. verna.* Four other parasitoid species were found, but they were not common.

Parasitism of *D. radicum* larva by *T. rapae* was generally about 11% when the estimations were based on larval samples. Parasitism based on puparial samples collected in fall was variable and related to locality. This estimate was influenced by adult emergence, and the interaction of *Aleochara* species through multiparasitism.

Synchronization of *T. rapae* with *D. radicum* was locality related and delay of occurrence of *T. rapae* compared to occurrence of *D. radicum* larvae led to asynchronization at Altamont and Melfort. Slight delay (3–7 days) of *T. rapae* did not affect parasitism.

Parasitism of *D. radicum* by *A. bilineata* was locality related and varied 5–23% among sampled locations. *Aleochara bilineata* occurred earlier than host puparia at Carman and Altamont leading to asynchronization.

Diapause of *T. rapae* and *A. bilineata* did not depend completely upon host physiology nor were diapause cues identical to those of *D. radicum.*

Table 1.1 Immature *Delia radicum* in weekly samples in canola in the Canadian Prairies in 2000, and immatures reared to adult emergence in the laboratory. Additional puparia were collected in October 2000.

Sampling Site	Sampling period	No. of Samples	Immatures collected			Immatures reared to adult			Additional puparia	
			Eggs	Larvae	Puparia	Eggs	Larvae	Puparia	Collected	Reared to adults
Altamont, MB	8 June – 9 Sep.	15	1185	859	1359	245	372	823	-	-
Carman, MB	8 June – 9 Sep.	16	1464	907	2296	472	355	1367	-	-
Melfort, SK	26 June – 31 July	6	117	390	0	78	151	0	-	-
Shellbrook, SK	11 July – 8 Aug.	6	0	369	85	0	143	34	1536	1127
Vegreville-1, AB	6 June – 7 Aug.	9	329	419	45	65	183	20	416	333
Vegreville-2, AB	6 June – 7 Aug.	9	241	337	17	12	182	14	601	384

Table 1.2 Parasitism of *Delia radicum* based on puparial samples collected in canola fields on the Canadian Prairies in late summer and fall 2000.

Sampling location	No of puparia reared	Puparia parasitized by different parasitoid species (%)[1]						Sampling date
		T. rapae	*A. bilineata*	*A. verna*	*Phygadeuon* spp.	Unidentified[2]	Total	
Carman	455	16.3	13.4	1.3	5.9	0.4	37.3	21 Aug.
Altamont	168	6.5	14.9	0.6	0	1.2	23.2	30 Aug.
Shellbrook	1124	21.4	4.7	2.4	0	0.6	29.1	5–6 Oct.
Vegreville-1	333	3.9	16.5	6.0	0	3.0	29.4	2 Oct.
Vegreville-2	384	7.0	23.4	13.3	0	4.1	47.8	3 Oct.

[1]Per cent of parasitism was estimated as number of parasitoid adults of a species divided by total number of adults x 100.
[2]Dead parasitoid larvae found upon dissection, and not identified to species.

Table 1.3 Immatures of *Delia radicum* collected in different sampling sites and reared to adulthood.

Sampling location	Instar	No. collected	*D. radicum*		*T. rapae*		*A. bilineata*		*A. verna*		*Phygadeuon* sp.		Unidentified[1] (No.)
			No.	%	No.	%	No.	%	No.	%	No.	%	
Carman	L1	51	12	85.7	2	14.3							
	L2	305	99	89.2	12	10.8							
	L3	551	205	89.1	25	10.9							
	Puparia	2327	878	63.2	212	15.3	218	15.7	18	1.3	49	3.5	15
Altamont	L1	140	42	97.7	1	2.3							
	L2	362	130	95.6	6	4.4							
	L3	357	181	93.8	11	5.7							1
	Puparia	1359	465	56.5	72	8.8	263	32.0	10	1.2	1	0.1	12
Shellbrook	L1	-											
	L2	8	1	100.0	0	0.0							
	L3	361	126	90.0	14	10.0							
	Puparia	1623	819	71.2	250	21.7	54	4.7	27	2.4	0	0.0	8
Melfort	L1	13	2	66.7	1	33.3							
	L2	59	23	95.8	1	4.2							
	L3	318	90	72.6	34	27.4							
	Puparia	-											

Continued.

Table 1.3 Continued.

Sampling location	Instar	No. collected	*D. radicum*		*T. rapae*		*A. bilineata*		*A. verna*		*Phygadeuon* sp.		Unidentified[1] (No.)
			No.	%	No.	%	No.	%	No.	%	No.	%	
Vegreville-1	L1	38	10	100.0	0	0.0							
	L2	173	60	95.2	2	3.2							1
	L3	208	105	95.5	5	4.6							
	Puparia	461	247	70.0	14	4.0	61	17.3	20	5.7	0	0.0	11
Vegreville-2	L1	8	2	100.0	0	0.0							
	L2	64	21	95.5	1	4.6							
	L3	265	151	95.6	7	4.4							
	Puparia	618	212	53.3	27	6.8	92	23.1	51	12.8	0	0.0	16
Beaverlodge	L1	-											
	L2	2	0										
	L3	60	37	97.4	1	2.6							
	Puparia	1	0	0	0	0	1						

[1]Dead parasitoid larvae found upon dissection, and not identified to species.

Table 1.4 Parasitism of *Delia radicum* by *Trybliographa rapae* estimated from a single sample collected when the third instar larvae were at their peak in canola in 2000.

Sampling location	No. collected			No. reared to adulthood			Parasitism (%)			Total larval parasitism (%)[1]	Sampling date
	L1	L2	L3	L1	L2	L3	L1	L2	L3		
Carman	2	80	282	0	40	122	-	17.5	7.4	9.9	10 July
Altamont	1	7	67	0	3	43	-	0	11.6	10.9	10 July
Shellbrook	0	0	95	0	0	31	-	-	9.7	9.7	31 July
Melfort	0	0	28	0	0	10	-	-	10.0	10.0	31 July
Vegreville-1	0	7	49	0	1	23	-	100	8.7	12.5	31 July
Vegreville-2	0	2	87	0	2	48	-	50.0	12.5	14.0	24 July

[1]Total larval parasitism was estimated as total number of *T. rapae* developed to adulthood divided by total number of *T. rapae* and *D. radicum* developed to adulthood in a given sample

Table 1.5 Parasitism of *Delia radicum* by its two major parasitoid species in brassica vegetable habitats in Canada.

Location	No of seasons sampled	Level of parasitism (%)				Remarks	Source
		A. bilineata		*T. rapae*			
		Average	Range	Average	Range		
Alberta	1	18.0	-	0.0	-	1 sample in 1 location, OWP	Wishart, 1957
British Columbia	2	25.7	1.6–50.7	0.3	0–1.7	6 samples in 6 places, OWP	Wishart, 1957
British Columbia, Abbotsford	3	44.4	17.7–70.6	-	-		Finlayson *et al.*, 1980
Manitoba, Portage la Prairie	1	0.0	-	12.0	-	OWP	Turnock *et al.*, 1995
Manitoba, Winnipeg	9	52.2	10–94	1.1	0–3	OWP	Turnock *et al.*, 1995
New Brunswick	1	7.7	-	8.5	-	1 sample in 1 location, OWP	Wishart, 1957
Newfoundland	2	9.5	8–11	5.0	1–9	OWP	Morris, 1960
Newfoundland	3	36.5	4.7–63.0	3.0	0–10.7	4 locations, OW puparia, OWP	Wishart, 1957
Newfoundland, St. Johns	1	74.0	-	0.0	-	OWP	Turnock *et al.*, 1995
Nova Scotia	3	9.6	2.7–13.2	28.5	1.5–46.3	5 samples in 3 locations, OWP	Wishart, 1957
Ontario	1	9.4	1.2–23.4	0.4	0–0.6	4 samples in 4 locations, OWP	Wishart, 1957
Ontario, London	5	11.8	0–38	4.2	2–6	OWP	Turnock *et al.*, 1995
Ontario, southwestern	3	18.3	9.3–32.4	3.8	1.7–7.6	OWP	Nair and McEwen, 1975
Ontario, southwestern	1	47.0	17–77	8.5	0–17	First and second generation	Nair and McEwen, 1975
Prince Edward Island	1	77.0	47–95			6 sequential samples	Read, 1962
Prince Edward Island	3	3.2	0–9.5	4.6	0.8–9.1	3 samples in 2 locations, OWP	Wishart, 1957
Quebec	2	28.9	0–52.5	5.0	0–24.6	10 samples in 9 locations, OWP	Wishart, 1957
Quebec, St. Jean	4	52.7	27–79	1.5	0–3	OWP	Turnock *et al.*, 1995

OWP=Overwintering puparia

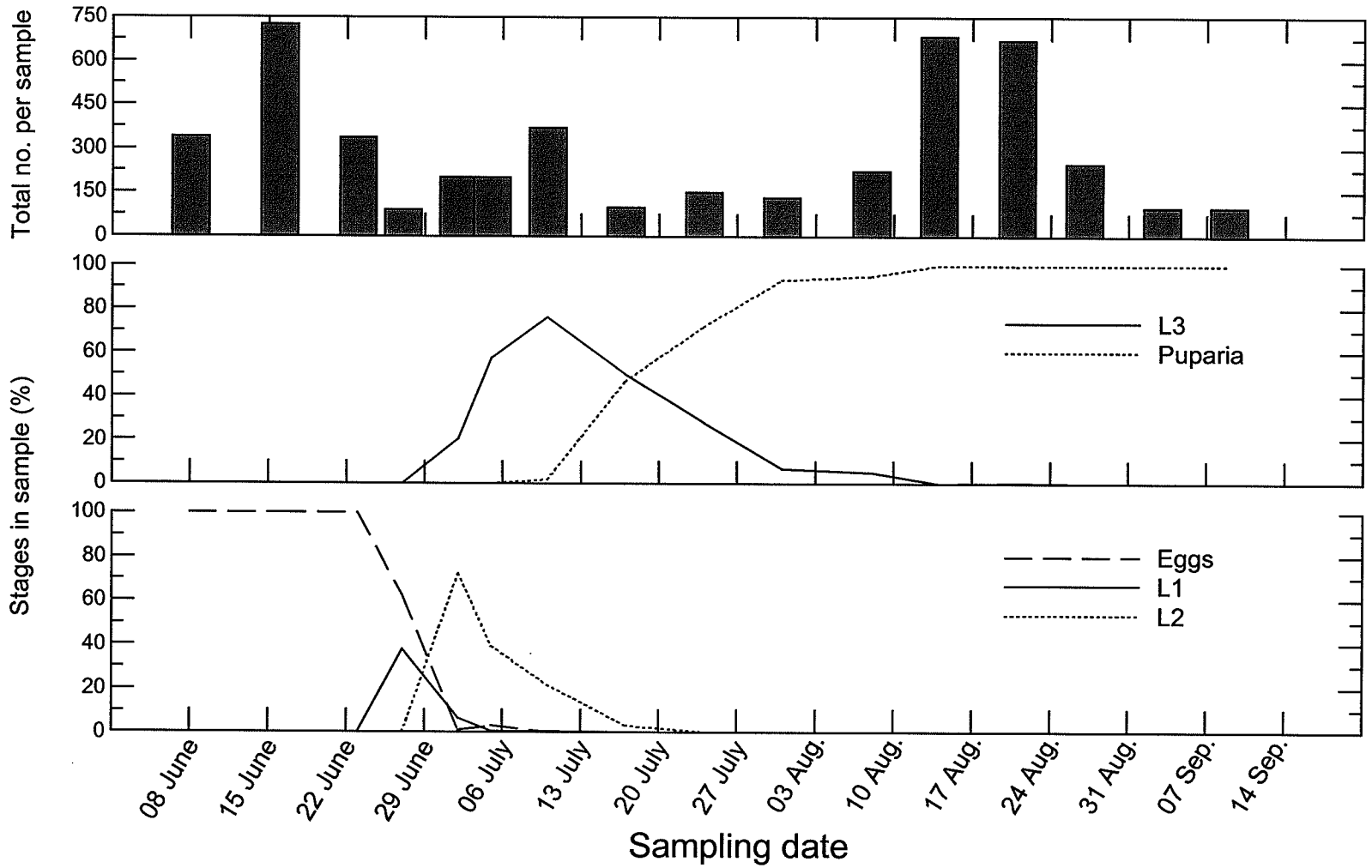

Figure 1.1 Number and stage composition of immature *Delia radicum* in samples collected in canola at Carman in 2000.

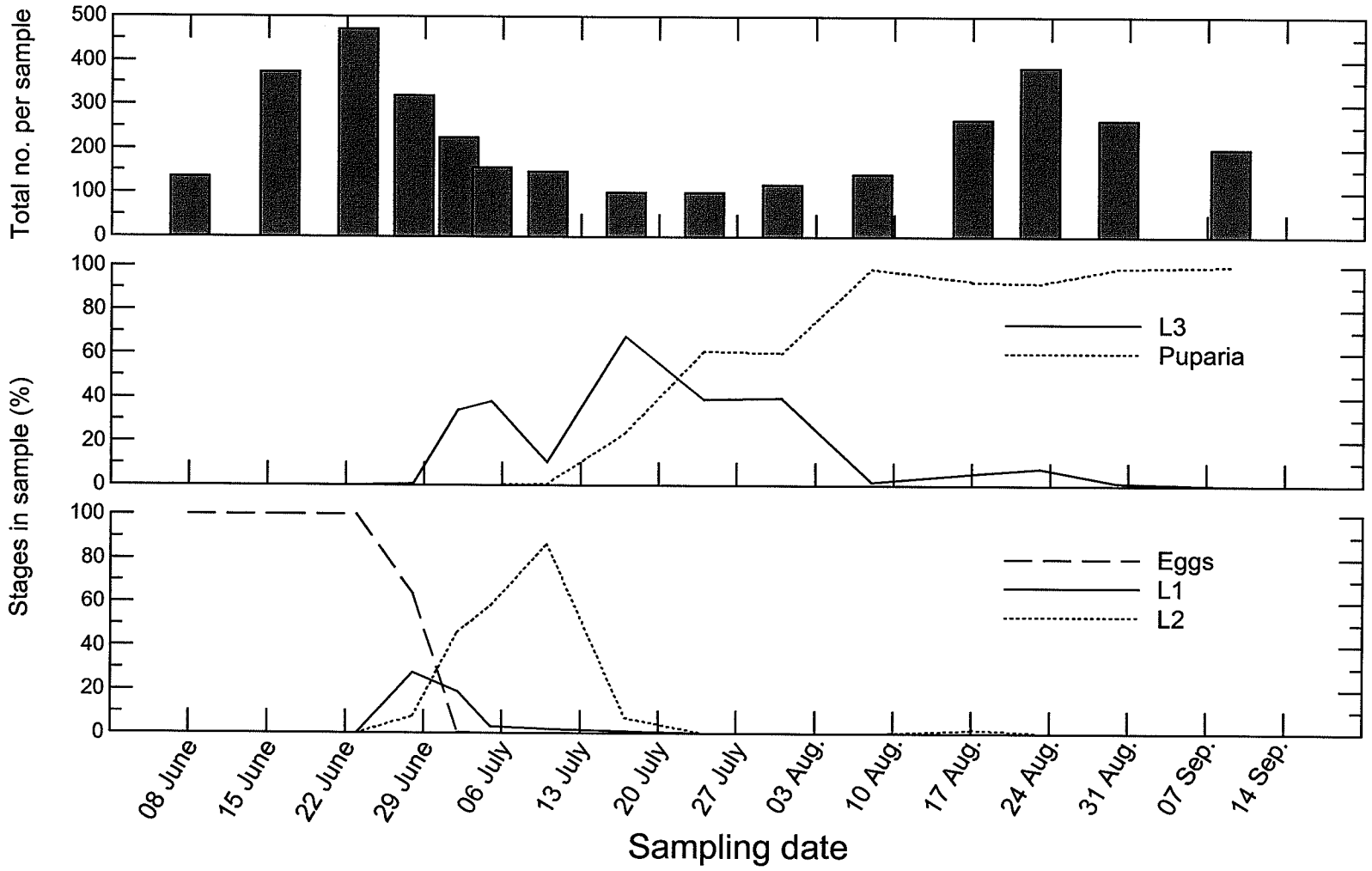

Figure 1.2 Number and stage composition of immature *Delia radicum* in samples collected in canola at Altamont in 2000.

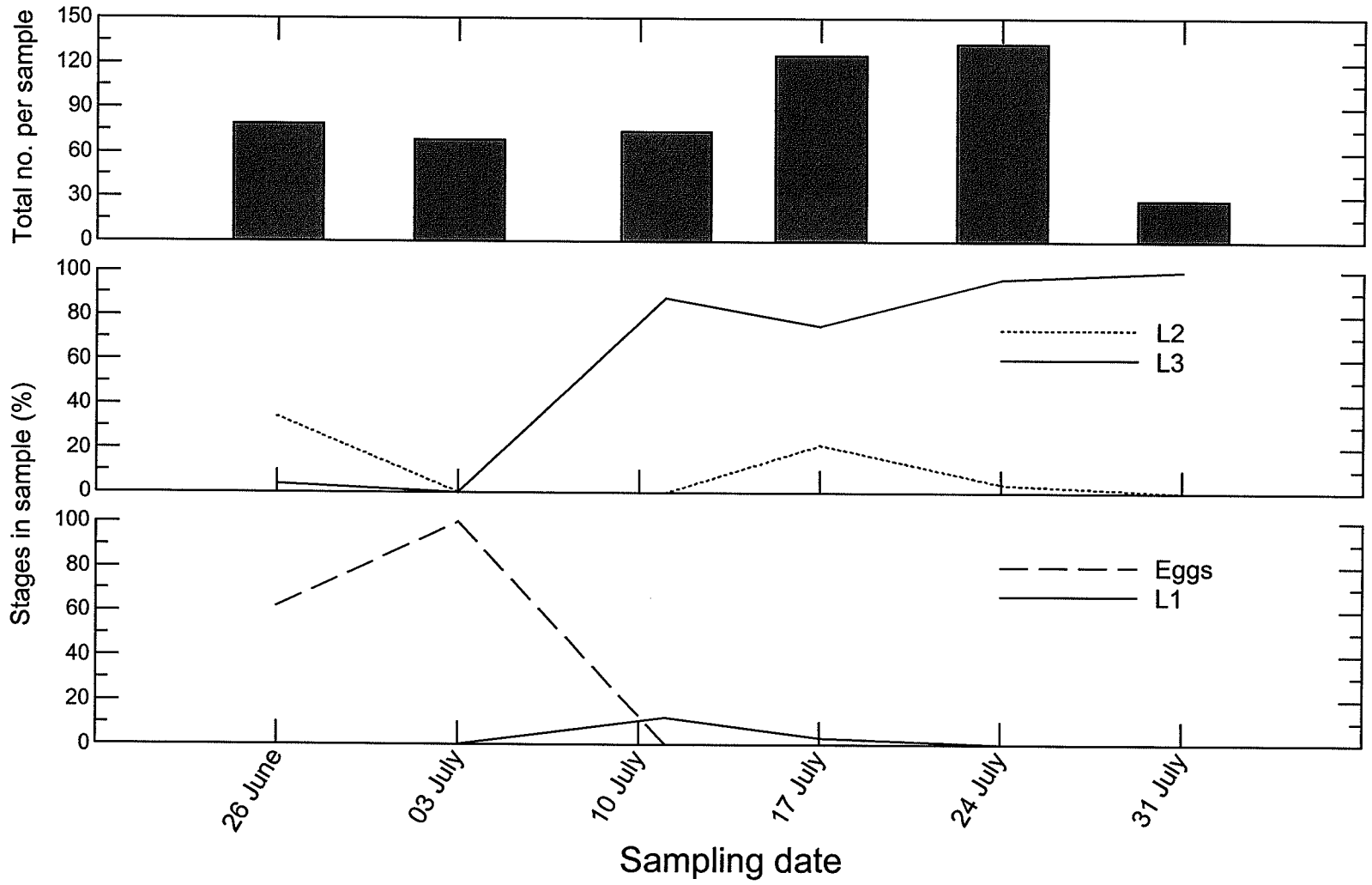

Figure 1.3 Number and stage composition of immature *Delia radicum* in samples collected in canola at Melfort in 2000.

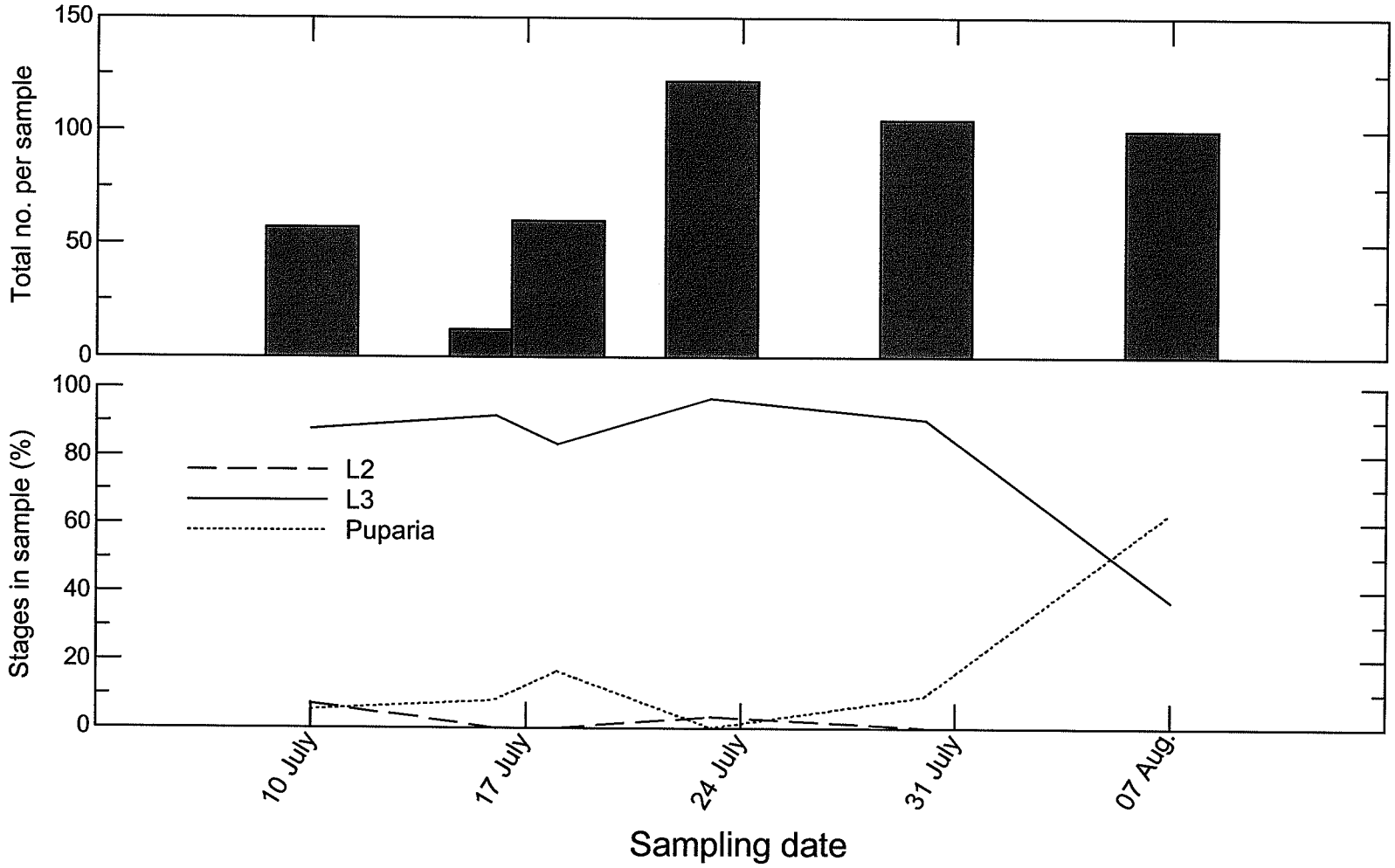

Figure 1.4 Number and stage composition of immature *Delia radicum* in samples collected in canola at Shellbrook in 2000.

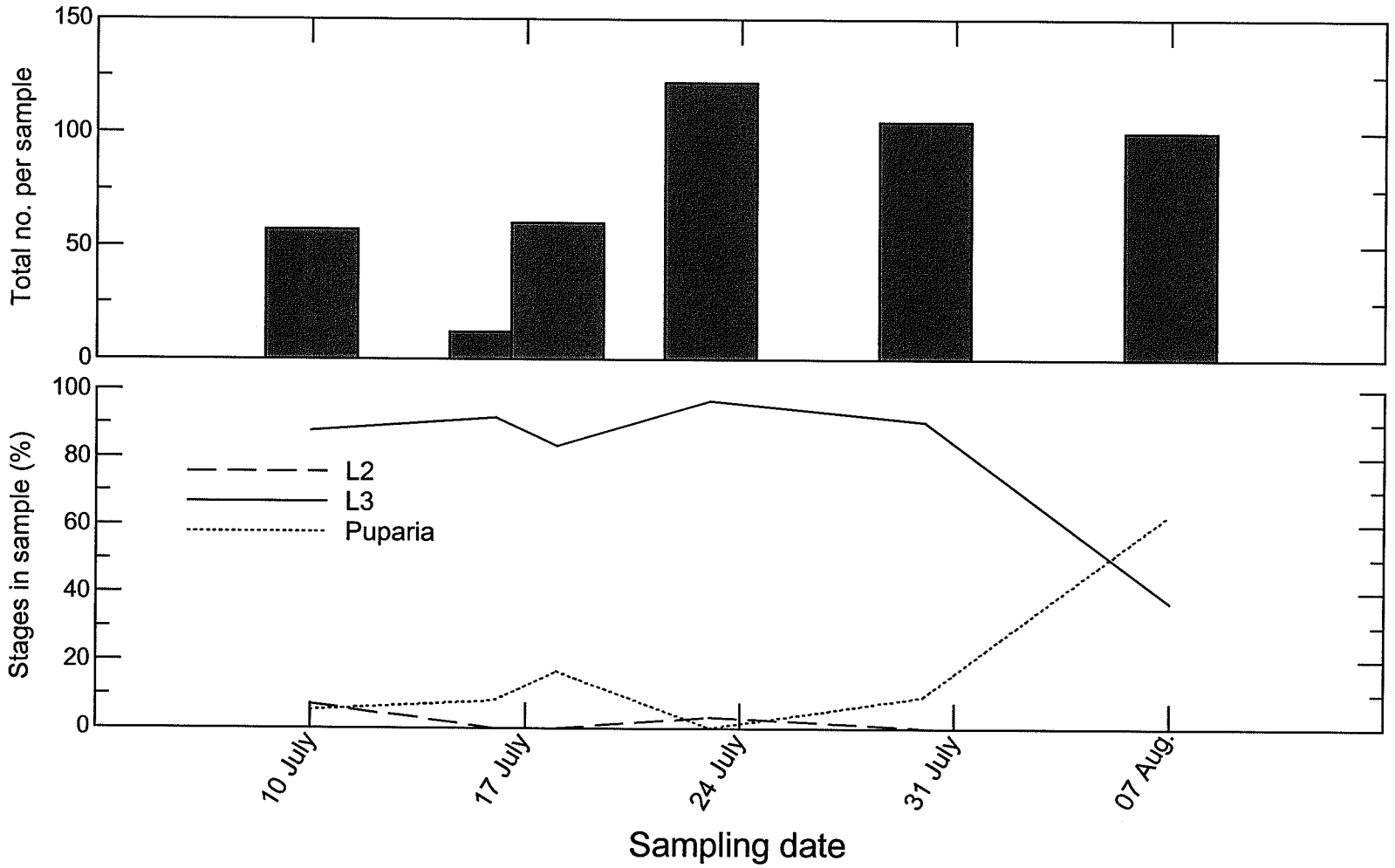

Figure 1.5 Number and stage composition of immature *Delia radicum* in samples collected in canola at Vegreville-1 in 2000.

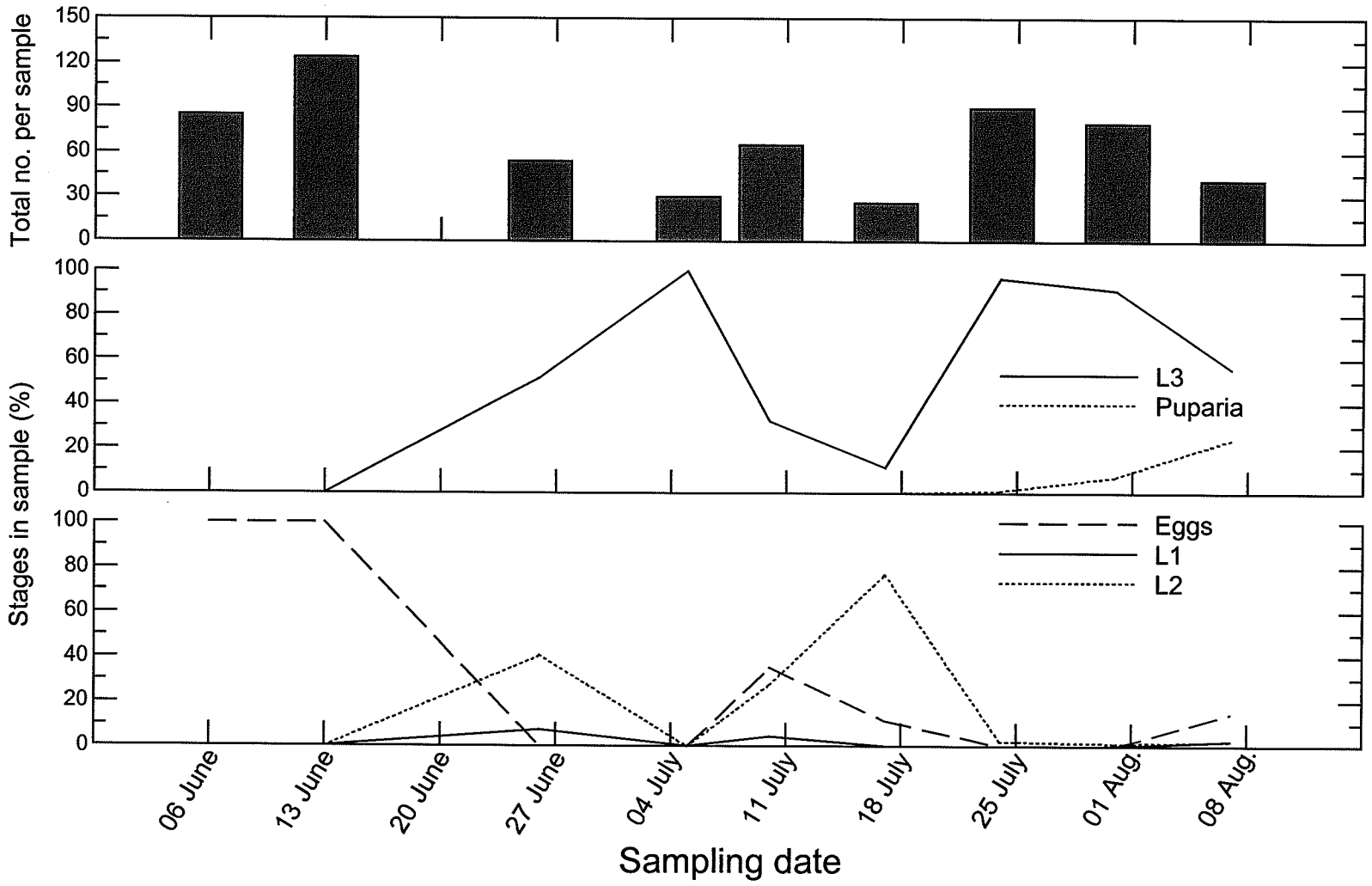

Figure 1.6 Number and stage composition of immature *Delia radicum* in samples collected in canola at Vegreville-2 in 2000.

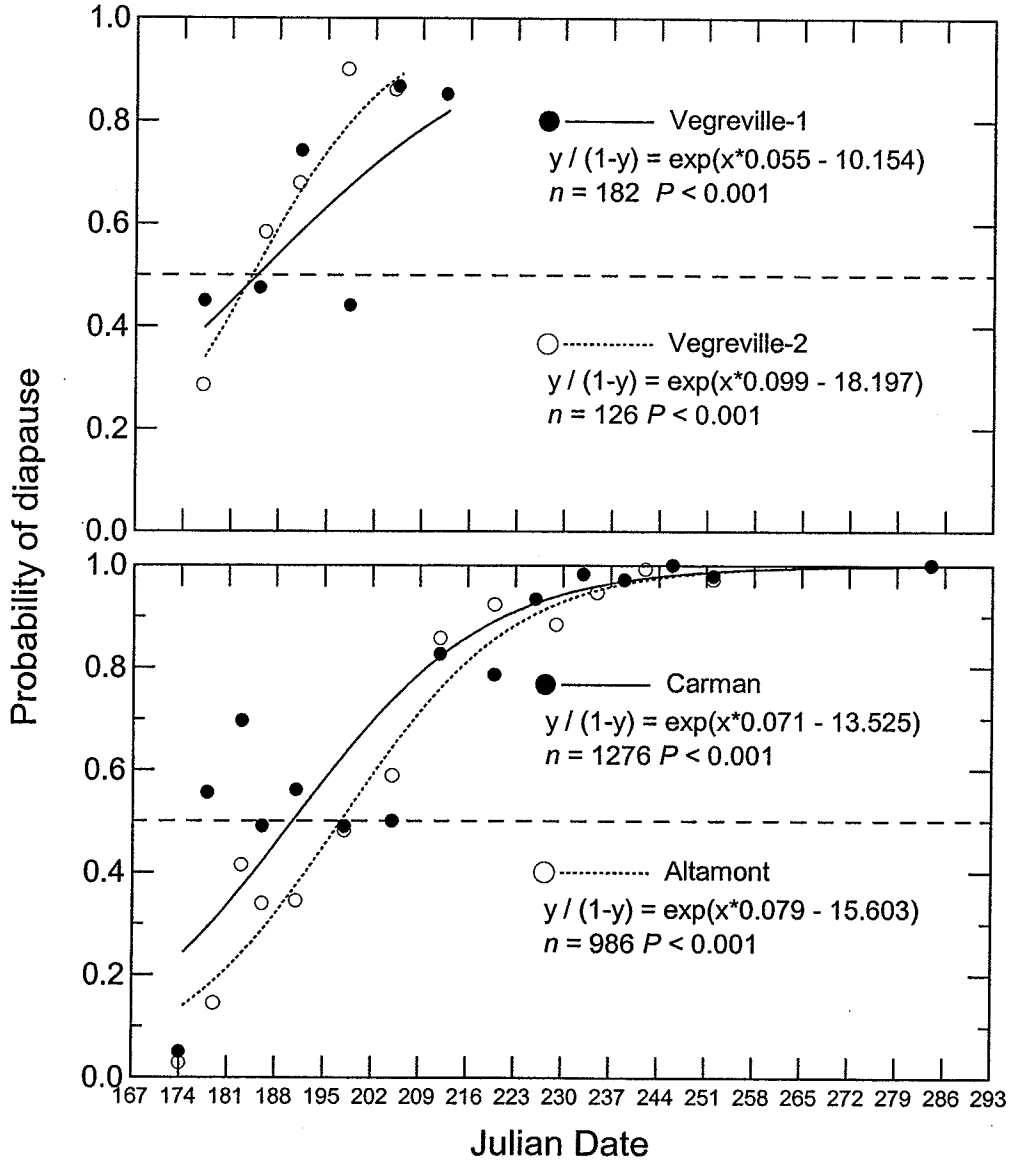

Figure 1.7 Probability of diapause of immature *Delia radicum* from canola in Carman, Altamont, Vegreville-1 and Vegreville-2 sampled in summer 2000.

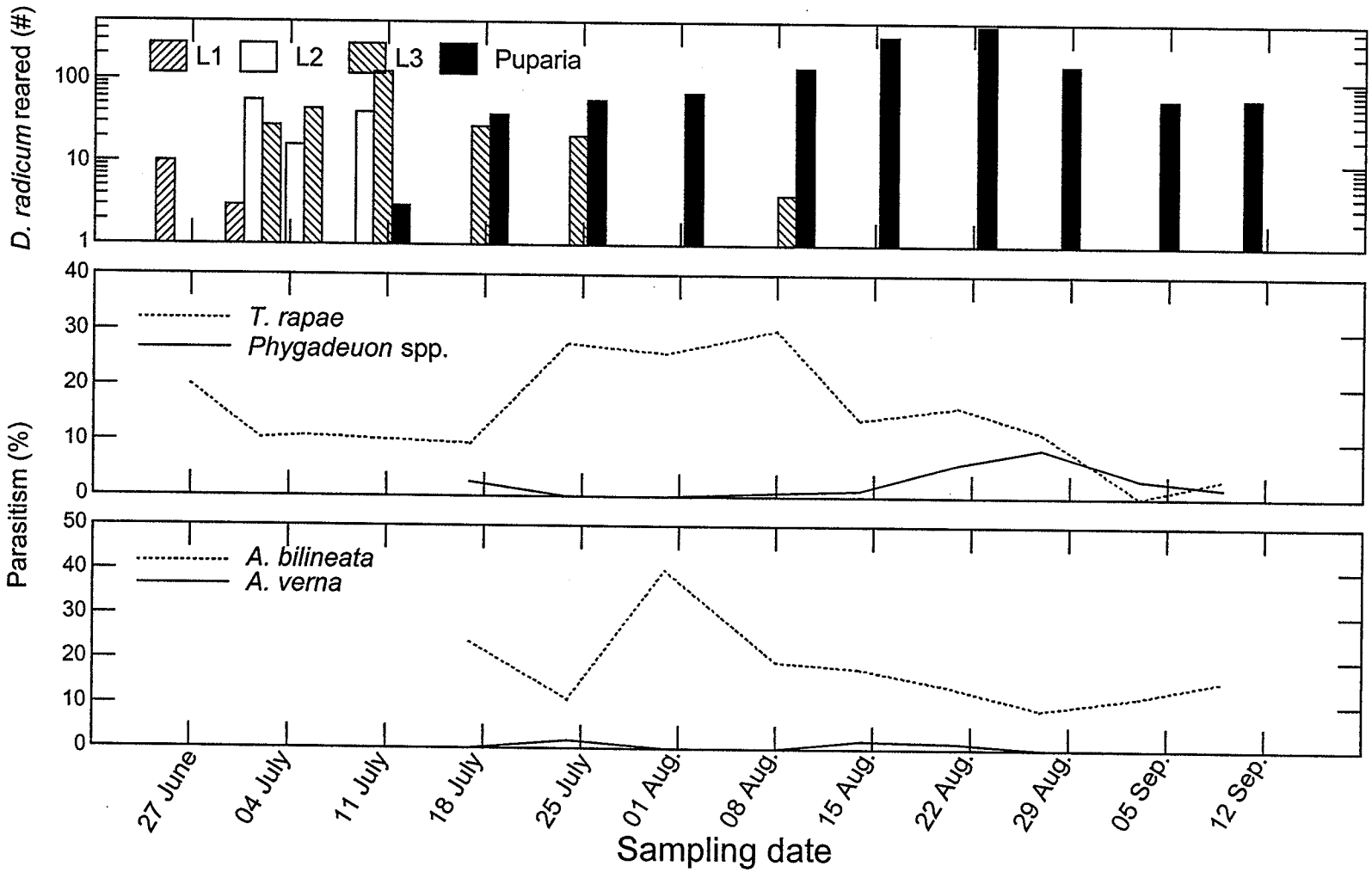

Figure 1.8 Parasitism of *Delia radicum* by its major parasitoids at Carman in relation to time of sampling in 2000 and number of immatures reared to adulthood.

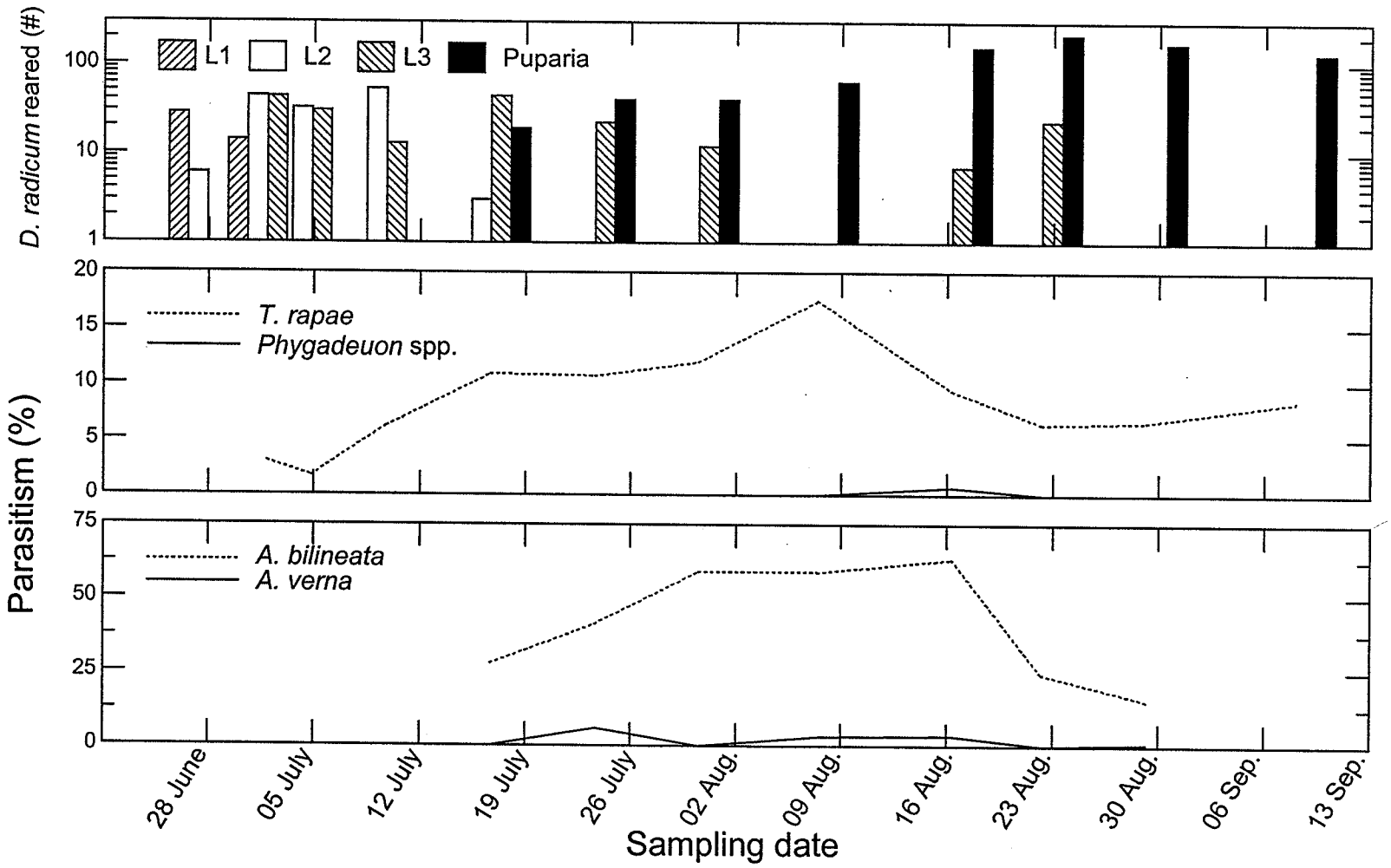

Figure 1.9 Parasitism of *Delia radicum* by its major parasitoids at Altamont in relation to time of sampling in 2000 and number of immatures reared to adulthood.

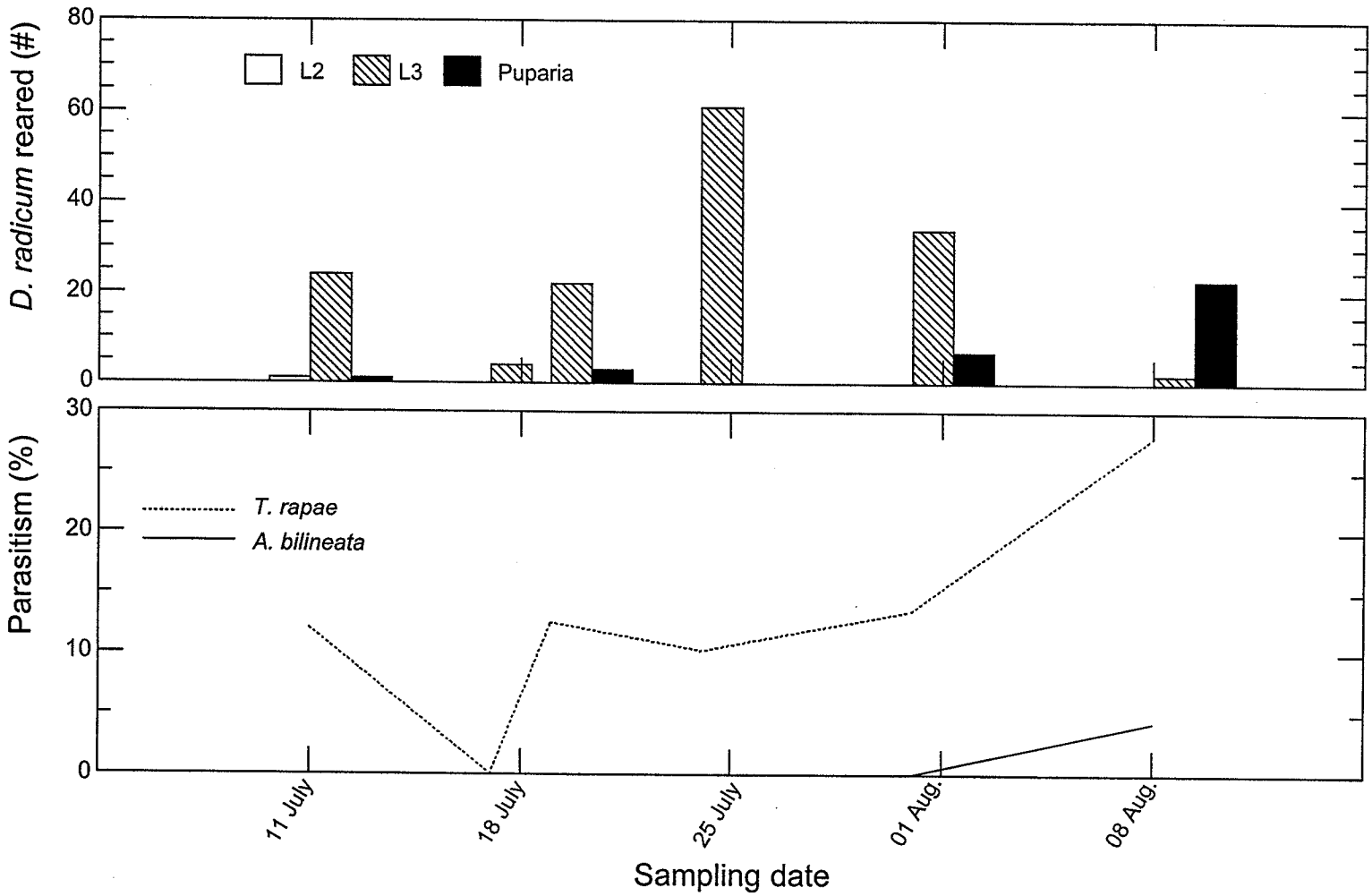

Figure 1.10 Parasitism of *Delia radicum* by its major parasitoids at Shellbrook in relation to time of sampling in 2000 and number of immatures reared to adulthood.

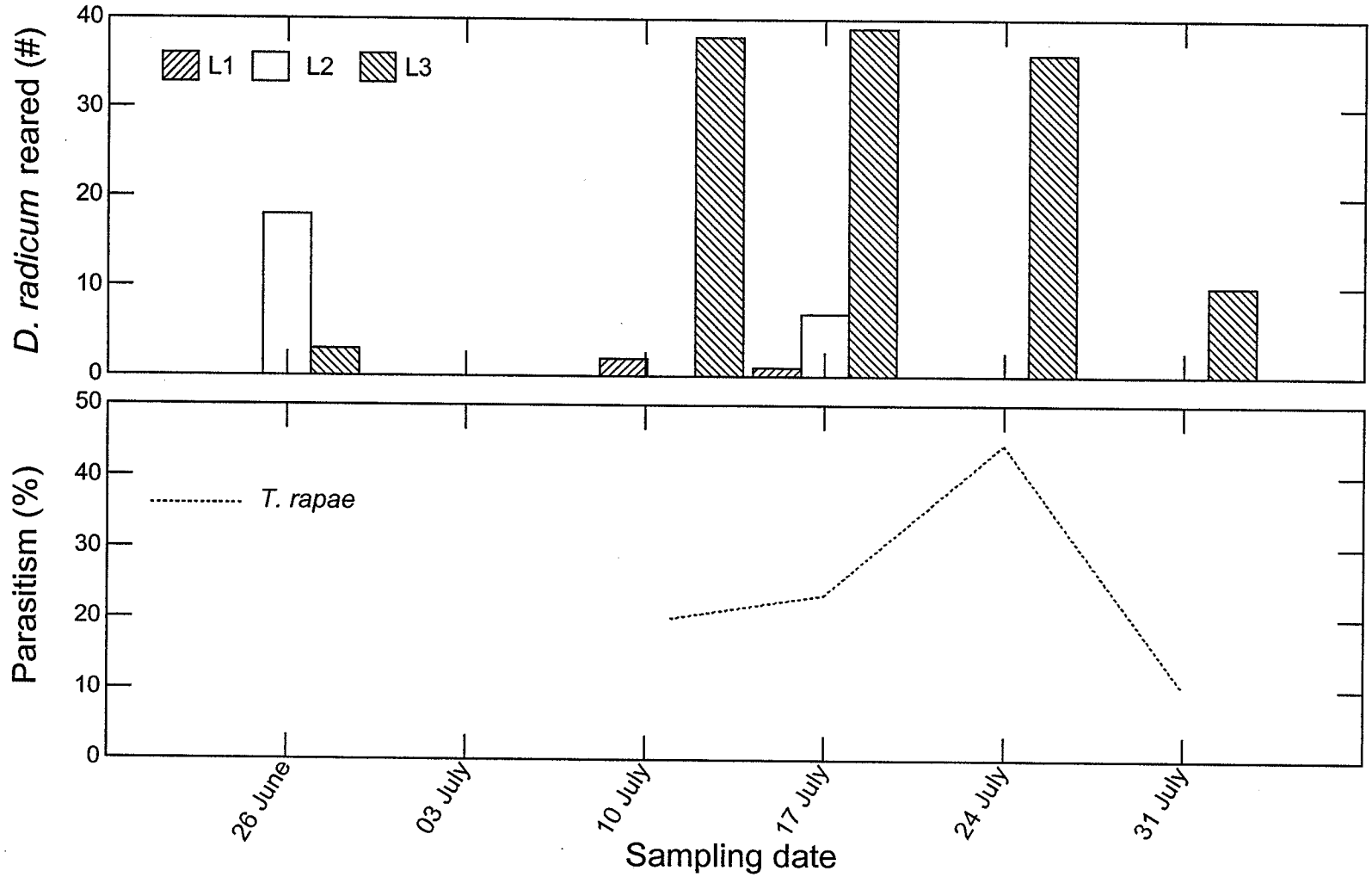

Figure 1.11 Parasitism of *Delia radicum* by its major parasitoids at Melfort in relation to time of sampling in 2000 and number of immatures reared to adulthood.

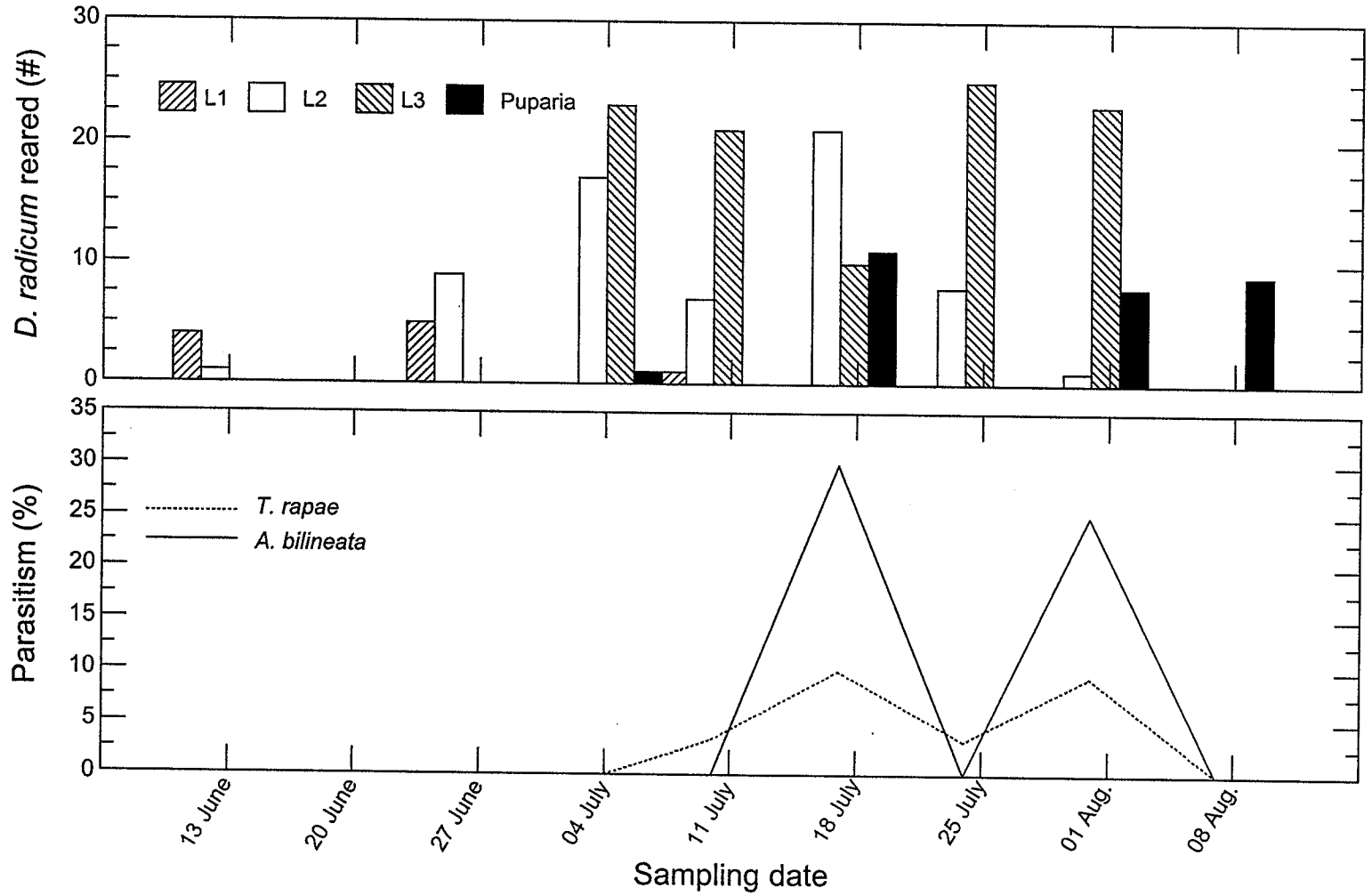

Figure 1.12 Parasitism of *Delia radicum* by its major parasitoids at Vegreville-1 in relation to time of sampling in 2000 and number of immatures reared to adulthood.

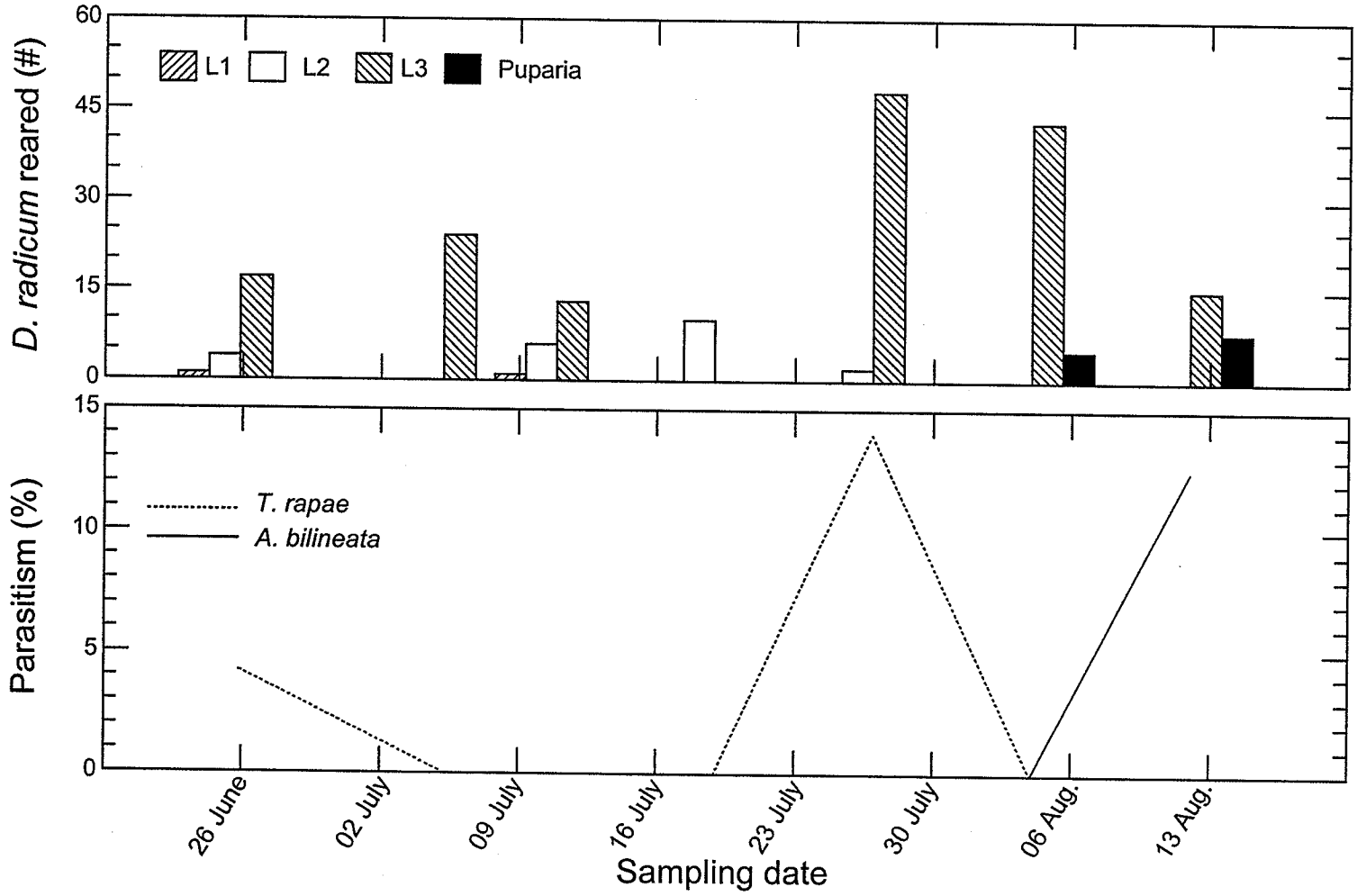

Figure 1.13 Parasitism of *Delia radicum* by its major parasitoids at Vegreville-2 in relation to time of sampling in 2000 and number of immatures reared to adulthood.

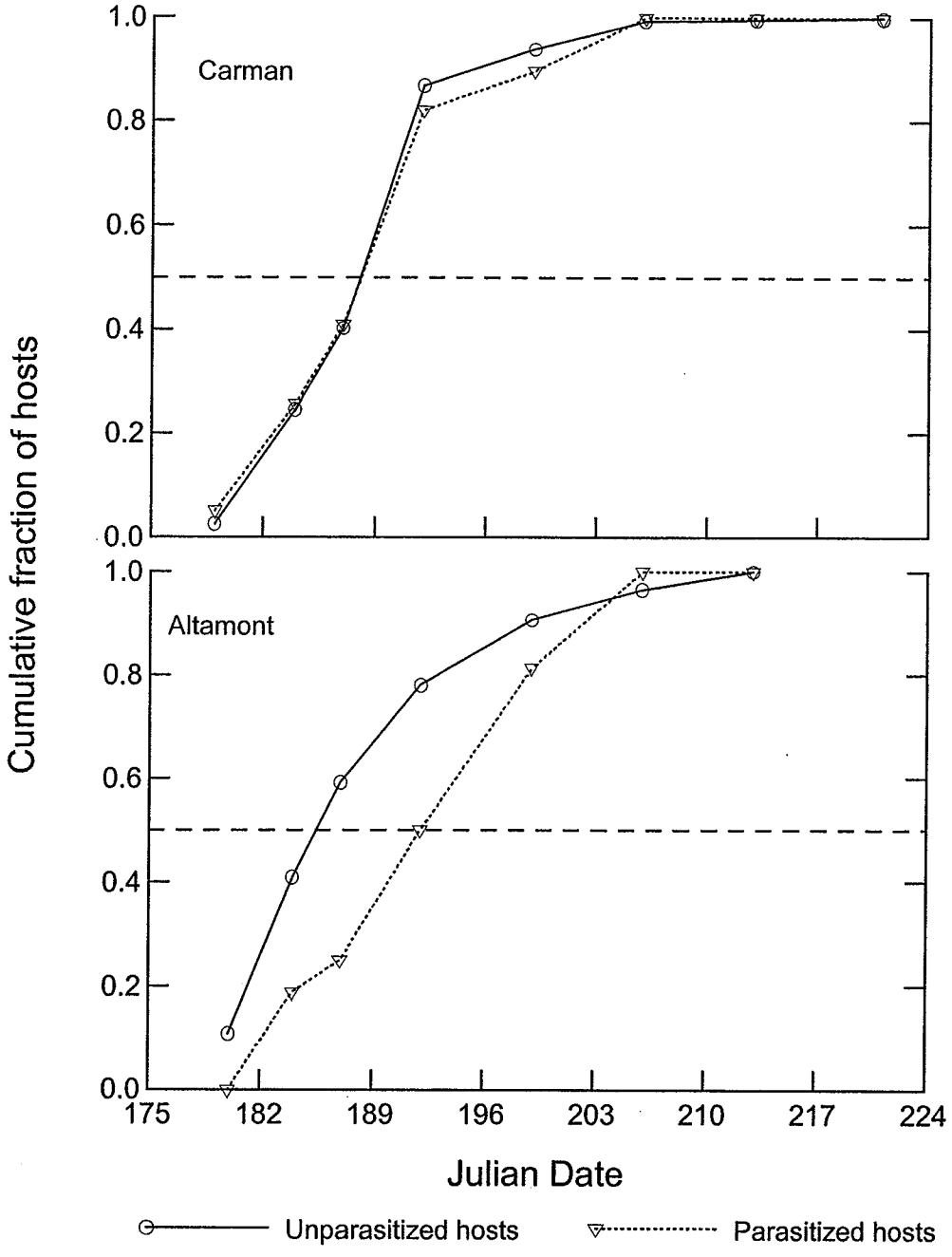

Figure 1.14 Temporal synchronization of *Delia radicum* larvae and *Trybliographa rapae* in canola at Carman and Altamont. Analysis is based on 313 adults of *D. radicum* and 39 adults of *T. rapae* in eight samples at Carman, and 324 adults of *D. radicum* and 16 adults of *T. rapae* in seven samples at Altamont.

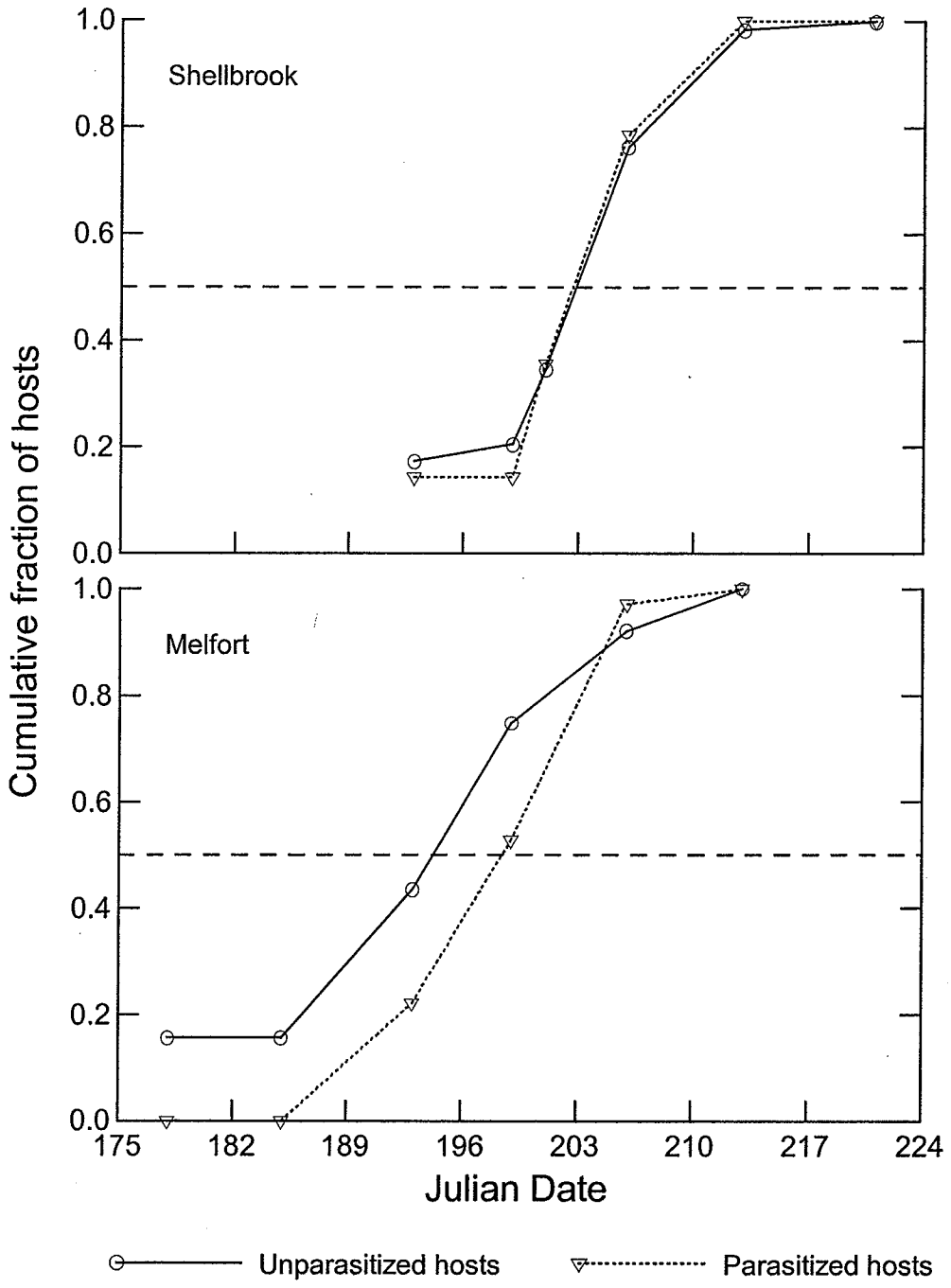

Figure 1.15 Temporal synchronization of *Delia radicum* larvae and *Trybliographa rapae* in canola at Shellbrook and Melfort. Analysis is based on 127 adults of *D. radicum* and 14 adults of *T. rapae* in six samples at Shellbrook and 115 adults of *D. radicum* and 36 adults of *T. rapae* in six samples at Melfort.

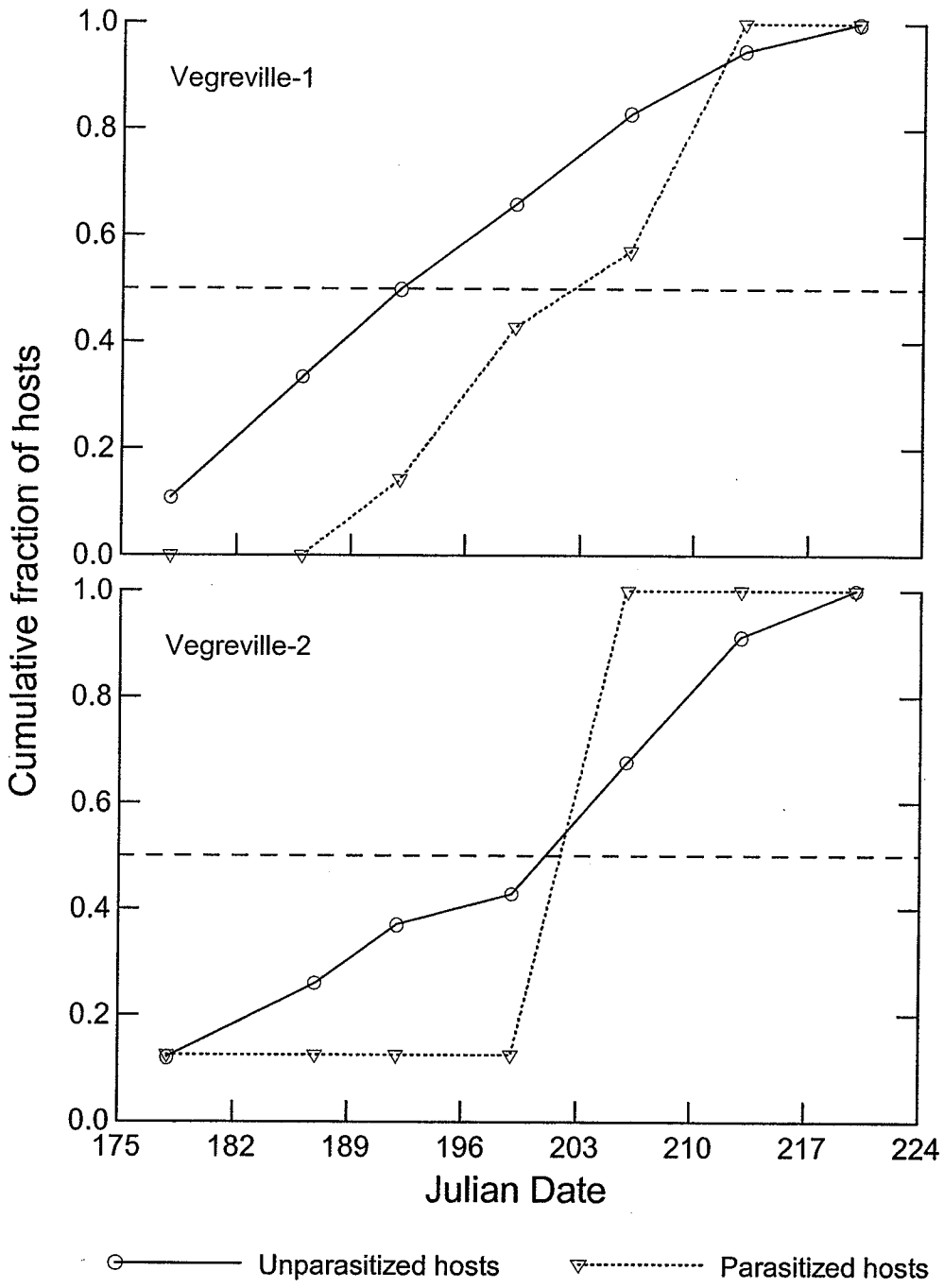

Figure 1.16 Temporal synchronization of *Delia radicum* larvae and *Trybliographa rapae* in canola at Vegreville-1 and Vegreville-2. Analysis is based on 176 adults of *D. radicum* and seven adults of *T. rapae* in seven samples at Vegreville-1 and 173 adults of *D. radicum* and eight adults of *T. rapae* in seven samples at Vegreville-2.

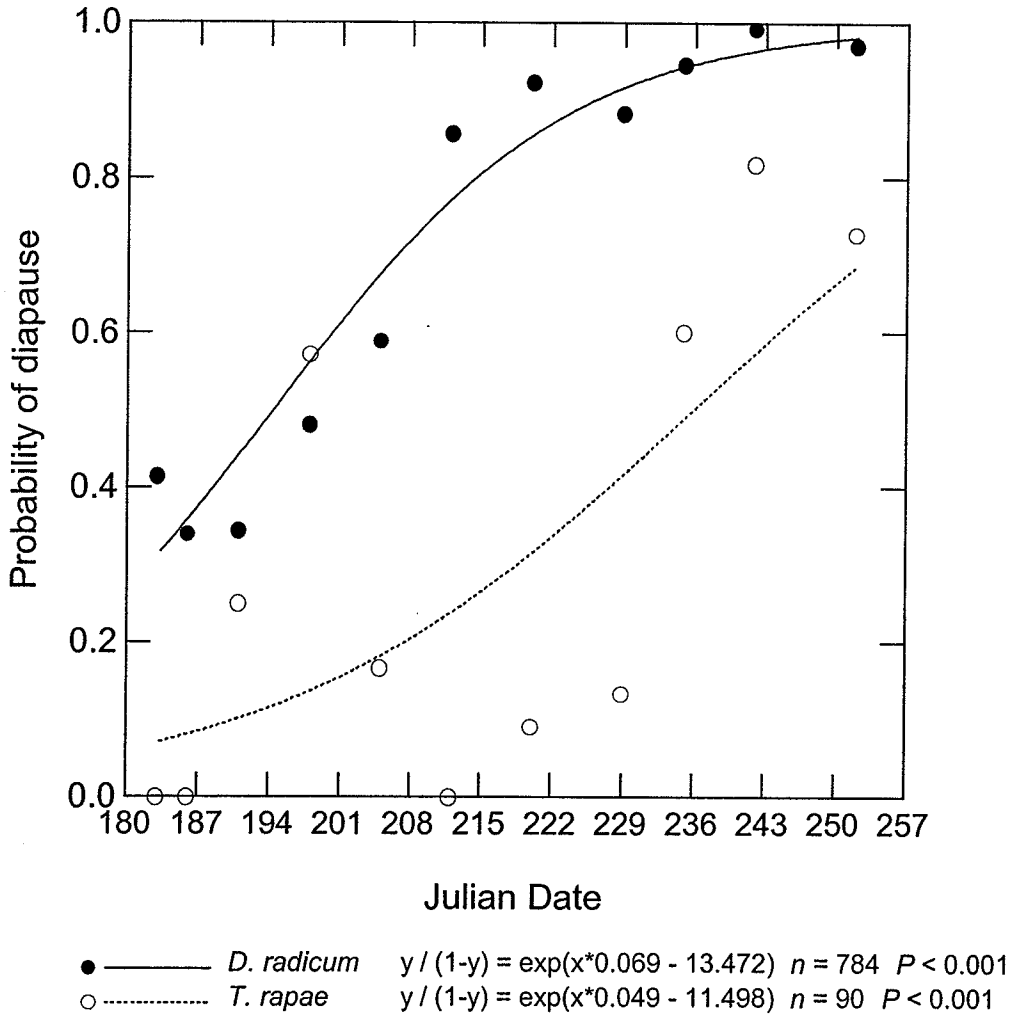

Figure 1.17 Probability of diapause of *Delia radicum* and *Trybliographa rapae* in samples collected at different times of the season at Altamont in summer 2000. Diapause was determined as numbers not emerged by fall.

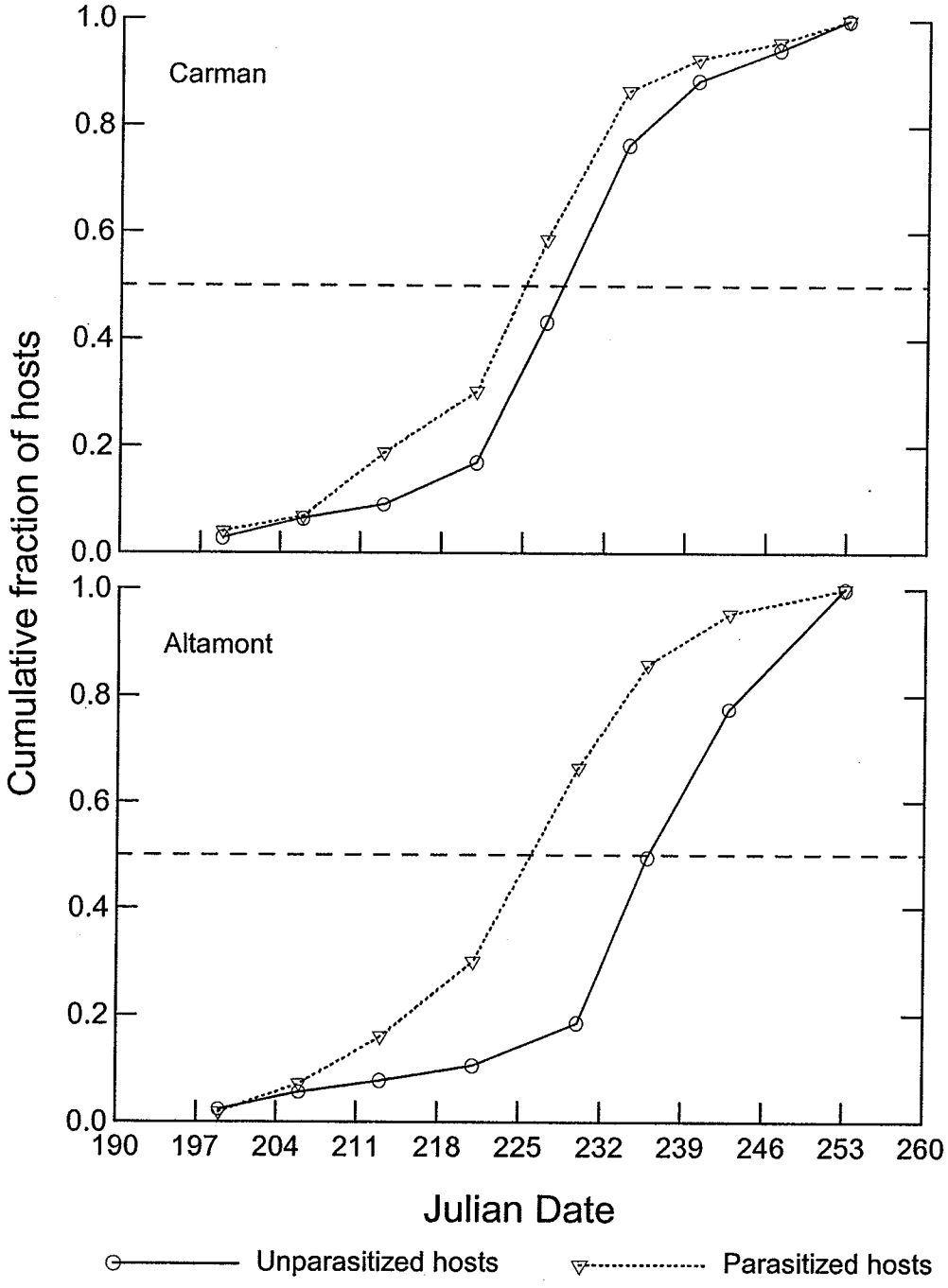

Figure 1.18 Temporal synchronization of *Delia radicum* puparia and *Aleochara bilineata* in canola at Carman and Altamont. Analysis is based on 859 adults of *D. radicum* and 218 adults of *A. bilineata* in 10 samples at Carman and 462 adults of *D. radicum* and 263 adults of *A. bilineata* in eight samples at Altamont.

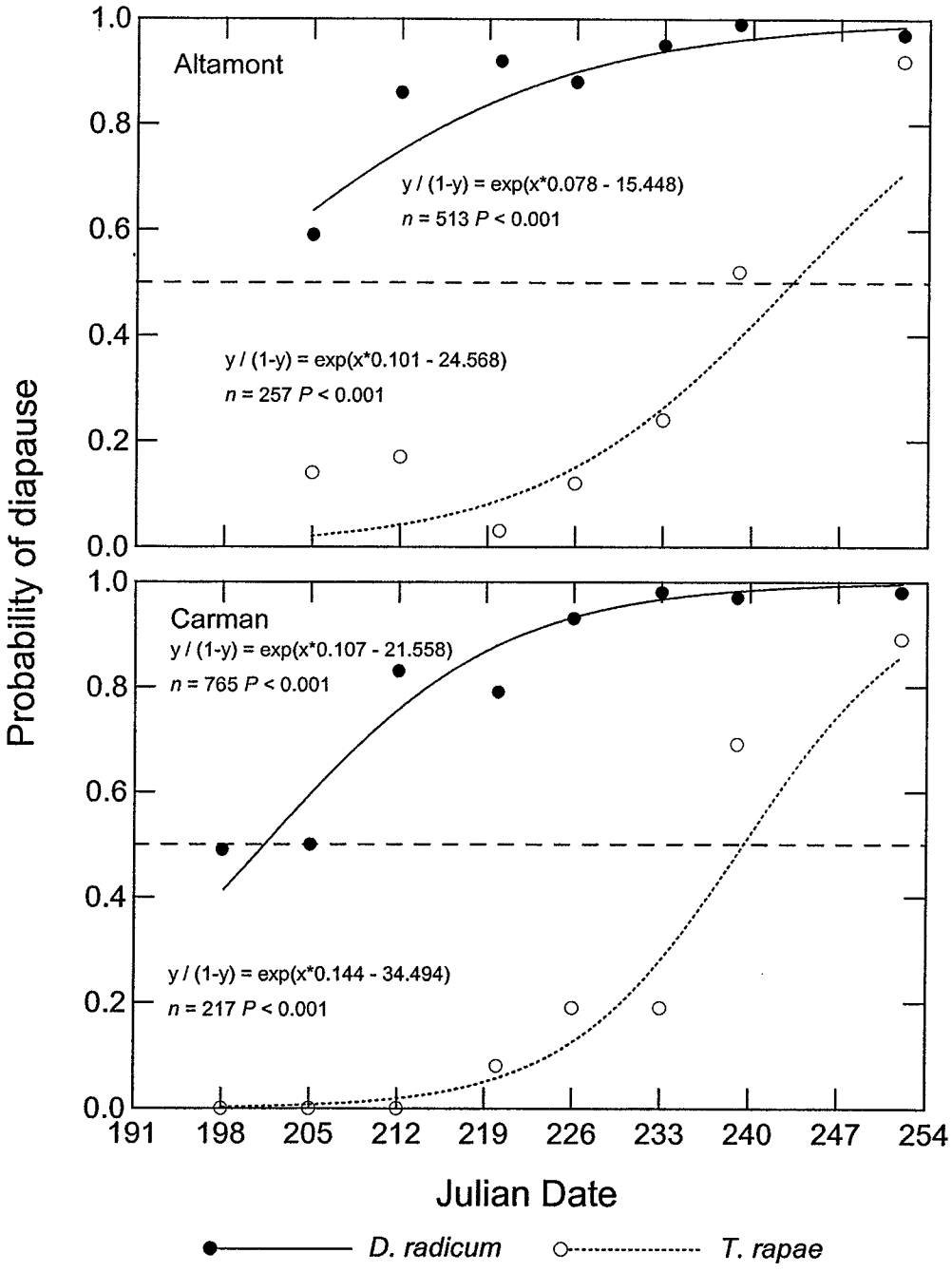

Figure 1.19 Probability of diapause of *Delia radicum* and *Aleochara bilineata* in samples collected at different times of the season at Carman and Altamont in summer, 2000. Diapause was determined as numbers not emerged by fall.

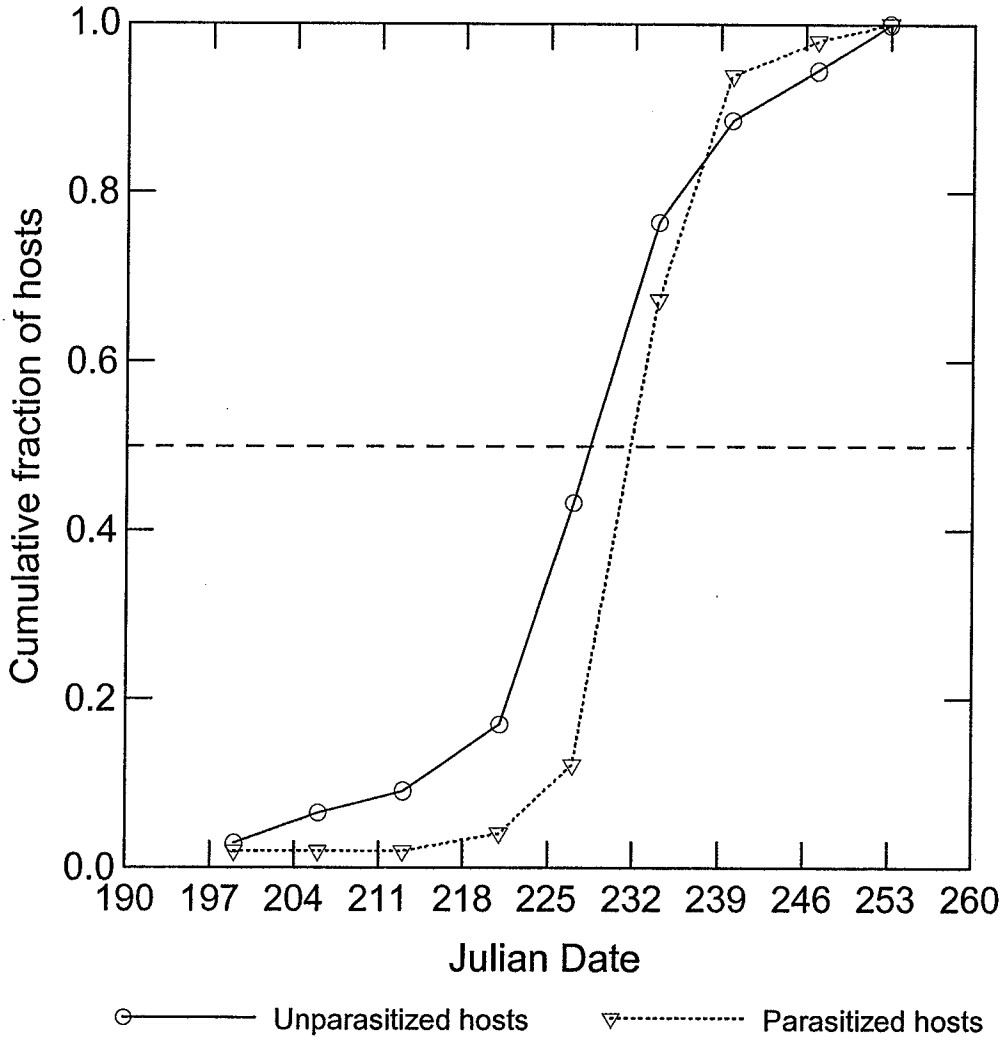

Figure 1.20 Temporal synchronization of *Delia radicum* pupae and *Phygadeuon* spp. in canola at Carman. Analysis is based on 859 adults of *D. radicum* and 49 adults of *Phygadeuon* spp. in ten samples from Carman.

CHAPTER 3 SECTION 2

Assessment of the parasitoids of *Delia radicum* in canola and brassica vegetables in Europe

Introduction

Delia radicum (L.) is an injurious insect in canola on the Canadian Prairies (Soroka *et al.,* 2002). On the Prairies, canola is grown extensively on an average of 4.6 million hectares per year (Canola Council of Canada, 2004); therefore, even a small yield loss per hectare amounts to a loss of millions of dollars annually (Soroka *et al.,* 2002). Larvae of *D. radicum* feed on canola roots causing considerable damage in some parts of the prairies (Liu and Butts, 1982; Griffiths, 1986a). Current management practices of *D. radicum* in the prairies are not adequate to prevent loss and additional management strategies are required. Conventional control methods for *D. radicum* that are used in brassica vegetables (Finch, 1987, 1989; Finch and Collier, 2000b) are not technically feasible in canola (Dosdall *et al.,* 1996b), and classical biological control has been suggested as a viable management strategy (Turnock *et al.,* 1995; Soroka *et al.*, 2002).

Potential biocontrol agents for *D. radicum* may exist in European canola habitats. The parasitoid community of *D. radicum* could be richer in Europe than elsewhere (Zwolfer *et al.,* 1976) because *D. radicum* is an insect of European origin (Griffiths, 1991; Biron *et al.,* 2000). *Delia radicum* inhabits many different habitats such as brassica vegetables, canola habitats (Soroka *et al.,* 2002) and natural habitats that have cruciferous weeds (Finch and Ackley, 1977), and its parasitoid community could differ among habitats (Zwolfer *et al.,* 1976). The parasitoid community of *D. radicum* has been studied in brassica vegetable habitats (Wilkes and Wishart, 1953; Wishart *et al.,* 1957; Finch and Collier, 1984; Jonasson, 1994; Jonasson *et al.,* 1995), but the parasitoid community of *D. radicum* in the canola habitat is unknown. Since the habitat in the potential target area of release is canola, it is desirable to look for parasitoids in similar habitats in the area of origin (Munroe, 1971).

The objectives of this study were to assess the parasitoid community of *D. radicum,* and to examine the relationship between hosts and parasitoids in canola habitats and the brassica vegetable habitat in Europe.

Methods

In the summers of 2001 and 2002, immature *D. radicum* were collected from selected fields in northern, southern and eastern Germany and in Switzerland, and individually reared to assess the parasitoid community. There were 12 sampling sites that had various canola crops or brassica vegetables (Table 2.1).

The field at Fehmarn was bordered by a highway on one side and by a hedgerow on the other three sides. There was a wheat field beyond the hedgerow. In 2001, the year of sampling, there were no canola fields nearby. Volunteer winter canola plants in this field were descended from a crop sown in fall 1999. Fehmarn is an island, and a famous cabbage growing area, and a long bridge connects the island to the German mainland.

The field at Rastorfer-Passau was in a major canola growing area. The volunteer canola field was bordered by a wood on one side, a highway on one side, and by country roads on the other two sides. Beyond the highway, there was a commercial winter canola field of about 50 ha. Volunteer winter canola plants in this field were descended from the crop sown in fall 1999.

The field at Neuenburg was in the Rhine valley, in an area with peas, corn, asparagus, strawberry, wheat, canola and many other crops. The average farm size was about 2–3 ha in the area. The sampled field was bordered by a pea field on the east, a farm road on the south, and hedgerows on the north and west.

The field at Birkenmoor was in a wheat-growing area and there were no canola fields nearby. This location was a research field prepared for another study, and was bordered by wheat fields in all four directions. The canola field was 20 x 20 m and consisted of 1 m wide beds. Root samples were taken from six beds at the west edge of the plot.

The field at Schuby was also in an area dominated by wheat; there were no canola fields in the area. The sampled field was a research field grown for another study, and was bordered by wheat fields on the north and south, by a hedgerow to the east and by a farm road to the west. The canola field was 20 x 20 m and consisted of 1 m wide beds. The samples were taken from six beds at the south side.

The field at Rostock was in an area with no summer canola, but there were scattered winter canola fields in the area. This location was a research field and canola was grown for another study. The field was surrounded by wheat fields.

The field at Dietingen was in an area with no other summer canola nearby and where wheat and barley were the major crops. The sampled field was bordered by woodland on the east and south by a farm road to the west and by a country road on the north.

The field at Dunningen was in an area with winter canola fields but no other summer canola. This sampled field was bordered by wheat fields to the east and south, by a farm road to the west and by a highway to the north.

The field at Grundhof was in an area with no summer canola, but scattered winter canola was available. This sample location was a research field prepared for another study.

The field at Galmiz was in a cabbage growing area. The nearby fields had mainly cabbages with some rhubarb, carrots and corn; carrots and an abandoned brassica crop were on either side of the sampled field, which was a 2 m wide bed of cv "Express" grown specifically for this study.

The field at Wünnewil was in an area where potato, corn, wheat and pasture were grown. The sampled plot was bordered by corn on the east and south, by a highway on the north, and by a country road on the west. Beyond the country road and within 25 m of the crop, was woodland. The canola plot was planted with *Brassica napus* cv 'Express' and no insecticides were used.

The field at Fraeschels was in an area dominated by organic vegetable production. The chosen field had cauliflower and broccoli during the sampling period. The field was bordered by a cabbage crop and a farm road. The nearby fields had carrots, corn and cabbage crops. Brassica vegetables had been grown organically in the same field for several years.

Delia radicum larvae were sampled by removing randomly selected plants from the chosen fields and processing samples in the laboratory to gather information on host plants, and *D. radicum* larvae. The plants were taken from the field margin at locations at least 3 m apart in commercial and volunteer canola fields. Depending on the size of the canola research fields, samples were taken 2–3 m apart. Two to five plants were taken from each sampling location and sampling was continued until 100 plants were taken from summer canola and late summer canola or until 30 plants were taken in commercial winter canola and brassica vegetables.

When *D. radicum* puparia were in the field, puparia and plants were sampled by collecting canola roots and the soil around the root (10 cm diameter and 6 cm deep). Summer canola or late summer canola plants and the soil around plants were individually packed in clear polyethylene bags (30 x 20 cm). In the case of commercial winter canola and cauliflower or broccoli plants, 2–3 liter of soil were collected and packed in 7 liter black polyethylene bags. In addition, bulk samples of *D. radicum* puparia were collected in some locations where necessary.

The sampled plants and immature *D. radicum* in Switzerland and southern Germany were transported in a picnic cooler by car to CABI Bioscience Switzerland Centre, Delémont, Switzerland. The samples collected in Northern Germany were sent to the Plant Protection Institute in Lörrach, southern Germany by mail, and on receipt in Lörrach were transported by car to CABI on the same day. These samples were transported as plant roots with larvae on them. When soil with puparia was collected in northern Germany, the soil was washed and the puparia were collected into Petri dishes. When puparia were collected on roots, the puparia and the corresponding root were wrapped together for transport to CABI Bioscience Switzerland Centre.

In the laboratory, larvae on roots were isolated by dissecting plant roots under the microscope (16 x). Larvae that were not *D. radicum* were discarded. When soil with puparia was sampled, it was washed in water in a plastic basin (35 cm long, 29 cm wide and 15 cm deep). The puparia floating on the water surface were collected using a tea strainer (Langer, 1996). The sampling date, sampling location, crop, plant number, root diameter at the soil surface, number of immatures per plant, and larval instar were recorded. Each larva or puparium was given a unique number and all of the above

information and follow up rearing results were linked to the unique number of the individual in a Microsoft® Access database.

Rearing

The immature *D. radicum* collected in the fields were reared in the laboratory at room temperature and natural light supplemented by artificial light until adult emergence. Larvae extracted from either canola or cabbage roots were individually placed on a cube of rutabaga or turnip within a plastic vial (5 cm high x 2.2 cm diameter). A small amount of fine moist sand or moist sand with fine grade vermiculite was placed in the vial to support the larva and facilitate establishment on rutabaga. Vials with larvae were examined once each week until pupation; food was replaced with a fresh cube of rutabaga when necessary. Upon pupation, the puparia were individually placed in a fresh vial with moist fine sand or moist fine vermiculite. When the sand was dry in the vial, it was replaced with moist sand. All rearing vials were held at room temperature until the emergence of adults.

Some of the collected samples did not emerge before November 2001 and these were stored at natural winter temperatures in a bunker at the CABI Bioscience Switzerland Centre, Delémont. Over-wintered materials were brought back to room temperature on 15 April 2002, and held at room temperature until adult emergence. Some puparia had not emerged by July 2002, and these puparia were dissected to determine whether they contained parasitoids. Puparia, in the samples that were collected in 2002 and did not emerge as adults, were dissected in March 2003. These materials were not kept at low temperature for diapause development. Information on rearing,

mortality, adult emergence dates, species, host identity, diapause status, and dissection were gathered and added to the database.

All the adults that emerged were examined under a microscope (60 x) and grouped based on external anatomy. Subsequently, the groups were identified using taxonomic keys and comparison with reference specimens. *Trybliographa rapae* (Westwood) specimens, received from Dr. Liliane Krespi-Bailhache, Université de Rennes, France, were also used for comparison. Representative samples of *Aleochara* specimens were dissected and genitalia were mounted on plastic slides, and structure of the aedeagus and spermatheca were compared with the drawings of Klimaszewski (1984) and Maus (1996, 1998). Most of the specimens were stored in 70% ethanol in 5 ml plastic vials and some specimens were mounted on paper points. Voucher specimens were deposited in the J.B. Wallis Museum at the University of Manitoba, CABI Bioscience Centre Delémont, Switzerland, and the Canadian National Collection in Ottawa.

Representative samples of *Aleochara* specimens were sent to Dr. J. Klimaszewski, Laurentian Forestry Centre, Canadian Forestry Service, Sainte-Foy (Québec), Canada and Dr. C. Maus, Institut für Biologie I, Freiburg, Germany for the confirmation of their identity. Similarly, *Phygadeuon* specimens were sent to Dr. K. Horstmann, Theodor-Boveri-Institut für Biowissenschaften, Universität Würzburg, Germany and *Trybliographa rapae* specimens were sent to Dr. G. Melika, Systematic Parasitoid Laboratory, Ministry of Agriculture of Hungary, Kszeg, Hungary. Specimens of *Trichopria* were sent to Dr. L. Masner, Eastern Cereal and Oilseed Research Centre,

Ottawa, Canada. A representative sample of *D. radicum* from each sample site was sent to G.C.D. Griffiths, Alberta, Canada for confirmation.

Data analysis

Percentage parasitism of host by a parasitoid was estimated as the number of parasitoids developed to adulthood divided by the total number of hosts collected in a susceptible stage for parasitization and developed to adults, and multiplied by 100. Parasitism of *T. rapae* was estimated based on a single larval sample and a single puparial sample. For the single larval sample, the sample that had the highest per cent of third-instar larvae was chosen. For the puparial sample, the sample that had the highest per cent of puparia, closest to the peak of third-instar larva was chosen. When these criteria were not met, the next appropriate sample was chosen. Levels of parasitism were compared using likelihood ratio chi-square analysis of contingency tables in relation to crops and sampling sites.

Synchronization of hosts and parasitoids was examined using the method of Macdonald and Cheng (1970), in which cumulative fractions of parasitized and unparasitized hosts are calculated for each sampling time. The distributions of parasitized and unparasitized hosts were compared using a Kolmogorov-Smirnov two-sample test. Preliminary analysis revealed that Kolmogorov-Smirnov two-sample test was more appropriate than contingency table analysis to detect the synchronization in host and parasitoids in my data.

Puparial samples that had parasitism by *Aleochara* species with sufficient numbers were used to examine the relationship between host density per plant and probability of one or more hosts being parasitized on a plant. In this analysis, samples

that had enough data for analysis were examined by logistic regression in which attributes of individual plants were the data. The effects of *Aleochara* species and crop on the logistic regression were investigated, in this analysis.

Puparia parasitized by *A. bilineata* were used to examine the relationship between parasitism per plant and host density. The locations were pooled when there was no significant effect of sample location on parasitism pattern. Parasitism was estimated for samples from plants as number of *Aleochara* sp. developed to adulthood divided by total number of puparia collected associated with the plant. Effect of crop and species on the relationship was examined using logistic regression.

Results

The population biology of *D. radicum,* phenology, infestation levels in different crops, and infestation and plant size, were examined and are reported in Chapter 3 Section 3.

Parasitoid community of *Delia radicum*

The parasitoid community of *D. radicum* in canola and brassica vegetables consisted of seven parasitoid species: one larval-pupal parasitoid and six pupal parasitoid species. The larval-pupal parasitoid was *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae). Three species of pupal parasitoids belonged to the order Hymenoptera, and the other three parasitoids species were Coleoptera. The hymenopteran species were *Phygadeuon trichops* Thomson, an undescribed *Phygadeuon* species (Ichneumonidae) and *Trichopria* sp. (Proctotrupidae). The *Trichopria* species was a gregarious parasitoid with an average of 30 adults emerging per host puparium. Three puparia parasitized by *Trichopria* sp. were collected at Neuenburg, one at Galmiz

and one at Dunningen. Because of its infrequent occurrence, this species will not be further discussed. The coleopteran parasitoids were *Aleochara bilineata* Gyllenhal, *Aleochara bipustulata* L. and *Aleochara brevipennis* Gravenhörst (Staphylinidae).

Trybliographa rapae

Trybliographa rapae was found in samples collected in all sites in all crops (Table 2.2). When parasitism of *D. radicum* was estimated based on a single sample of puparia, there was overall variation among the five crop types (Likelihood Ratio (L.R.) $\chi^2 = 68.9$, df = 4, $P = 0.001$). Variability of parasitism within crops (L.R.$\chi^2 = 68.1$, df = 7, $P < 0.001$) accounted for 49.7% of the L.R.χ^2 among 12 larval samples. There was no significant amount attributable to the difference between brassica vegetables and canola (L.R.$\chi^2 = 2.2$, df = 1, $P < 0.14$), but there was considerable variation among the four types of canola (L.R.$\chi^2 = 66.7$, df = 3, $P < 0.001$). Variation of parasitism within volunteer winter canola (L.R.$\chi^2 = 34.8$, df = 1, $P < 0.001$), summer canola (L.R.$\chi^2 = 13.5$, df = 4, $P = 0.009$), and late summer canola (L.R.$\chi^2 = 19.8$, df = 2, $P < 0.001$) were significant.

When total parasitism of *T. rapae* was estimated based on a single sample of larvae (Table 2.3), there was significant overall variation among the five crops (L.R.$\chi^2 = 98.8$, df = 4, $P < 0.001$). The variation within crops (L.R.$\chi^2 = 46.2$, df = 7, $P < 0.001$) was significant and accounted for 31.9% of the L.R.χ^2 among the 12 larval samples. There was a significant variation between parasitism in brassica vegetables and canola (L.R.$\chi^2 = 24.0$, df = 1, $P < 0.001$), and also among the four canola crops (L.R.$\chi^2 = 74.8$, df = 3, $P < 0.001$). Parasitism within late summer canola (L.R.$\chi^2 = 1.9$, df = 2, $P = 0.391$) did not differ significantly. Average parasitism in late summer canola

was 37.4%. In addition, parasitism levels varied across the sampling dates in a given sampling site, and there was often a trend of increasing parasitism as the season progressed (Fig. 2.1–2.10).

Synchronization of *T. rapae* and *D. radicum* larvae appeared to be related to locality. Six of the sampling sites had sufficient numbers of samples and *T. rapae* adults for analysis. Of these six sites, lack of synchronization was not significant at Fehmarn, Rastorfer-Passau, and Wünnewil (Fig. 2.11, 2.14). Lack of synchronization was significant at Birkenmoor (Kolmogorov-Smirnov Two Sample Test $P < 0.001$) and Galmiz (Kolmogorov-Smirnov Two Sample Test $P < 0.001$) and Fraeschels (Kolmogorov-Smirnov Two Sample Test $P = 0.006$) (Fig. 2.12–2.14). At Birkenmoor, the occurrence of 50% host population was 4 days earlier than that of parasitized hosts (Fig. 2.13) and at Galmiz this difference was 5 days (Fig. 2.14). In contrast, at Fraeschels 50% parasitized hosts occurred 3 days before 50% of the host population (Fig. 2.12). Neuenburg (Fig. 2.12), Schuby (Fig. 2.13) and Rostock sites did not have sufficient numbers of parasitoids for statistical analysis of synchronization.

Trybliographa rapae collected in samples emerged in the same summer or diapaused and emerged in the following spring. The proportion of *T. rapae* that diapaused was 7.2% of the 2089 *T. rapae* individuals reared to adulthood. Therefore, the numbers were too low to allow comparisons of time of diapause induction of parasitoid and host.

Aleochara bilineata

Aleochara bilineata was found in samples collected in all sites except Fehmarn, Neuenburg, Dunningen and Dietingen (Table 2.2). When estimates were based on a

single sample of puparia, there was a overall significant variation of parasitism among the five crops (L.R.χ^2 = 50.8, df = 4, $P < 0.001$). Variation within crops was significant (L.R.χ^2 = 153.1, df = 7, $P < 0.001$), and accounted for 75.1% of the L.R.χ^2 among the 12 puparial samples. Variation of parasitism between brassica vegetables and canola was not significant (L.R.χ^2 = 0.2, df = 1, $P = 0.64$), but variation among the four canola crops was significant (L.R.χ^2 = 50.6, df = 3, $P < 0.001$). In canola, parasitism of *D. radicum* in winter crops was significantly lower than the parasitism in summer crops (L.R.χ^2 = 44.2, df = 1, $P < 0.001$). There was significant variation in parasitism among locations within volunteer winter canola (L.R.χ^2 = 6.9, df = 1, $P = 0.009$) and late summer canola (L.R.χ^2 = 136.9, df = 2, $P < 0.001$). Variation in parasitism was not significant within summer canola (L.R.χ^2 = 9.3, df = 4, $P = 0.053$); on average the parasitism was 3.7%.

Parasitism of *A. bilineata* appears to be fluctuating with time with an increasing trend in some sites e.g. Fig. 2.5, 2.8, but this pattern was not evident in all sites e.g. Fig. 2.4.

Delia radicum puparia parasitized by *A. bilineata* were found in sufficient numbers in late summer canola at Galmiz for analysis of density relationships. The relation between the probability of one or more hosts being parasitized per plant and host density followed a logistic regression at Galmiz (L.R.χ^2 = 27.9, df = 1, $P < 0.001$) (Fig. 2.15). However, there was no significant logistic regression between the probability of an individual host being parasitized and host density (L.R.χ^2 = 0.3, df = 1, $P = 0.586$).

Aleochara bipustulata

Aleochara bipustulata was found in samples collected from Birkenmoor, Schuby, Rostock, Grundhof, Galmiz, Wünnewil and Fraeschels (Fig. 2.4–2.10). It was not found

in volunteer winter canola and winter canola. It coexists with *A. bilineata* in all these sites. When parasitism was based on a single sample of puparia, there was significant overall variation of parasitism among the five crops (L.R.χ^2 = 45.4, df = 4, $P < 0.001$). Variation within crops (L.R.χ^2 = 12.3, df = 7, $P = 0.092$) was not significant. Variation between brassica vegetables and canola was significant (L.R.χ^2 = 4.8, df = 1, $P = 0.028$), and variation among the four canola crops was significant (L.R.χ^2 = 40.6, df = 3, $P < 0.001$). Variation of parasitism within late summer canola (L.R.χ^2 = 0.8, df = 2, $P = 0.68$) was not significant. On average, parasitism in late summer canola was 1%. Variation of parasitism among locations of summer canola (L.R.χ^2 = 11.5, df = 4, $P = 0.02$) was significant.

Delia radicum puparia parasitized by *A. bipustulata* were found in sufficient numbers at Schuby for analysis of density relationships. Relationship between probability of one or more host being parasitized per plant, and host density followed a significant logistic regression (L.R.χ^2 = 3.9, df = 1, $P = 0.047$) (Fig. 2.15). When this pattern was compared with that of *A. bilineata* in late summer canola, the effect of species was significant (L.R.χ^2 = 11.3, df = 1, $P < 0.001$), but species x density interaction was not significant (L.R.χ^2 = 0.8, df = 1, $P = 0.363$) (Fig. 2.15). However, the logistic regression between probability of individual hosts being parasitized by *A. bipustulata* and host density was not significant (L.R.χ^2 = 3.2, df = 1, $P = 0.08$).

<u>*Phygadeuon* species</u>

Phygadeuon species were found in all sites except Rastorfer-Passau, Schuby, Rostock and Dunningen (Fig. 2.1–2.10). There were two species of *Phygadeuon* in samples collected in sampling sites. The species found at Neuenburg was *P. trichops*

Thomson and the species found in northern Germany was an undescribed *Phygadeuon* species. In addition, *Phygadeuon* insects were found in several other locations (Table 2.2) and identified only to genus level. Therefore, all *Phygadeuon* insects collected were treated as one group.

Overall, there was variation in parasitism among the five crops (L.R.χ^2 = 15.3, df = 4, P = 0.04). Variation within crops was not significant (L.R.χ^2 = 13.3, df = 7, P = 0.07). Variation between brassica vegetables and canola was not significant (L.R.χ^2 = 1.0, df = 1, P = 0.032), but variation among the four canola crops was significant (L.R.χ^2 = 14.3, df = 3, P = 0.002). There was significant variation among locations within volunteer winter canola (L.R.χ^2 = 5.7, df = 1, P = 0.017), but that was not significant within late summer canola (L.R.χ^2 = 2.6, df = 2, P = 0.28) and summer canola (L.R.χ^2 = 5.0, df = 4, P = 0.283). Average levels of parasitism levels in late summer canola and summer canola were 1.8 and 1.3% respectively (Table 2.2).

Discussion

Implication of methods

The methodology of this study was planned to assess the parasitoid community, therefore many different canola habitats were sampled. Field selection was based on level of *D. radicum* infestation and geographical area. On some occasions, number of sampling sites per crop was limited to one, e.g. winter canola, due to lack of fields with adequate levels of infestation. In this situation the effects of crop type and of location on parasitism cannot be separated.

Sampling of *D. radicum* in small plots of canola is comparable with the edge of commercial canola fields. Therefore, sampling at the edge of the field avoids many of

the influences of field size on assessment of parasitism. Parasitism in small plots may be influenced by the crop type and by characteristics of the geographical location. This is especially true when the canola plots were in brassica vegetable growing areas. However, the canola habitat is quite different to the brassica vegetables habitat, and area of habitat overlap or transition is minimal.

Parasitism was compared among crops and sites using puparial samples collected before the emergence of host and parasitoid adults. These avoid effects associated with the number of generations in the area, and provide a consistent measure of parasitism among the sites. However, this technique might lead to an under estimate of the parasitism of pupal parasitoids and parasitoid species that are present in puparia for a short period of time.

The strengths of the sampling protocol for assessment of host-parasitoid synchrony, diapause, and response of parasitoids were discussed in Chapter 3 Section 1.

Parasitoid community

This study is the first investigation of *D. radicum* parasitoids in the canola habitat in Europe, but there have been several investigations of *D. radicum* parasitoids in brassica vegetables (Wadsworth, 1915a; Smith, 1927; Wilkes and Wishart, 1953; Wishart *et al.,* 1957; Bromand, 1980; Finch and Skinner, 1980; Finch and Collier, 1984; Jonasson, 1994; Jonasson *et al.,* 1995; Brunel and Fournet, 1996). In those studies, *T. rapae* and *A. bilineata* or *A. bipustulata* were the major parasitoid species of *D. radicum*. In addition, two species of ichneumonids, *Phygadeuon trichops* Thomson (Finch and Collier, 1984) and *Phygadeuon fumator* (Gravenhörst) (Wadsworth, 1915a; Wishart *et al.,* 1957), three species of braconids, *Aphaereta difficilis* Nees, *Aphaereta*

tennuicornis Nix (Wishart *et al.*,1957); *Dacnusa stramineipes* Halid (Smith, 1927), one diapriid, *Loxotropa tritoma* (Thomson) (Wishart *et al.*, 1957), one proctotrupid, *Trichopria cilipes* Kieff, (Adashkevich, 1983) and three species of staphylinids, *Aleochara verna* (Jonasson, 1994), *Aleochara binotata* Kraatz (Jonasson, 1994) and *Aleochara brundini* Bernh (syn. *suffusa*) (Jonasson *et al.*, 1995) were found as minor parasitoids of *D. radicum*. The major parasitoids found in this study in canola were the same as the species in brassica vegetables in previous studies.

Some of the rare species found in previous studies were not found in this study. This may be associated with the time of sampling, sample size, and history of sampling sites. In many previous studies, puparia were collected in fall, whereas samples in this study were collected during the summer. In contrast, I found two species that have not been documented previously. *Aleochara brevipennis* Gravenhörst was reared from a puparium from Galmiz; this is the first record of *D. radicum* as a host of *A. brevipennis*. Generally, *A. brevipennis* parasitizes *D. antiqua* Meigen, *Calliphora vicina* Rob.-Desv. and *Lucilia caesar* L. (Maus *et al.*, 1998). The other species was an undescribed *Phygadeuon* sp. collected in northern Germany.

Parasitism of *Delia radicum*

Parasitism levels can be assessed on different bases, therefore parasitism levels from previous studies should be compared with caution. For example, Finch and Collier (1984) and Jonasson *et al.* (1995) calculated the parasitism level as the number of parasitoids that emerged in relation to the initial number of hosts. In this method, the hosts that die during rearing are considered as unparasitized, which is erroneous, especially if the mortality was associated with parasitism (Reader and Jones, 1990).

Smith (1927) did not indicate the method of calculation of parasitism. In this study, parasitism was calculated based on the total number of hosts and parasitoids developing to adulthood (Driesche, 1983).

Trybliographa rapae

Trybliographa rapae parasitizes a variable proportion of *D. radicum* in brassica vegetable habitats in Europe (Table 2.4). Parasitism level varies among countries, as well as among the locations within a country. In my study, the parasitism level of *T. rapae* ranged from 10–64% (Table 2.2). Levels of parasitism were generally higher in this study than in the previous studies (Table 2.4).

The parasitism of a host population depends on the population levels of both host and parasitoid, their temporal synchronization (Huffaker *et al.*, 1976; Driesche, 1983) and degree of multiparasitism (Jones, 1986; Hassell, 2000). In addition, parasitism level varies with weather, soil type, geographical location and history of sampling sites (Wishart, 1957; Wishart *et al.,* 1957; Nair and McEwen, 1975). In this study, *T. rapae* parasitism levels in canola fields varied at a local scale and this local variability overwhelmed any general patterns of parasitism among crops.

The high level of *T. rapae* parasitism at Fehmarn may be associated with its locality and the absence of *Aleochara* species, which can have a negative effect on *T. rapae* through multiparasitism (Jones, 1986). The Fehmarn sampling site was in the vicinity of a cabbage growing area, and multiple generations of the host on cabbage would allow the parasitoid population to build up (Thompson, 1939). Comparatively high parasitism levels in the cabbage growing area of Fraeschels further support this speculation.

Parasitism of *D. radicum* by *T. rapae* was not high at Neuenburg compared with Fehmarn, and *Aleochara* spp. were also not found at Neuenburg. Therefore, it appears that absence of *A. bilineata* alone was not sufficient for a population build up of *T. rapae.* Availability of host insects and of their host plants has a considerable effect on the local parasitoid population (Thompson, 1939). Brassica plants were not common at the Neuenburg area, except *Alliaria petiolata* Beib., garlic mustard along roadsides, so there were probably of few multivoltine host and parasitoid populations in the area. In addition, insecticides and other agricultural chemicals were used in vegetables and field crops in the area. Therefore, it can be speculated that availability of host and host plants, absence of multiparasitism, and field history all affect parasitism.

Estimates of parasitism based on a single sample of larvae are free from interference associated with multparasitism by *A. bilineata. Delia radicum* larvae are susceptible to *T. rapae* until they become puparia (Neveu *et al.*, 2000), but samples contained third-instar larvae that were of different ages. The lifespan of third-instar larvae is about two weeks (McDonald, 1985). Thus my estimates of parasitism are likely to underestimate the true parasitism, because larvae were collected before completion of their period of vulnerability to attacking parasitoids.

The parasitism level of different larval instars of *D. radicum* indicates the accumulation of parasitism within the *D. radicum* population in the field (Table 2.3). Whenever there was a reasonable number of second-instar larvae in the sample, the per cent parasitism of second-instar larvae was close to the parasitism level of third-instar larvae (Table 2.3). This may be associated with estimating parasitism based on a small number of larvae, or may indicate that *D. radicum* larvae were mostly parasitized by

T. rapae when they are in the first- or second-instar. Generally, first- and second-instar larvae feed closer to the soil surface than third-instar larvae (Schoene, 1916). Therefore, female *T. rapae* searching for hosts by burrowing from the soil surface may have a higher probability of encountering a first- or second-instar larva than encountering a third-instar larva. Larvae that feed and pupate close to the soil surface have higher parasitism by *T. rapae* than puparia at deeper levels in the soil (Block *et al.,* 1987), possibly as a consequence of a higher probability of encounter.

Estimation of parasitism based on puparial samples was influenced by emergence of host and parasitoids, and also by interference of *Aleochara* species (Jones, 1986; Reader and Jones, 1990) through multiparasitism. The differences in estimates of parasitism of *T. rapae* based in larval samples (Table 2.3) and puparial samples (Table 2.2) were negatively correlated with the parasitism of *A. bilineata* though the relationship was not significant ($r = -0.45$, $P = 0.142$).

Variability of parasitism at local scale prevents statistical comparisons of parasitism in relation to crops. However, in general, the parasitism in late summer canola was higher than in summer canola. The difference in parasitism may be related to field size, availability of host plants for *D. radicum* and the parasitoid in relation to time of the season, availability of host plants around the sampling site, and cropping history of adjacent fields.

Aleochara bilineata

Parasitism levels of *D. radicum* by *A. bilineata* varied with the geographical location in Europe (Table 2.2); weather, host-plant availability and interaction with parasitoids such as *T. rapae* may influence *A. bilineata* parasitism (Bromand, 1980;

Reader and Jones, 1990). In this study, *A. bilineata* was found in all sampling sites where adequate numbers of puparia were collected, except at Neuenburg and Fehmarn. At Fehmarn, weather, host plants, and hosts appeared favourable for survival of *A. bilineata*; however, Fehmarn is an island connected to the mainland by a >1 km bridge. Therefore, there is a possibility that *A. bilineata* has not colonized this island. Tomlin *et al.* (1992) found that *A. bilineata* dispersed 5 km among urban gardens following inundative release of adults, but perhaps *A. bilineata* does not fly across water.

Aleochara bilineata was not found in winter canola. However, volunteer winter canola is not very different from winter canola in terms of plant architecture, phenology and plant density and *A. bilineata* was found in a volunteer winter canola site (Fig. 2.2). Therefore, absence of *A. bilineata* in winter canola could be locality-related rather than crop related in general. The puparial samples collected in summer canola in southern Germany did not have *A. bilineata,* and this could be related to small sample size. Parasitism of *D. radicum* by *A. bilineata* was low in winter crops. This could be influenced by the small number of plants sampled, but might also relate to resource availability in winter crops to retain adult *A. bilineata.* If the objective is to collect large numbers of *Aleochara*, field collections in future work should be focused on summer crops.

Generally parasitoids respond to host density during host search (Jones, 1986), and they use chemical cues emanating from the host plant, the host-insect or its frass to locate hosts (Vet and Groenewold, 1990). *Aleochara bilineata* also uses chemical cues to choose oviposition sites (Royer and Boivin, 1999). Therefore, it can be assumed that the probability of finding a plant with high host density is higher than that of finding a plant

with low host density (Langer, 1996). In this study, in agreement with Langer (1996), host density and the probability of at least one host being parasitized by *A. bilineata* were positively correlated.

Discovery by parasitoids of host plants with high host density does not necessarily translate into high levels of parasitism on those plants (Godfray, 1994); parasitism levels could be density dependent or density independent (Stiling, 1987). It appears that the relationship between parasitism by *A. bilineata* and host density is inconsistent. Positive and negative density dependence and density independence have all been observed (Jones *et al.*, 1993; Turnock *et al.*, 1995; Langer, 1996). In this study, the relationship was density independent.

Adult *A. bilineata* find the host plant by responding to semiochemicals (Royer and Boivin, 1999) and lay eggs on soil near host plants (Fuldner, 1960). Emerging first-instar larvae search randomly for a host (Fuldner, 1960), and enter the host puparia (Fuldner, 1960). The free-living lifespan of the first-instar larva is 5–6 days (Fuldner, 1960). Therefore, the relationship between host density and parasitism is the result of behaviour of both the adult female and the first-instar larva. If the number of eggs laid by the adult female is responsive to host density, density dependent parasitism could result. However, females may lay consistent numbers of eggs when they find a plant showing symptoms of *D. radicum* attack or the distribution of puparia in soil could interfere with density dependent parasitism. Generally, *D. radicum* pupate at a depth of 0–20 cm with >75% at 0–5 cm (Jones, 1986). It is unlikely that a first-instar larva searches for a patch of high host density as it uses only one host. The larva's limited mobility and short lifespan restrict the exploitation of patch searching for suitable hosts.

The relationships of host plant finding and parasitism in relation to host density in *A. bilineata* were similar to that in *A. bipustulata,* and the similarity of behaviour may indicate similar host finding in the two species.

Aleochara bipustulata

Previously, *A. bipustulata* and *A. verna* have rarely been found as parasitoids of *D. radicum* in western Europe. One or both species are present in France, Belgium, Netherlands (Wishart *et al.,* 1957) and the United Kingdom (Wishart *et al.,* 1957; Finch and Collier, 1984). These assessments were based on a collection of overwintering puparia, so there was a chance that *A. bipustulata* was not present in the samples. Jonasson (1995) indicated without experimental data that *A. bipustulata* overwinter as adults; if it overwinters as a free adult, then *A. bipustulata* would not be in puparial samples collected in fall. In my study, *A. bipustulata* was rare in Switzerland and absent in Southern Germany.

Aleochara bipustulata may be more abundant in northern parts of Europe. In a study in Sweden, 13.2% of *D. radicum* puparia were parasitized by *A. bipustulata* (Jonasson, 1994), and the species has been found in several locations in Norway (Anderson and Eltun, 2000). In my study, *A. bipustulata* was most common in northern Germany (Table 2.2).

Conclusions

Major parasitoid species of the parasitoid community of *D. radicum* in Europe include *T. rapae, A. bilineata,* and *A. bipustulata* and found in brassica vegetables and canola. Minor parasitoids found varied with sampling locations and include *Phygadeuon trichops,* undescribed *Phygadeuon* sp., *Trichopria* sp. and *A. brevipennis.*

Trybliographa rapae was widely distributed and its parasitism varied from 0% to 64% and was related to locality. Occurrence of host larvae and *T. rapae* were synchronized in some locations, but degree of synchronization was not related to parasitism. *Aleochara bilineata* was found only in some locations and parasitism varied between 0% and 57%. Variation of parasitism among locations was large enough to mask any effect of crop type on parasitism levels, but in general parasitism was low in winter crops. *Aleochara bipustulata* was not found in all sampling locations, and never found in winter crops. Parasitism level varied between 0% and 14%. Therefore, role of *Aleochara* species in suppression of *D. radicum* population in European canola was limited. Both *Aleochara* species responded similarly to host density in that the probability of at least one host being parasitized was positively related to host density, but parasitism level of pupae on a plant was not related to host density. *Phygadeuon* species were found in some locations and included two species, an undescribed *Phygadeuon* sp. and *P. trichops*; parasitism varied from 0% to 11%, and was related to locality.

Table 2.1 Geographical location and characteristics of sampling sites where immature *Delia radicum* were collected in 2001 and 2002.

Crop and Sampling site	Latitude and longitude	Field size (ha)	Plant density (No. / m^2)	Sampling period	No. of samples
Volunteer winter canola					
Fehmarn, Schleswig-Holstein, NG	54° 28' N, 11° 7' E	5	48	24 May – 24 June, 01	6
Rastorfer-Passau, Schleswig-Holstein, NG	54° 16' N, 10° 20' E	5	68	24 May – 18 June, 01	5
Winter canola					
Neuenburg, Baden-Wuerttemberg, SG	47° 49' N, 7° 34' E	1	80	22 May – 10 July, 01	8
Summer canola					
Birkenmoor, Schleswig-Holstein, NG	54° 45' N, 10° 6' E	0.04	75	31May – 8 July, 02	5
Schuby, Schleswig-Holstein, NG	54° 31' N, 9° 38' E	0.04	75	31May – 8 July, 02	5
Rostock, Mecklenburg-Vorpommern, EG	54° 4' N, 12° 7' E	0.25	75	30 May – 20 June, 02	4
Dietingen, Baden-Wuerttemberg, SG	48° 11' N, 8° 38' E	10	100	11 June and 5 July, 02	2
Dunningen, Baden-Wuerttemberg, SG	48° 12' N, 8° 32' E	5	100	11 June and 5 July, 02	2
Late summer canola					
Grundhof, Schleswig-Holstein, NG	54° 46' N, 9° 39' E	0.03	463	31 July – 04 Sep., 01	6
Galmiz, Seeland, CH	46° 57' N, 7° 9' E	0.02	83	11 July – 21 Aug., 01	6
Wünnewil, Mittleland, CH	46° 52' N, 7° 16' E	0.003	438	17 July – 21 Aug., 01	5
Brassica vegetables					
Fraeschels, Seeland, CH	47° 0' N, 7° 12' E	3	2	1 June – 21 Aug., 01	11

NG = northern Germany, SG = southern Germany, EG = eastern Germany, CH = Switzerland

Table 2.2 Percentage parasitism of *Delia radicum* puparia by its major parasitoid species in canola and brassica vegetables. Assessments were based on one sample of puparia.

Crop and sampling site	*T. rapae*	*A. bilineata*	*A. bipustulata*	*Phygadeuon* spp.	No. of puparia	Sampling date
Volunteer winter canola						
Fehmarn	64.2	0	0	6.6	106	1 July, 01
Rastorfer-Passau	15.7	5.9	0	0	51	18 June, 01
Winter canola						
Neuenburg	13.6	0	0	11.4	44	27 June, 01
Summer canola						
Birkenmoor	15.8	2.6	13.2	0	38	8 July, 02
Schuby	9.7	10.8	14	0	93	24 June, 02
Rostock	21.1	5.3	5.3	0	19	20 June, 02
Dietingen	50.0	0	0	6.3	16	5 July, 02
Dunningen	18.5	0	0	0	27	5 July, 02
Late summer canola						
Grundhof	50.0	7.7	1.9	1.9	52	4 Sep., 01
Galmiz	28.9	56.7	0.7	0.7	135	7 Aug., 01
Wünnewil	52.4	0	0.5	2.7	187	14 Aug., 01
Brassica vegetables						
Fraeschels (1st Gen.)	44.3	9.1	0	1.1	88	25 June, 01
Fraeschels (2nd Gen.)	44.8	0	0	1.7	58	24 Sep., 01

Table 2.3 Parasitism of *Delia radicum* larvae by *Trybliographa rapae* in canola and brassica vegetables. Assessments were based on one sample of larvae.

Crop and sampling site	No. of larvae collected			No. of larvae reared to adulthood			Parasitism (%)			Total parasitism	Sampling date
	L1	L2	L3	L1	L2	L3	L1	L2	L3		
Volunteer winter canola											
Fehmarn	0	5	129	0	3	99	-	0	30.3	29.4	26 May, 01
Rastorfer-Passau	0	2	97	0	1	69	-	0	11.6	11.4	26 May, 01
Winter canola											
Neuenburg	0	1	63	0	1	55	-	0	10.9	10.7	31 May, 01
Summer canola											
Birkenmoor	25	114	431	11	74	321	27.3	14.9	17.1	17.0	17 June, 02
Schuby	1	7	67	1	3	40	0	66.7	12.5	15.9	10 June, 02
Rostock	1	5	17	0	3	9	-	66.7	44.4	50.0	6 June, 02
Dietingen	9	39	37	5	18	20	0	0	0	0	11 June, 02
Dunningen	38	19	2	32	7	0	0	0	0	0	11 June, 02
Late summer canola											
Grundhof	1	13	76	0	10	61	-	60.0	36.1	39.4	7 Aug., 01
Galmiz	2	20	47	2	14	36	0	42.9	50.0	46.2	24 July, 01
Wünnewil	3	47	66	2	23	50	0	43.5	56.0	50.7	24 July, 01
Brassica vegetables											
Fraeschels (1st Gen.)	0	20	385	0	12	239	-	41.7	37.7	37.8	1 June, 01

Table 2.4 Parasitism of *Delia radicum* by *Trybliographa rapae* and *Aleochara bilineata* in brassica vegetables in Europe where assessments were based on puparial samples collected in fall.

Country	No of locations	Level of parasitism (%)		Source
		T. rapae	*A. bilineata*	
Belgium	-	22.0	33	Wishart *et al.*, 1957
Belgium	-	8	-	Hertveldt, 1970
Denmark	-	0–3	0–74	Wishart *et al.*, 1957
Denmark	5 – 6[a]	4.5±1.6	55.2±9.1	Bromand, 1980
Denmark	3	21.5	24.8	Langer, 1996
France	-	1–10	4–65	Wishart *et al.*, 1957
Netherlands	14	16.0±2.8	14.3±3.1	Wilkes and Wishart, 1953
Norway	-	0–29	0–25	Wishart *et al.*, 1957
Poland	1	4	37	Kaczorowski, 1993
Sweden	-	5–8	83	Wishart *et al.*, 1957
Sweden	1	7.9	40.2	Jonasson, 1994
Switzerland	-	5–12	1–17	Wishart *et al.*, 1957
United Kingdom	1	16.0	18.0	Finch and Collier, 1984
United Kingdom	1	>30	-	Smith, 1927
United Kingdom	-	0–13	1–44	Wishart *et al.*, 1957

[a]Five samples for *T. rapae* and six samples for *A. bilineata* for assessment.

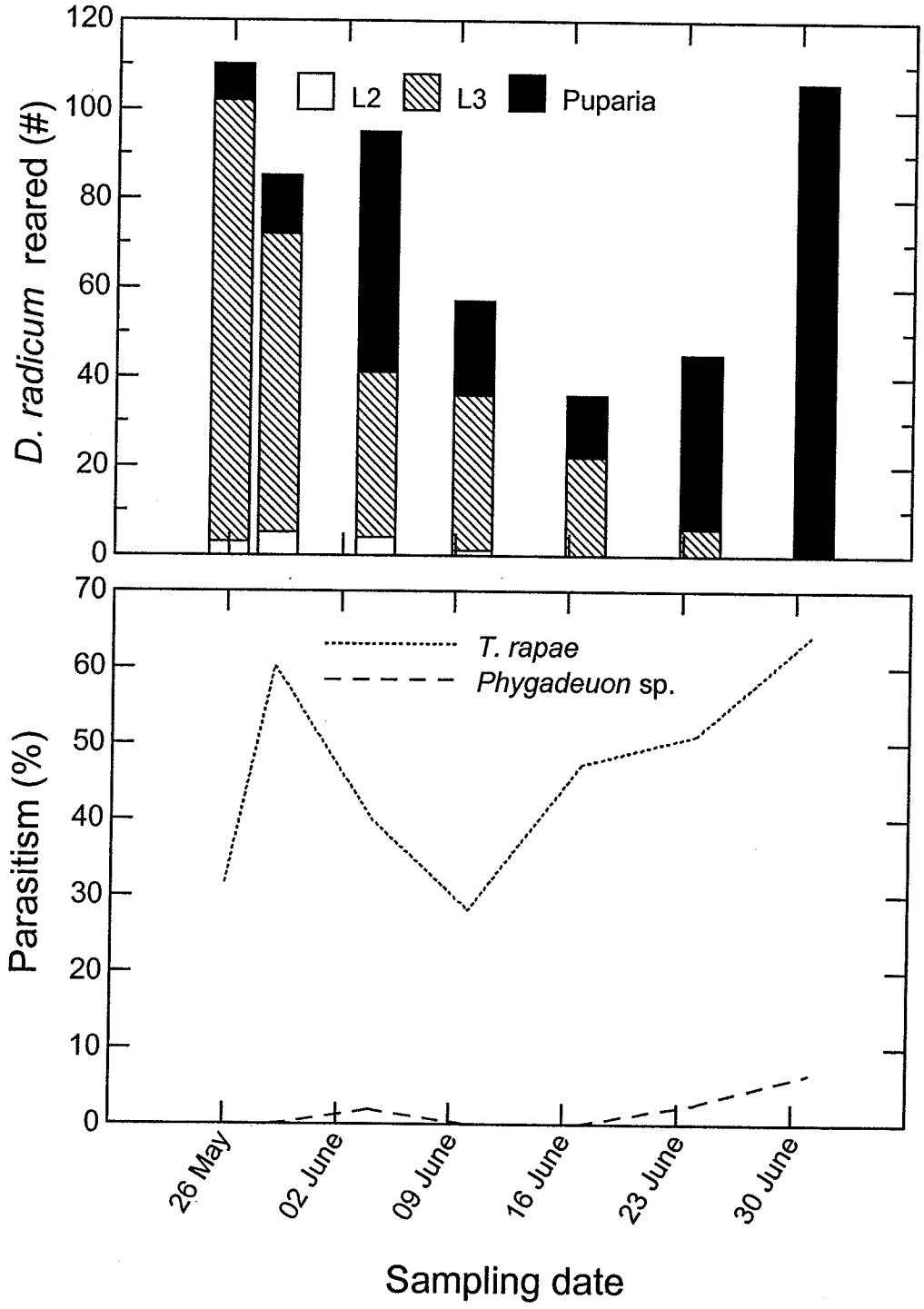

Figure 2.1 Parasitism of *Delia radicum* by its major parasitoid species in volunteer winter canola at Fehmarn in relation to time of sampling in 2001 and number of immatures reared to adulthood.

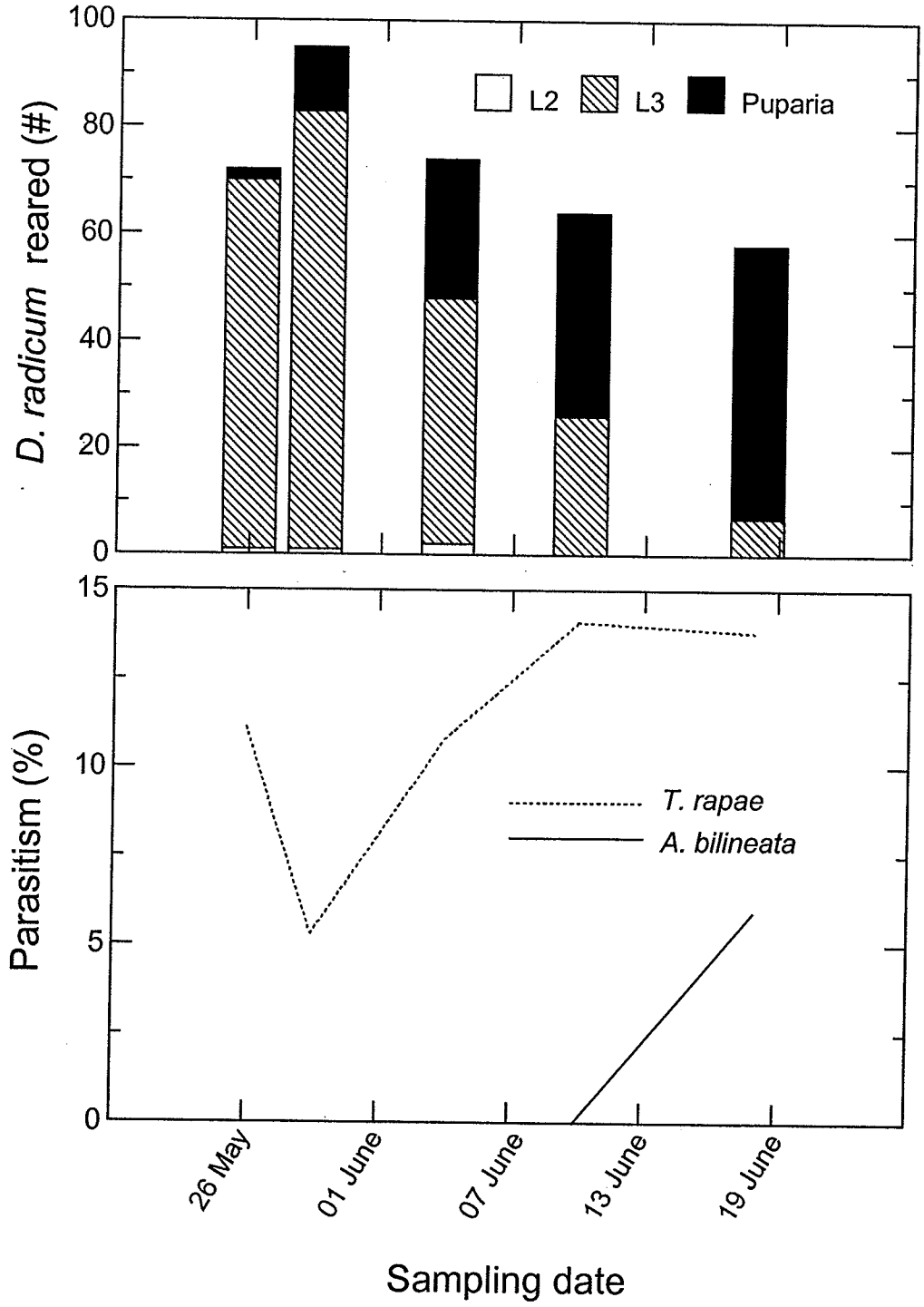

Figure 2.2 Parasitism of *Delia radicum* by its major parasitoid species in volunteer winter canola at Rastorfer-Passau in relation to time of sampling in 2001 and number of immatures reared to adulthood.

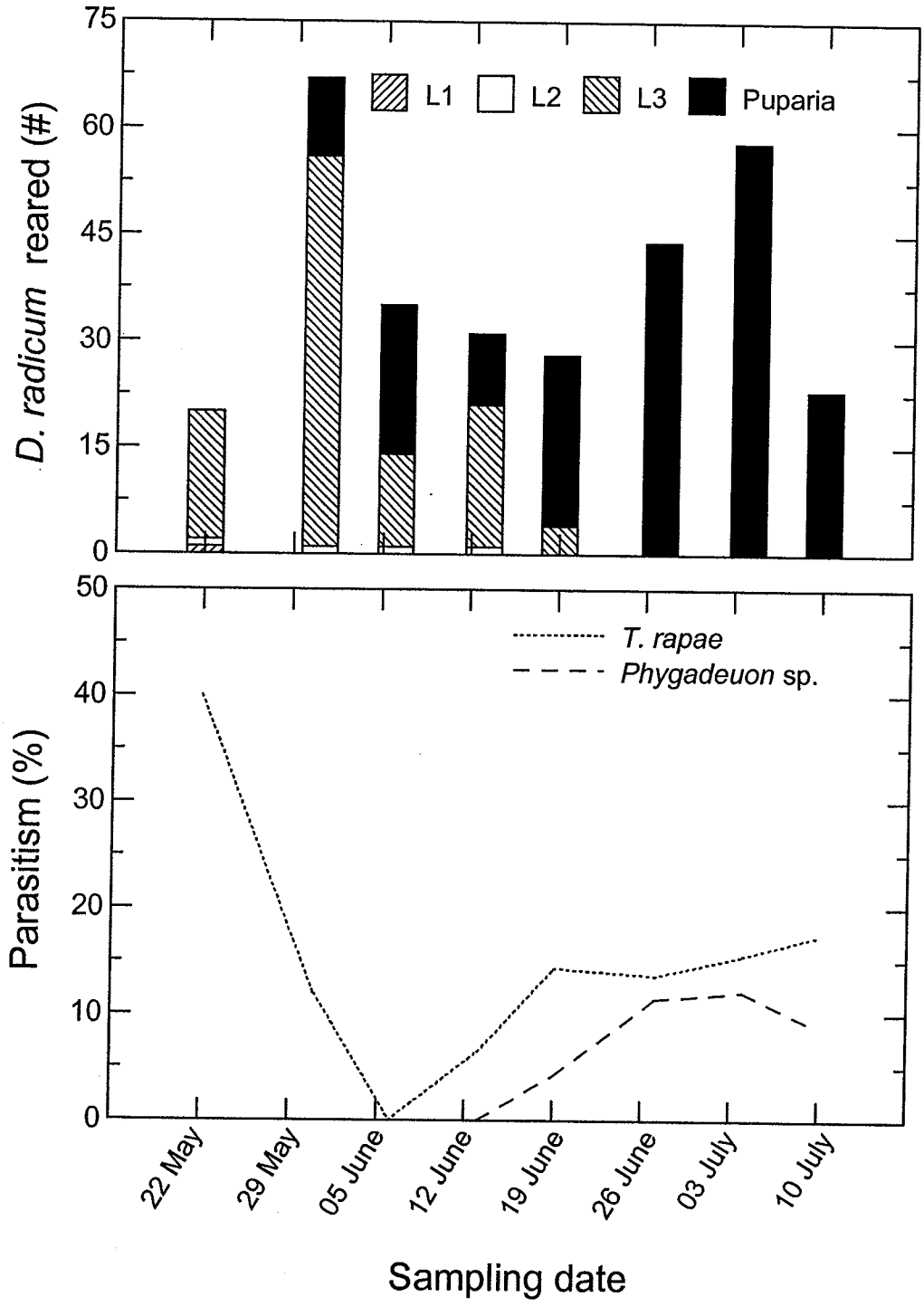

Figure 2.3 Parasitism of *Delia radicum* by its major parasitoid species in winter canola at Neuenburg in relation to time of sampling in 2001 and number of immatures reared to adulthood.

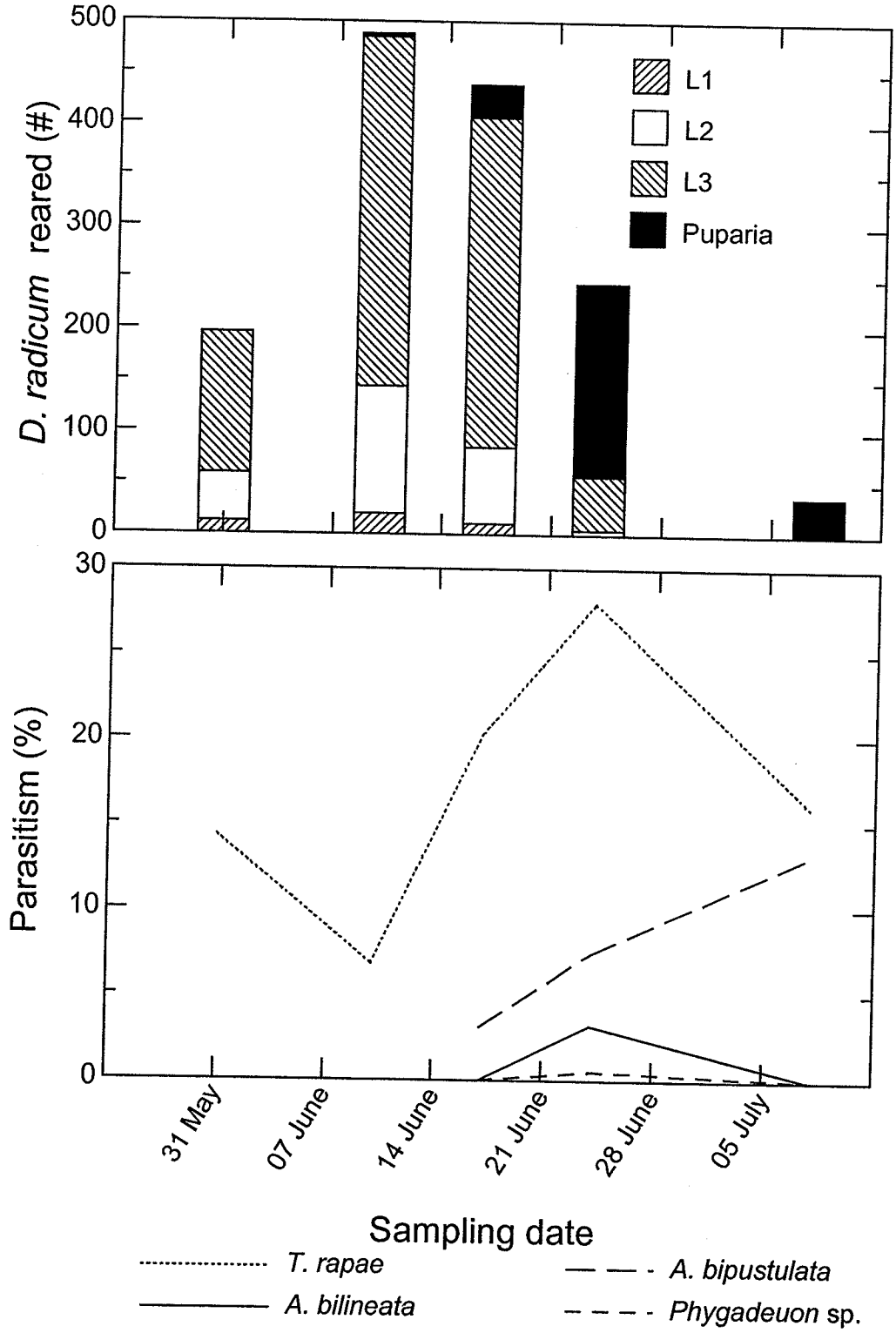

Figure 2.4 Parasitism of *Delia radicum* by its major parasitoid species in summer canola canola at Birkenmoor in relation to time of sampling in 2002 and number of immatures reared to adulthood.

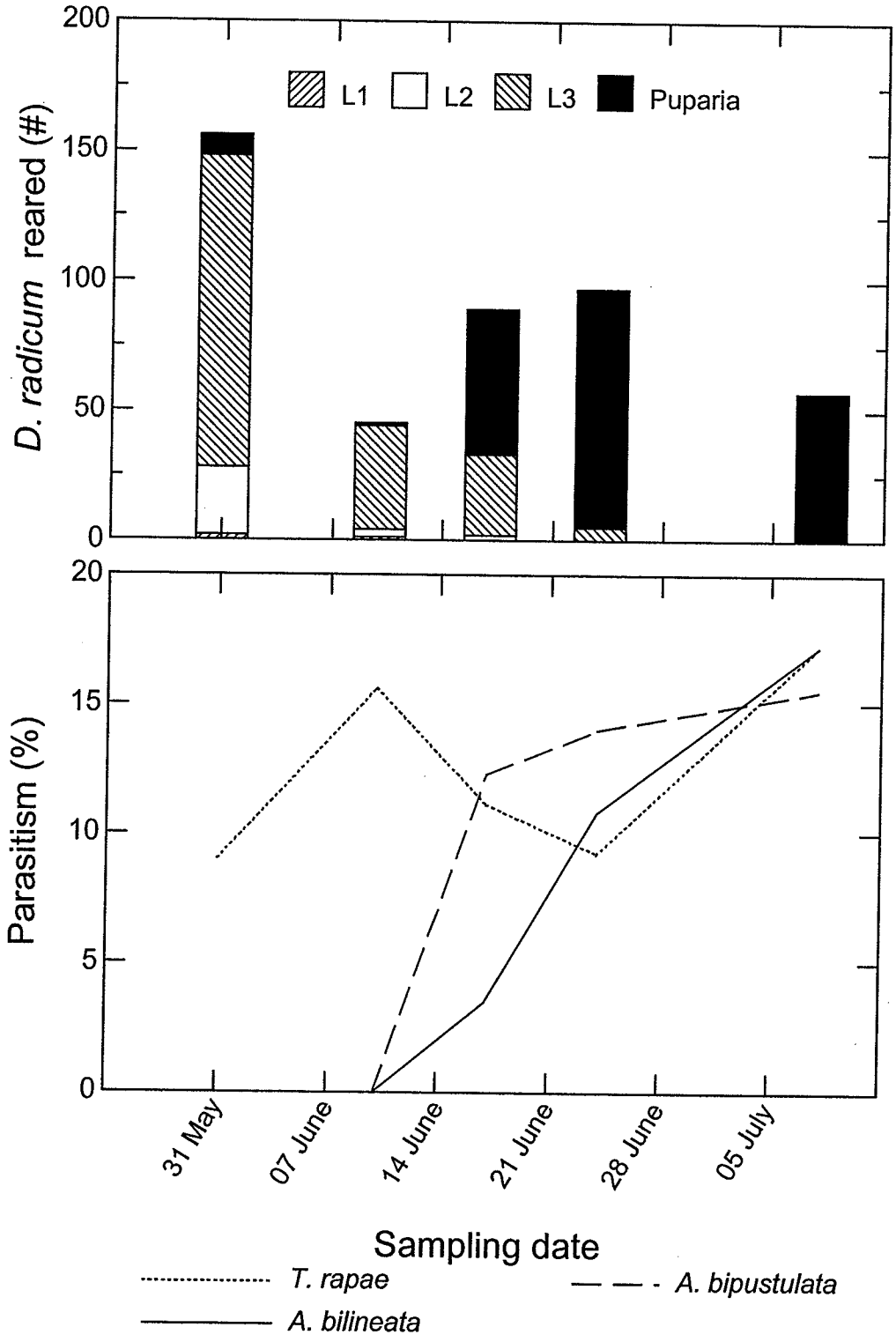

Figure 2.5 Parasitism of *Delia radicum* by its major parasitoid species in summer canola at Schuby in relation to time of sampling in 2002 and number of immatures reared to adulthood.

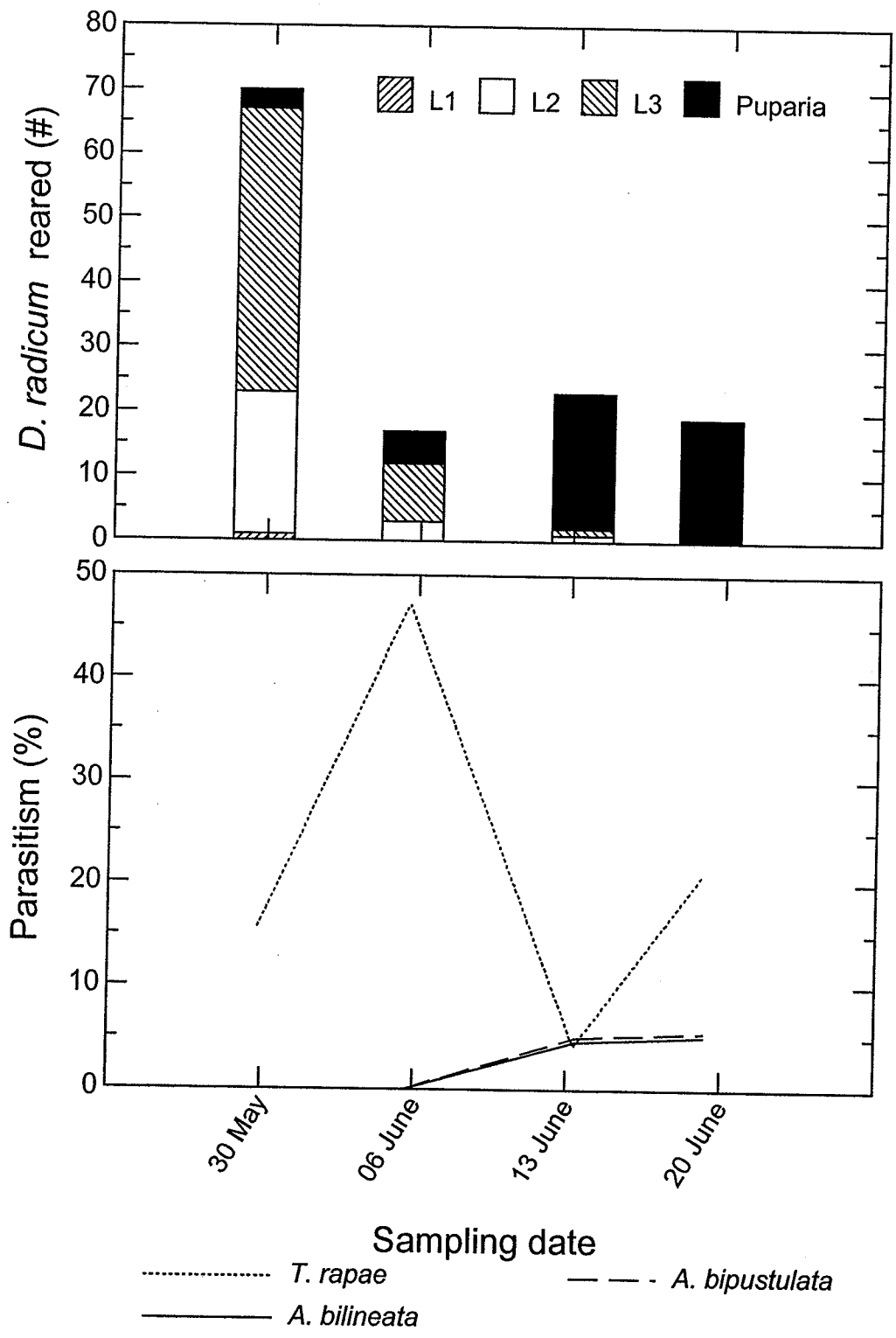

Figure 2.6 Parasitism of *Delia radicum* by its major parasitoid species in summer canola at Rostock in relation to time of sampling in 2002 and number of immatures reared to adulthood.

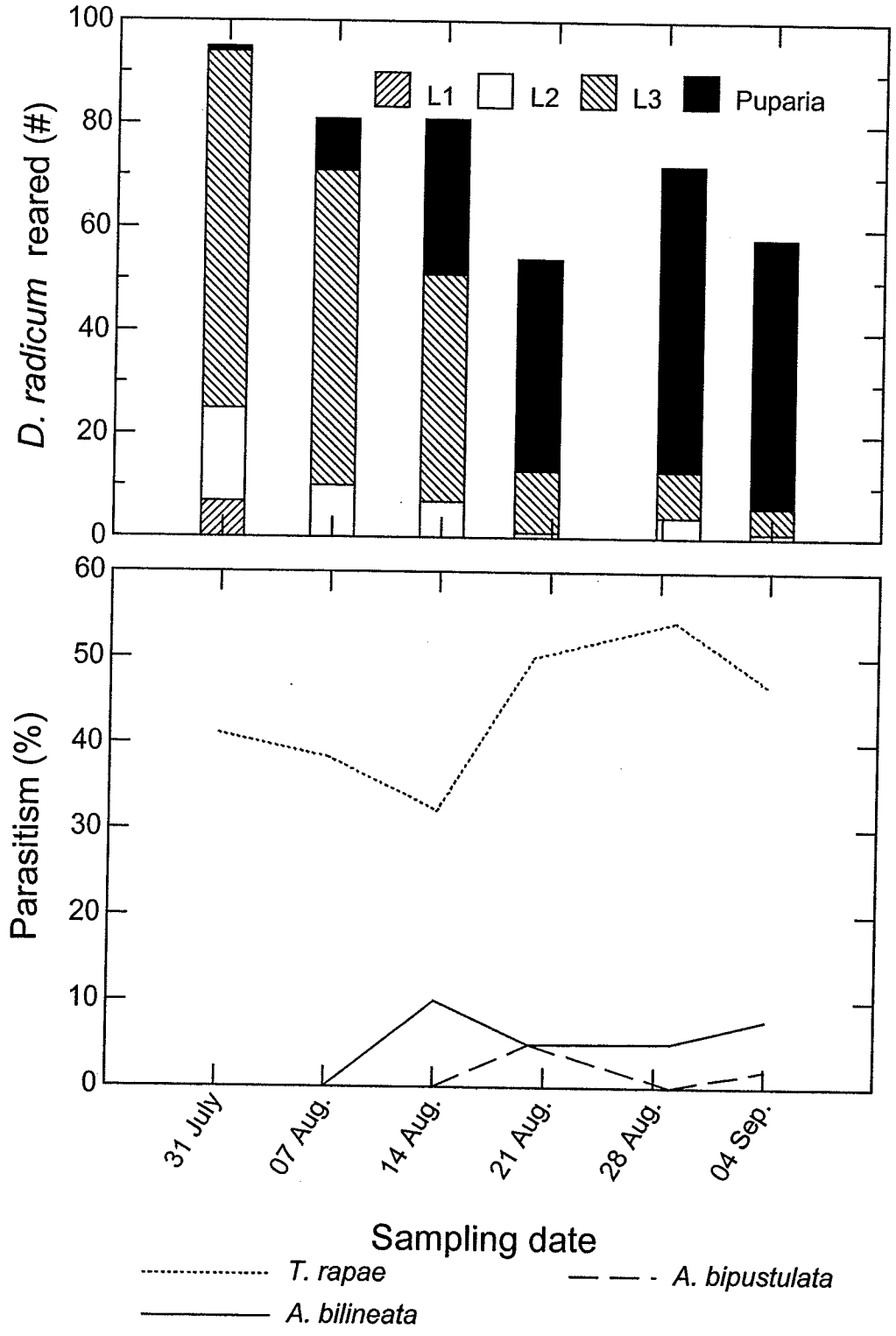

Figure 2.7 Parasitism of *Delia radicum* by its major parasitoid species in late summer canola at Grundhof in relation to time of sampling in 2001 and number of immatures reared to adulthood.

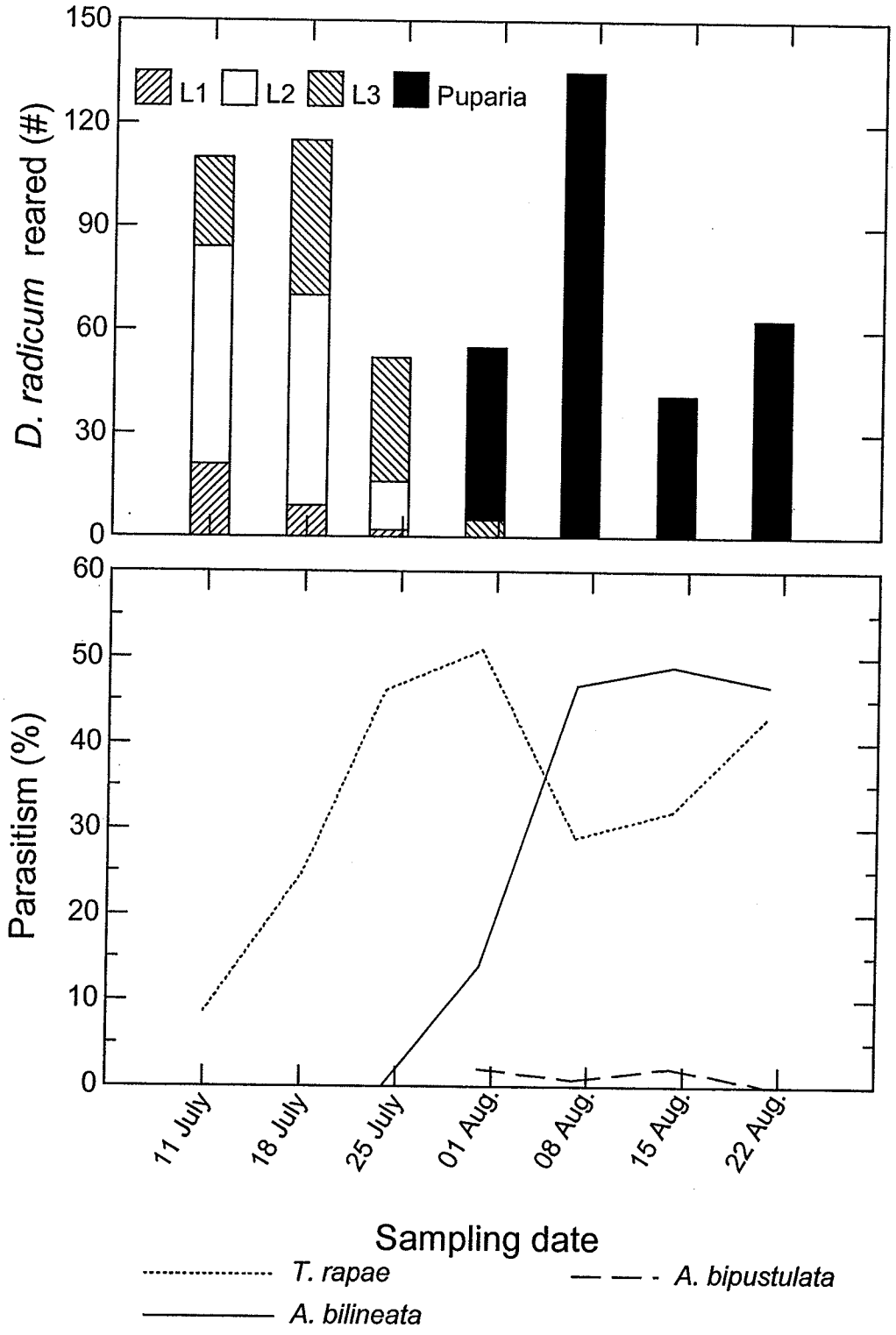

Figure 2.8 Parasitism of *Delia radicum* by its major parasitoid species in late summer canola at Galmiz in relation to time of sampling in 2001 and number of immatures reared to adulthood.

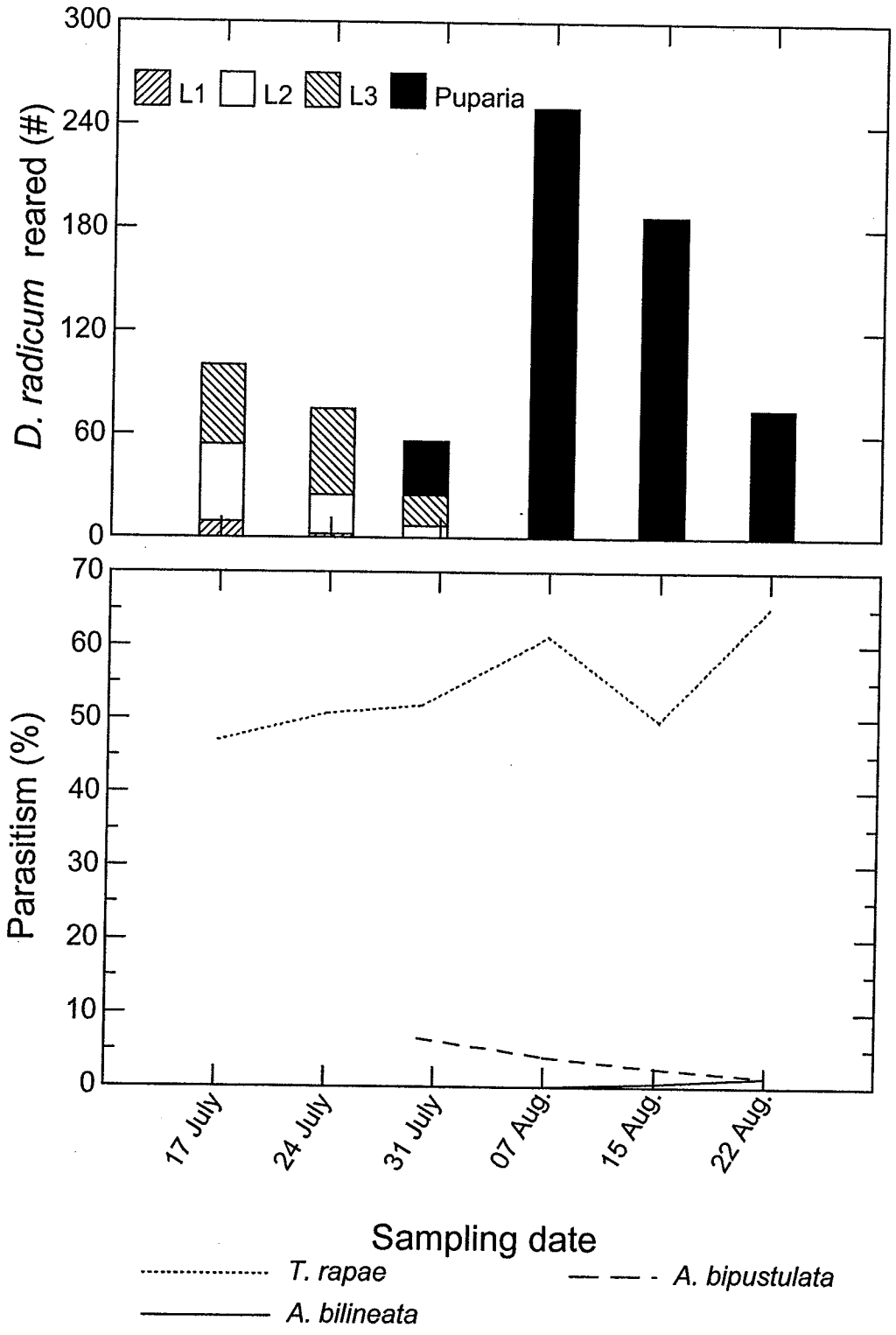

Figure 2.9 Parasitism of *Delia radicum* by its major parasitoid species in late summer canola at Wünnewil in relation to time of sampling in 2001 and number of immatures reared to adulthood.

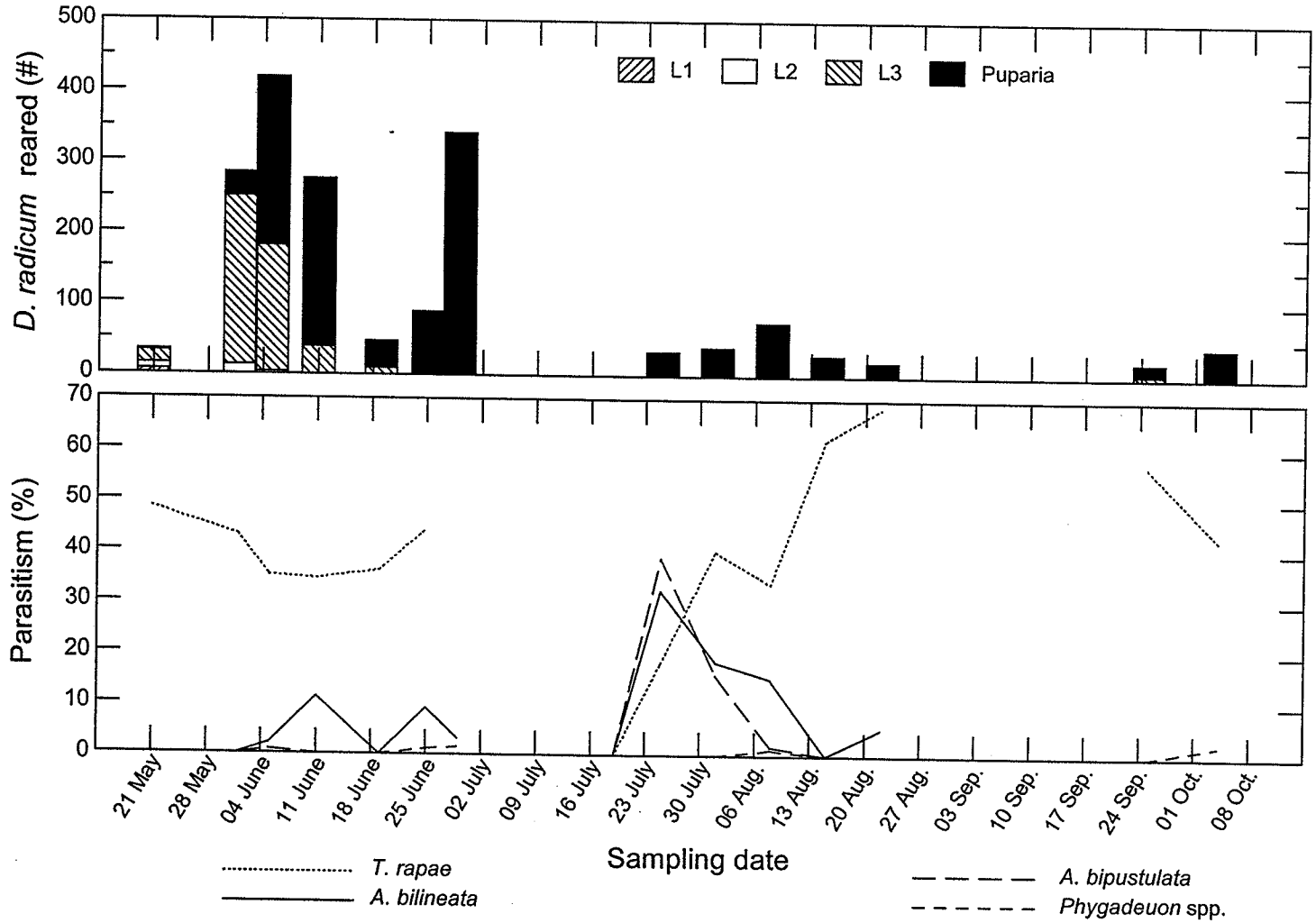

Figure 2.10 Parasitism of *Delia radicum* by its major parasitoid species in brassica vegetables at Fraeschels in relation to time of sampling in 2001 and number of immatures reared to adulthood.

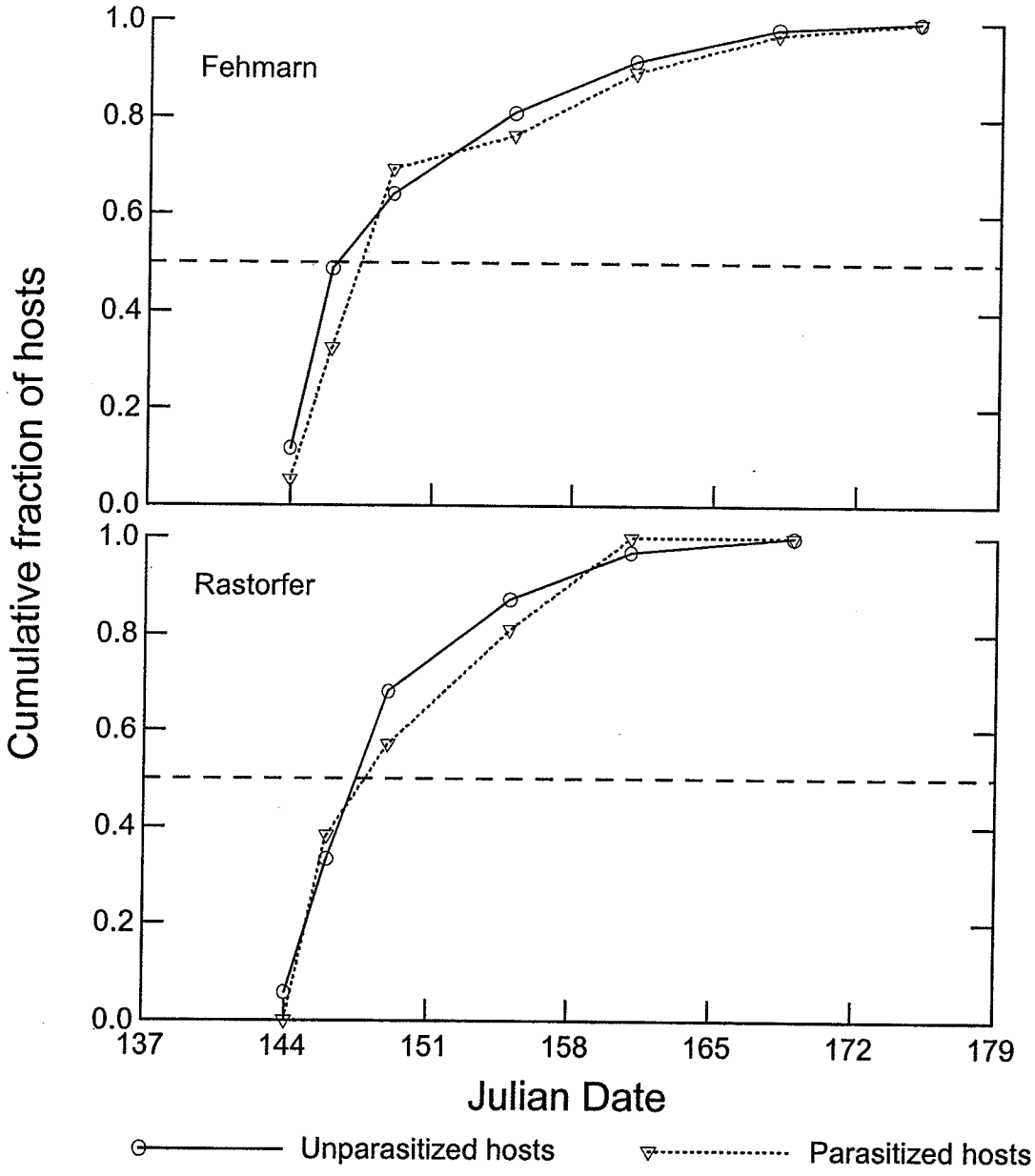

Figure 2.11 Temporal synchronization of *Delia radicum* larvae and *Trybliographa rapae* in canola at Fehmarn and Rastorfer-Passau. Analysis is based on 195 adults of *D. radicum* and 114 adults of *T. rapae* in seven samples in Fehmarn, and 226 adults of *D. radicum* and 21 adults of *T. rapae* in six samples in Rastorfer-Passau.

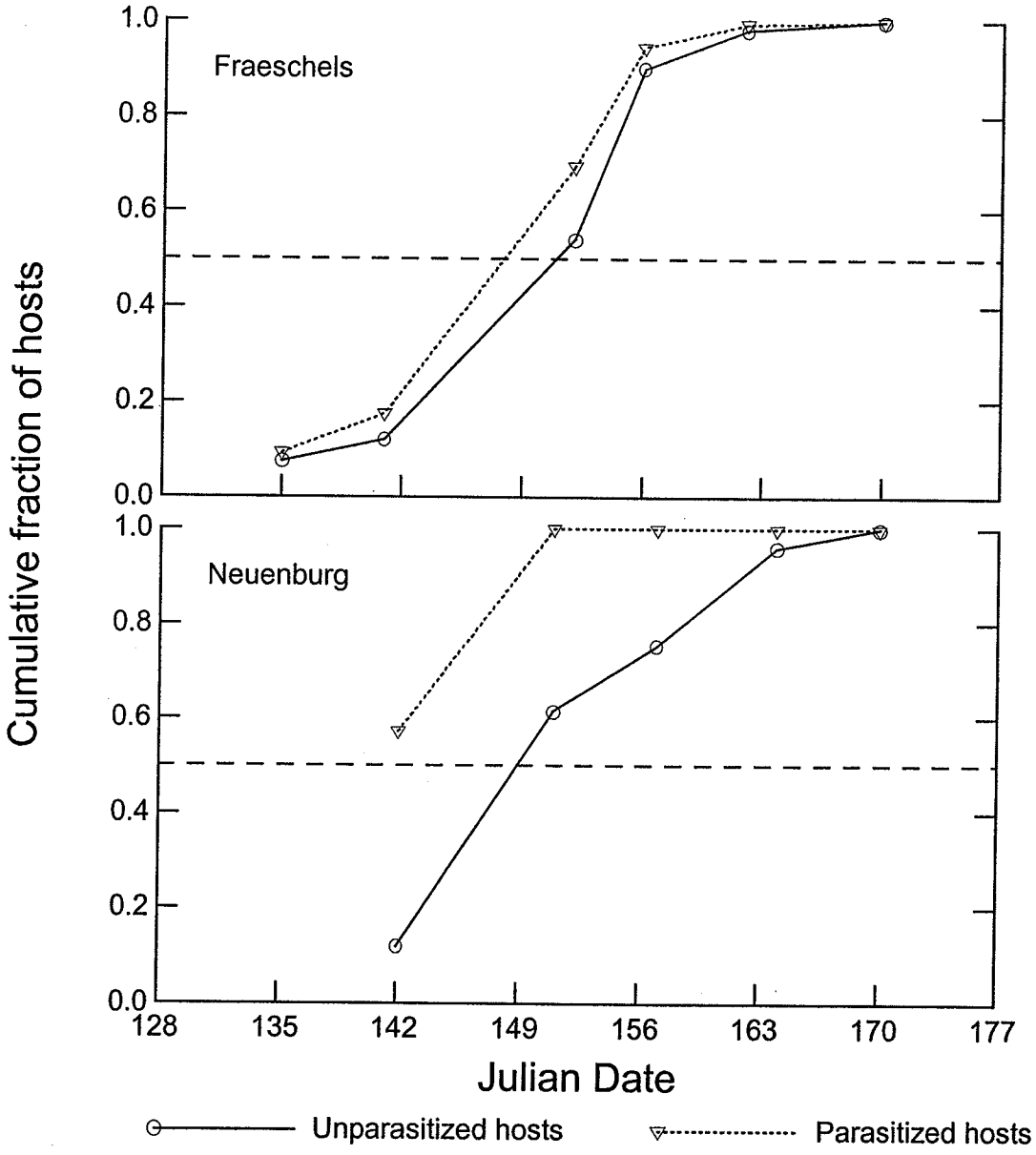

Figure 2.12 Temporal synchronization of *Delia radicum* larvae and *Trybliographa rapae* at Fraeschels and Neuenburg. Analysis is based on 372 adults of *D. radicum* and 183 adults of *T. rapae* in six samples at Fraeschels, and 101 adults of *D. radicum* and 14 adults of *T. rapae* in five samples at Neuenburg.

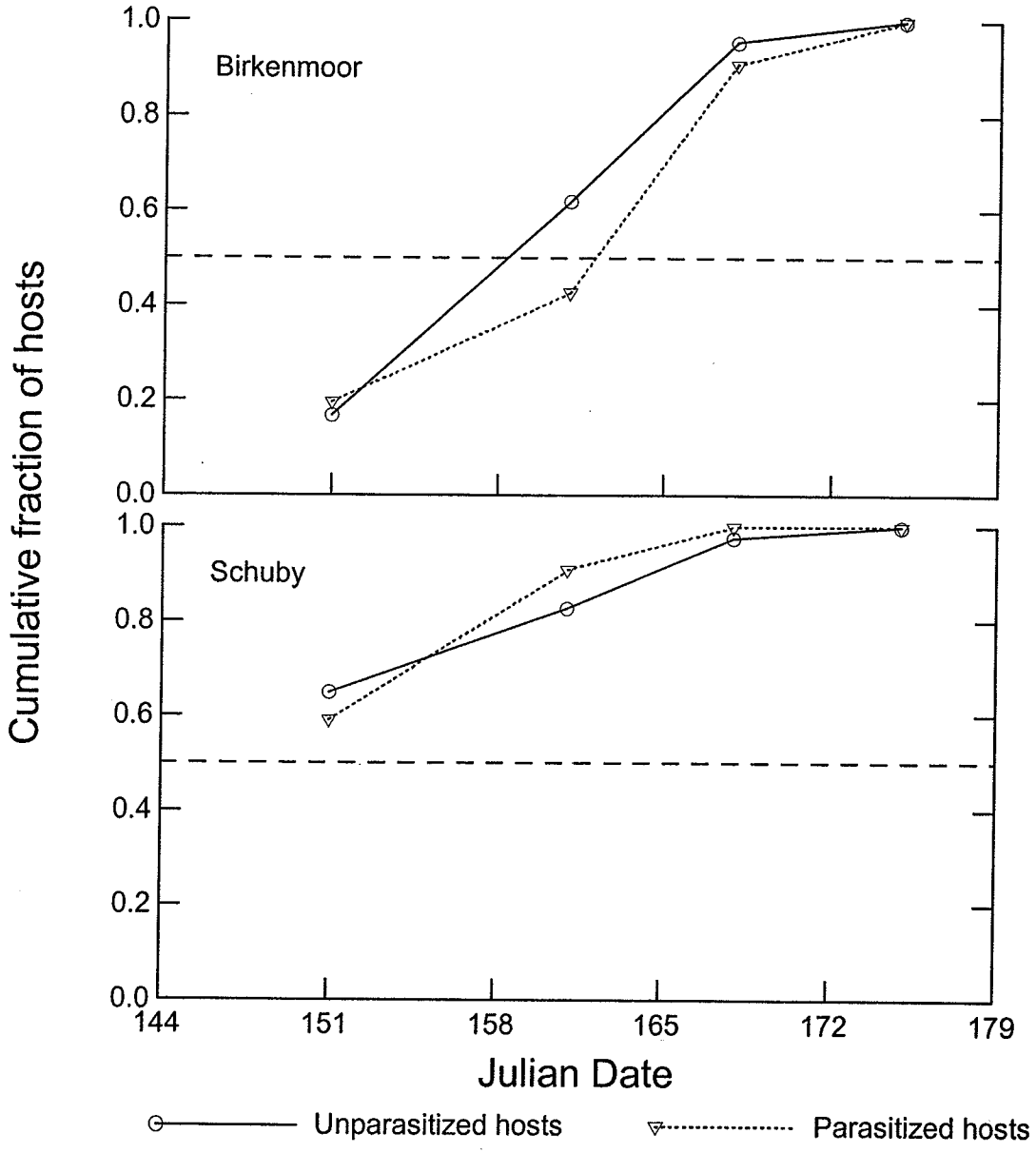

Figure 2.13 Temporal synchronization of *Delia radicum* larvae and *Trybliographa rapae* in canola at Birkenmoor and Schuby. Analysis is based on 1001 adults of *D. radicum* and 143 adults of *T. rapae* in four samples at Birkenmoor, and 208 adults of *D. radicum* and 22 adults of *T. rapae* in four samples at Schuby.

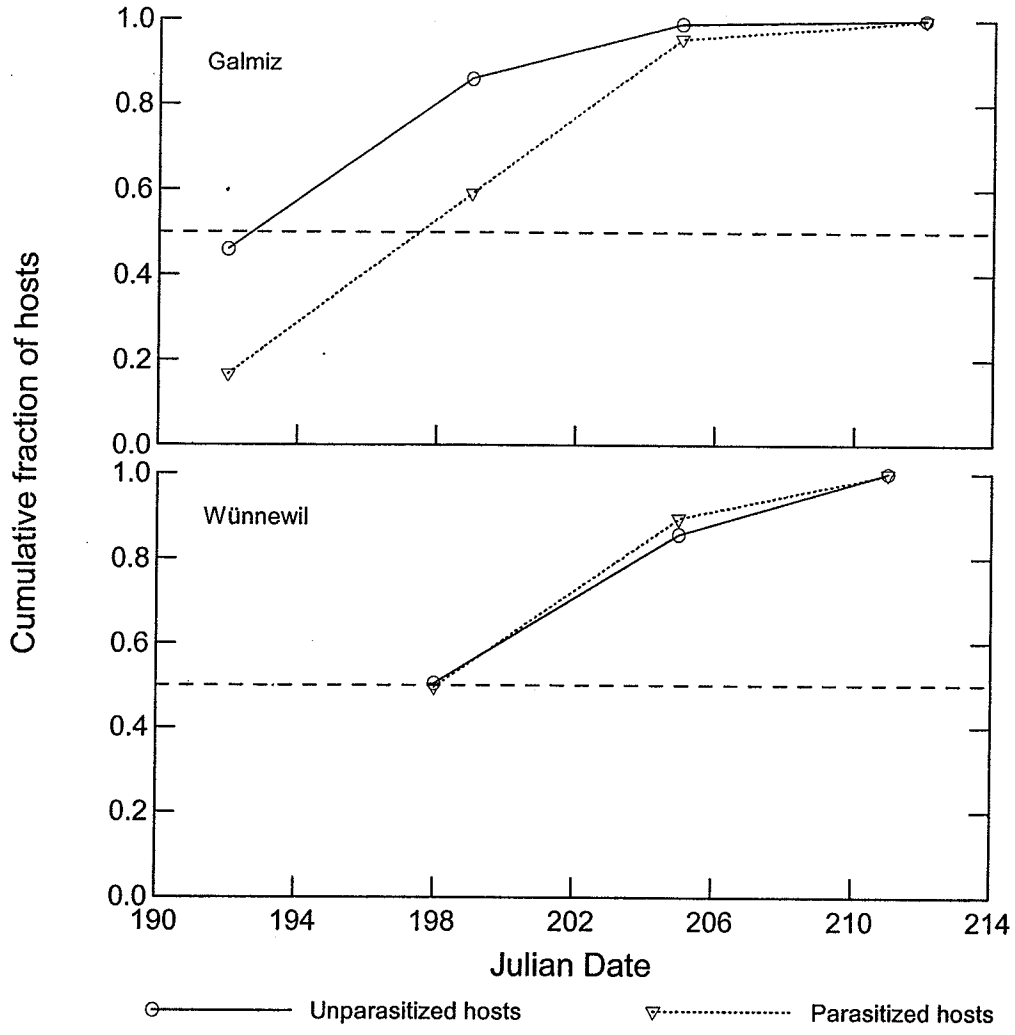

Figure 2.14 Temporal synchronization of *Delia radicum* larvae and *Trybliographa rapae* in canola at Galmiz and Wünnewil. Analysis is based on 215 adults of *D. radicum* and 66 adults of *T. rapae* in four samples at Galmiz, and 105 adults of *D. radicum* and 95 adults of *T. rapae* in three samples at Wünnewil.

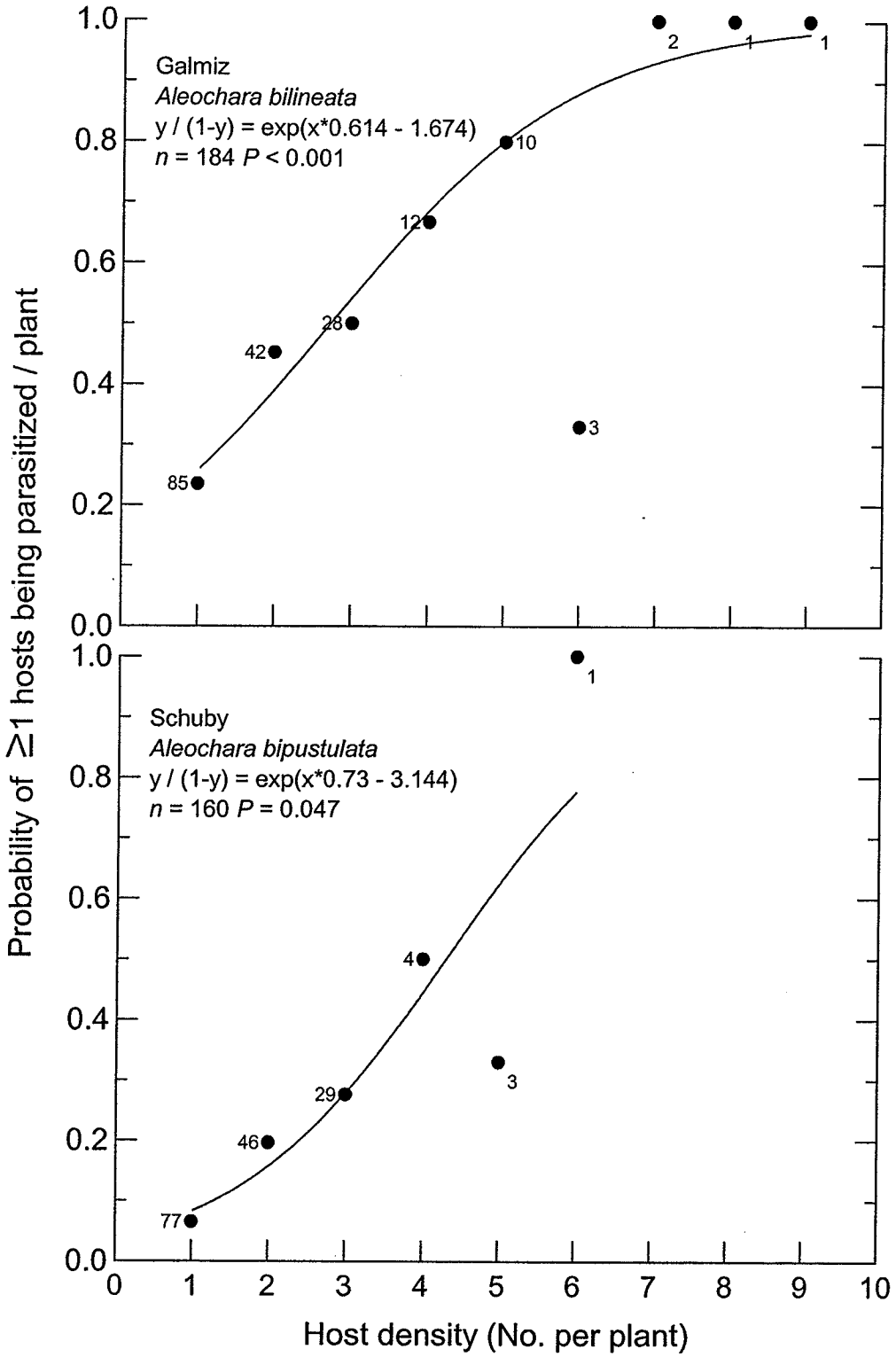

Figure 2.15 The probability of at least one *Delia radicum* on a plant being parasitized by *Aleochara* species in relation to density of puparia associated with roots. Number of plants studied at each host density is given beside the symbols.

CHAPTER 3 SECTION 3

Population biology of *Delia radicum* in European canola

Introduction

Delia radicum (L.) infests a wide range of crucifers which includes brassica vegetables, brassica field crops e.g. canola, and brassica weeds (Finch and Ackley, 1977; Griffiths, 1991). *Delia radicum* is an economic pest of brassica vegetables (Miles, 1953, 1954; Finch, 1987, 1989; Finch and Collier, 2000b), and its biology including adult emergence, oviposition, feeding, diapause and phenology has been well studied in brassica vegetables (Miles, 1953, 1954; Finch, 1971; Finch and Collier, 1983; Finch *et al.*, 1986; Finch and Skinner, 1975, 1976, 1980; Collier and Finch, 1983a, 1983b ; Collier *et al.*, 1988, 1989; Roessingh and Stadler, 1990; Nottingham, 1988; Kostal, 1991, 1993a, 1993b; Kostal and Finch, 1994a, 1994b, 1996). Management of *D. radicum* in brassica vegetables relies on cultural, biological and chemical control (Finch, 1987, 1989; Finch and Collier, 2000b). Canola has been an important crop in Europe since the 1970s (Bromand, 1990), and the acreage of canola in the United Kingdom alone increased ten fold from 1974–1987 (Finch and Jones, 1987). *Delia radicum* is a problem in canola on the Canadian Prairies (Griffiths, 1986a; Dosdall *et al.*, 1996a, 1996b; Soroka *et al.*, 2002) and in Europe (Bromand, 1990; Alford *et al.*, 2003). The biology of *D. radicum* in Canadian canola is relatively well known (Griffiths, 1986a), but that in European canola is poorly known. Therefore, the objective of this study was to study the population biology, and infestation levels of *D. radicum* in canola in Europe.

Methods

This study was carried out as a part of a study to assess the parasitoid community of *D. radicum* in European canola (Chapter 3, Section 2). The sampling protocol and sampling sites (Table 2.1) for this study were described in Chapter 3, Section 2. Canola

plants were sampled in different geographical locations and in different canola crops, and reared until adults emerged in the laboratory as described in Chapter 3 Section 2. In commercial canola fields, sampling was limited to the borders of the fields.

Data analysis

Delia radicum infestation levels were assessed based on a single sample per site. The sample that had the highest percentage of third-instar larvae was chosen for the assessment. The frequency distributions of plants with different levels of infestation were compared using likelihood ratio chi-square analysis of contingency tables. The relationship between level of infestation and diameter of root at soil surface was also examined in those samples. The number of larvae per plant was ($\log_{10}(x)$) transformed to minimize heteroscedasticity and the relationship with root diameter was examined using linear regression followed by analysis of covariance.

The diapause of *D. radicum* was examined at sites where sufficient numbers entered diapause and emerged the following spring. *Delia radicum* that did not emerge by November, and emerged in the spring, 2002 or developed to adulthood but failed to emerge were considered to be in diapause. The relationship between probability of diapause and the time of year at different sites was compared using logistic regression.

Results

The proportion of plants infested by *D. radicum* in a field differed among crops. In canola, the percentage of plants infested by *D. radicum* ranged from 18 to 86%, depending on the crop type, and was 100% in brassica vegetables (Table 3.1). Type of crop significantly affected the percentage of infested plants (Likelihood Ratio (L.R.) $\chi^2 = 61.9$, df = 4, $P < 0.001$), but there was no significant difference in the percentage of

infested plants between late summer canola and summer canola (L.R.$\chi^2 = 0.7$, df = 1, $P = 0.418$) or between volunteer winter canola and winter canola (L.R.$\chi^2 = 1.5$, df = 1, $P = 0.225$). It appears that field size did not influence the percentage of infested plants in a field. The field at Schuby was an experimental field with a moderate level of infestation, and the proportion of infested plants at Schuby was not different from the proportions of infested plants at Dietingen and Dunningen (L.R.$\chi^2 = 2.5$, df = 2, $P = 0.28$) which were commercial summer canola fields (Table 3.1).

Plants infested by *D. radicum* had variable numbers of immatures (larvae and puparia) per root (Fig. 3.1). The frequency distribution (pooled into six classes) of numbers of immatures per infested root was significantly different among crops and sampling locations (L.R.$\chi^2 = 295.7$, df = 55, $P < 0.001$). All the crops were grouped into four frequency distributions that were significantly different from each other (L.R.$\chi^2 = 242.6$, df = 15, $P < 0.001$) (Fig. 3.1). Volunteer winter canola and winter canola formed the first group and there was no significant location effect within the group (L.R.$\chi^2 = 17.3$, df = 10, $P = 0.067$). The second group consisted of summer canola and late summer canola except for the Birkenmoor site, and there was no significant location effect within the group (L.R.$\chi^2 = 35.8$, df = 30, $P = 0.214$). Summer canola at Birkenmoor and brassica vegetables at Fraeschels were the other two frequency distributions (Fig. 3.1).

The mean number of immature *D. radicum* per root was significantly different among crops ($F_{(4,1029)} = 62.17$, $P < 0.001$), and brassica vegetables had the highest numbers per plant (Table 3.1). Among canola crops, the level of infestation did not differ

significantly ($F_{(3,1000)} = 3.33$, $P = 0.019$) when crops were compared using experimental wise error ($\alpha = 0.013$) in Dunn-Šidak method.

Delia radicum larval density was positively related to the diameter of the root of host plants. There was a significant linear regression between root diameter at soil level and (Log_{10} (x)) number of larvae per root ($F_{(1,462)} = 170.21$, $P < 0.001$). The gradient ($F_{(4,454)} = 0.74$, $P = 0.566$) and intercept ($F_{(4,454)} = 0.68$, $P = 0.60$) of the relationship did not differ significantly among crops. However, the relationship differed significantly among locations. The intercept ($F_{(11, 440)} = 2.40$, $P = 0.006$) was significantly different among locations but not the gradient 0.53±0.04 ($F_{(11, 440)} = 1.36$, $P = 0.197$) (Fig. 3.2).

Phenology of *D. radicum* in different geographical locations was compared in relation to the occurrence of immatures. Third-instar larvae were on roots at the end of May in northern and southern Germany in canola and in Seeland, Switzerland in brassica vegetables (Fig. 3.3–3.12). The date on which there were equal percentages of third-instar larvae and puparia is a useful benchmark. This date occurred earlier in brassica vegetables (5 June) (Fig. 3.12) than in volunteer winter canola (except Rastorfer-Passau), winter canola and summer canola (except Rostock). Generally equality of third-instar and puparia occurred in the second and third week of June in volunteer winter canola, winter canola and summer canola in northern and southern Germany. Late summer canola, which was probably infested by the second generation of *D. radicum,* was sampled in a similar time period in northern Germany and in Switzerland. A similar proportion of third-instar larvae and puparia occurred in mid August in Grundhof (Fig. 3.9), which was late compared with Swiss late summer canola at Galmiz (Fig. 3.10) and Wünnewil (Fig. 3.11).

A large proportion of immature *D. radicum* collected in May and June in all locations emerged in summer 2001, and only 2.8% entered diapause (n = 1671). The proportion of *D. radicum* that entered diapause increased considerably beginning with collections in July and more than 80% of puparia was in diapause by the end of August in canola fields at Galmiz and Grundhof (Fig. 3.13). The logistic regressions of proportions in diapause against time differed between these two locations (L.R.χ^2 = 32.3, df = 1, $P < 0.001$); however, location did not significantly interact with time (L.R.χ^2 = 0.1, df = 1, P = 0.81).

Discussion

Oviposition behaviour of *D. radicum* is a general phenomenon, and influenced by weather (Miles, 1954), and crop (Pond, 1965). Oviposition behaviour includes habitat selection, host plant location, host plant finding, and oviposition (Schoonhoven *et al.*, 1998). Adult females use chemical cues to locate their host plant habitat, and *D. radicum* females respond to allyl isothiocyanate, a hydrolysed product of glucosinolates present in brassica plants (Nair *et al.*, 1973; Nair and McEwen, 1976; Tuttle *et al.*, 1988). *Delia radicum* also respond to visual cues including colour and shapes in host selection (Kostal, 1991; Vernon and Broatch, 1996). Females respond to the physiological age of the plant, plant characteristics, plant density and plant diversity (Ellis *et al.*, 1979; McDonald and Sears, 1992; Finch and Skinner, 1976; McKinlay *et al.*, 1996). Oviposition behaviour of *D. radicum* dictates the pattern of infestation such as the proportion of plants infested and the number of immatures per plant.

Generally, the number of *D. radicum* eggs in a field is a function of the number of gravid females present. If the number of available plants for oviposition is limited, then

flies may oviposit on all the plants. In this study, all the sampled vegetable brassica plants were infested with *D. radicum* larva. If the number of available plants for oviposition is less limited such as in canola, flies may use only a proportion of the plants available to them in the field as was observed in this study. In addition, the oviposition preference of *D. radicum* females varies among subspecies of brassica vegetables (Mukerji, 1969), and difference in oviposition preference may be related to the proportion of infested plants in canola and brassica vegetables. The population level of *D. radicum* flies varies with geographic location; hence proportion of infested plants of a crop also varies with location. Furthermore, within a sub species *D. radicum* favours some plant cultivars more than others, and generally a higher proportion of plants is infested in favoured cultivars than other cultivars (Pond *et al.*, 1962; Pond, 1965).

Delia radicum lay eggs as small batches (2–5 eggs) on soil close to the brassica root collar (McDonald and Sears, 1991), and average fecundity is about 78 eggs per female (Nair and McEwen, 1976). More eggs are found on soil close to bigger plants and egg number correlates with the basal diameter of plant (Dosdall *et al.*, 1996a). In this study, a linear relationship between root diameter and $\log_{10}$ number of larvae per plant was found. There is a linear relationship between number of eggs laid and root diameter, and the gradient has 1.47 eggs per mm of root diameter in canola, *B. napus* (Dosdall *et al.*, 1996a). The difference in number of eggs and larvae at a particular root size may be related to egg mortality through predation and infertility of eggs (Mukerji, 1971). Differences of intercepts of the relationships in my study probably relate to size of population of egg laying females in the field.

The frequency distribution of numbers of larvae per infested root was similar for phenologically and morphologically similar crops such as winter canola and volunteer winter canola (Fig. 3.1). In summer canola and late summer canola, except at Birkenmoor, had 41% of plants with one or two larvae per root. The variation of larval numbers per plant may relate to variation of root size in the field. Furthermore, the level of infestation is a product of size of population of egg laying females, synchronization of susceptible stage of crop and peak fly activity (Pond, 1965). Susceptible stage of brassica vegetables is the 5–6 leaf stage (Brunel and Fournet, 1996), whereas the susceptible stage in canola is the bolting stage (Griffiths, 1986a).

In this study, infestation level of *D. radicum* is generally low in canola compared with the infestation level in brassica vegetables. High infestation in brassica vegetables (Miles, 1952a, 1953) and low infestation in canola by *D. radicum* (Finch and Jones, 1987) have been found in previous studies. It appears that increased availability of brassica host plants did not affect on level of infestation over the years.

Adult *D. radicum* generally emerge in April and May (Finch *et al.*, 1986), depending on thermal accumulations (Coaker and Wright, 1963), but the time varies with geographical location (Finch and Collier, 1983; Finch *et al.*, 1986). Flies usually emerge with a major early peak followed by two minor peaks consisting of intermediate and late emerging flies (Finch and Collier, 1983). In this study, oviposition must have occurred in mid May or earlier to have third-instar larvae had late in May in both northern and southern Germany.

Diapause in *D. radicum* is induced by temperature and photoperiod (Hughes, 1960; Read, 1965a; 1968, 1969; Soni, 1976; Collier and Finch, 1983a, 1983b; Collier *et*

al., 1988). In addition, light intensity affects diapause induction (Read, 1969). The number of generations that *D. radicum* completes depends on geographical location (Griffiths, 1991), host plant availability and weather (Leather *et al.*, 1993). In this study, *D. radicum* went into diapause earlier at Galmiz than those at Grundhof. It had been expected that *D. radicum* at Grundhof would enter diapause earlier than that of at Galmiz due to its more northerly latitude (Collier *et al.*, 1988). This result suggests that there may be other factors involved in induction of diapause. However, further assessment of these populations with larger samples is needed for confirmation of the results.

Table 3.1 Level of infestation by *Delia radicum* in canola and brassica vegetable plants in 12 sampling sites in Germany and Switzerland.

Crop and sampling site	% of plants infested	Mean ± SE number of immatures per plant	Number of Plants sampled	Sampling date
Volunteer winter canola				
Fehmarn	30.9	1.7 ± 0.4	84	26 May, 01
Rastorfer-Passau	32.7	1.0 ± 0.2	98	26 May, 01
Winter canola				
Neuenburg	18.0	1.7 ± 0.5	30	31 May, 01
Summer canola				
Birkenmoor[1]	86.0	6.1 ± 0.6	100	17 June, 02
Schuby[1]	48.0	0.8 ± 0.1	100	10 June, 02
Rostock[1]	18.0	0.3 ± 0.1	100	6 June, 02
Dietingen	45.0	0.9 ± 0.1	100	11 June, 02
Dunningen	34.0	0.6 ± 0.1	92	11 June, 02
Late summer canola				
Grundhof[1]	45.0	1.0 ± 0.2	100	7 Aug., 01
Galmiz[1]	36.0	0.7 ± 0.2	100	24 July, 01
Wünnewil[1]	51.0	1.2 ± 0.2	100	24 July, 01
Brassica vegetables				
Fraeschels	100.0	14.7 ± 1.4	30	1 June, 01

[1]Field size was less than 1 ha.

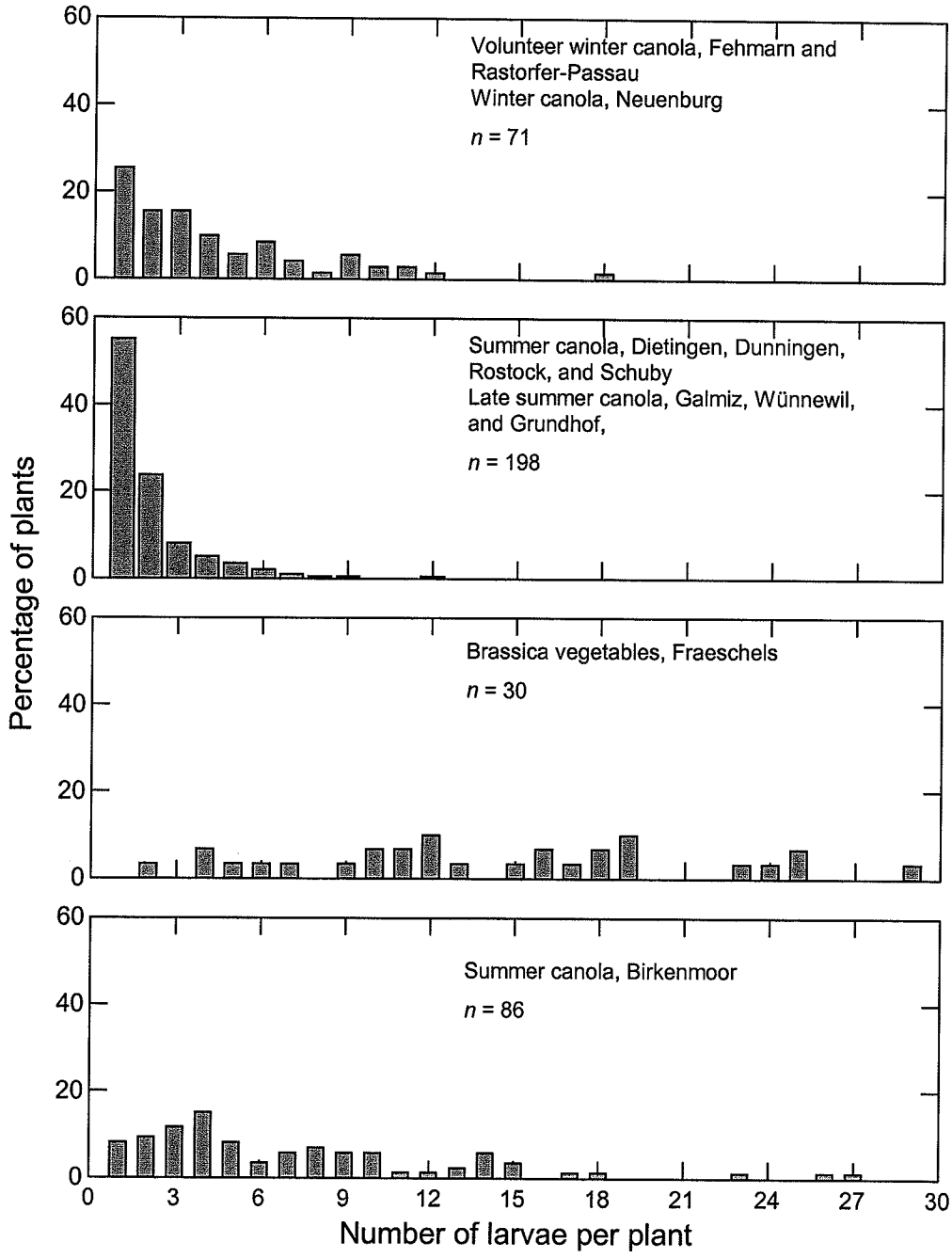

Figure 3.1 Frequency distribution of *Delia radicum* numbers on infested canola and brassica vegetable plants.

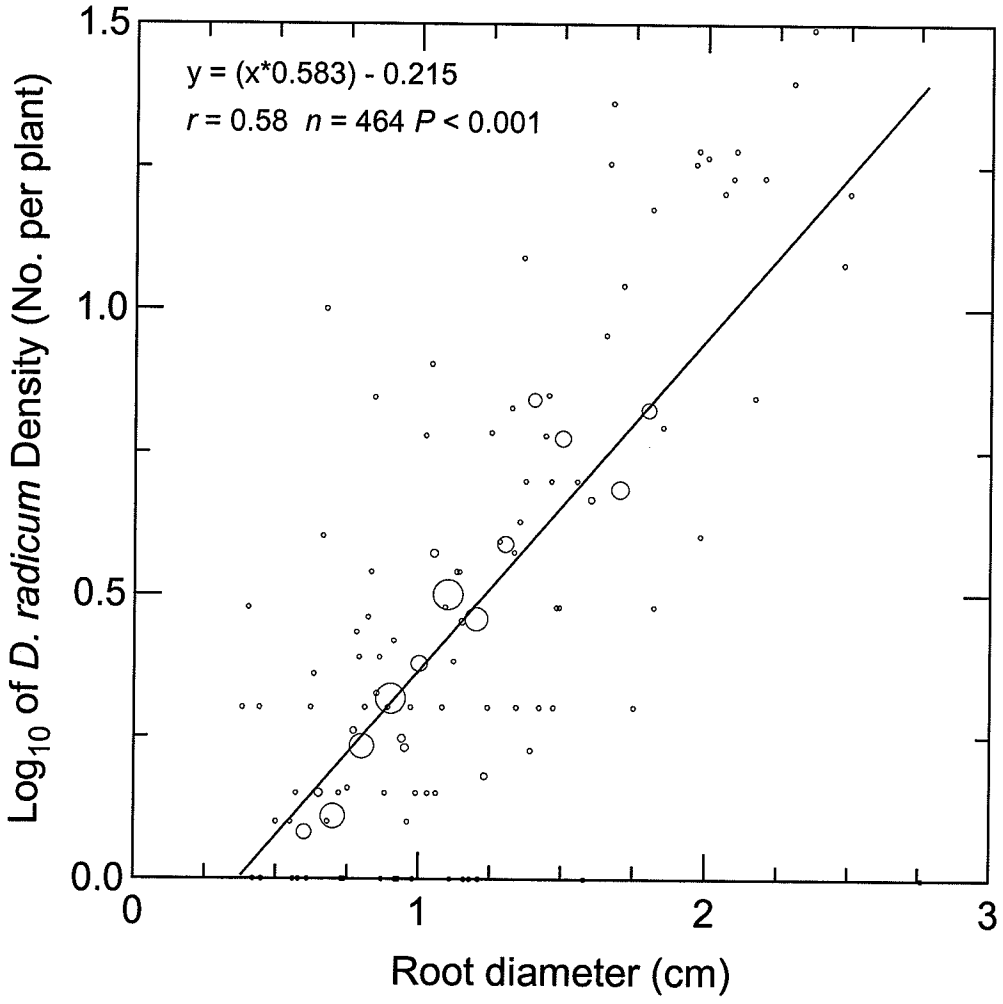

Figure 3.2 Relation between number of *Delia radicum* on infested plants and root diameter at soil level. Number of plants studied at each root size varied from 1 to 22. Symbol size represents the number of plants studied at each root size.

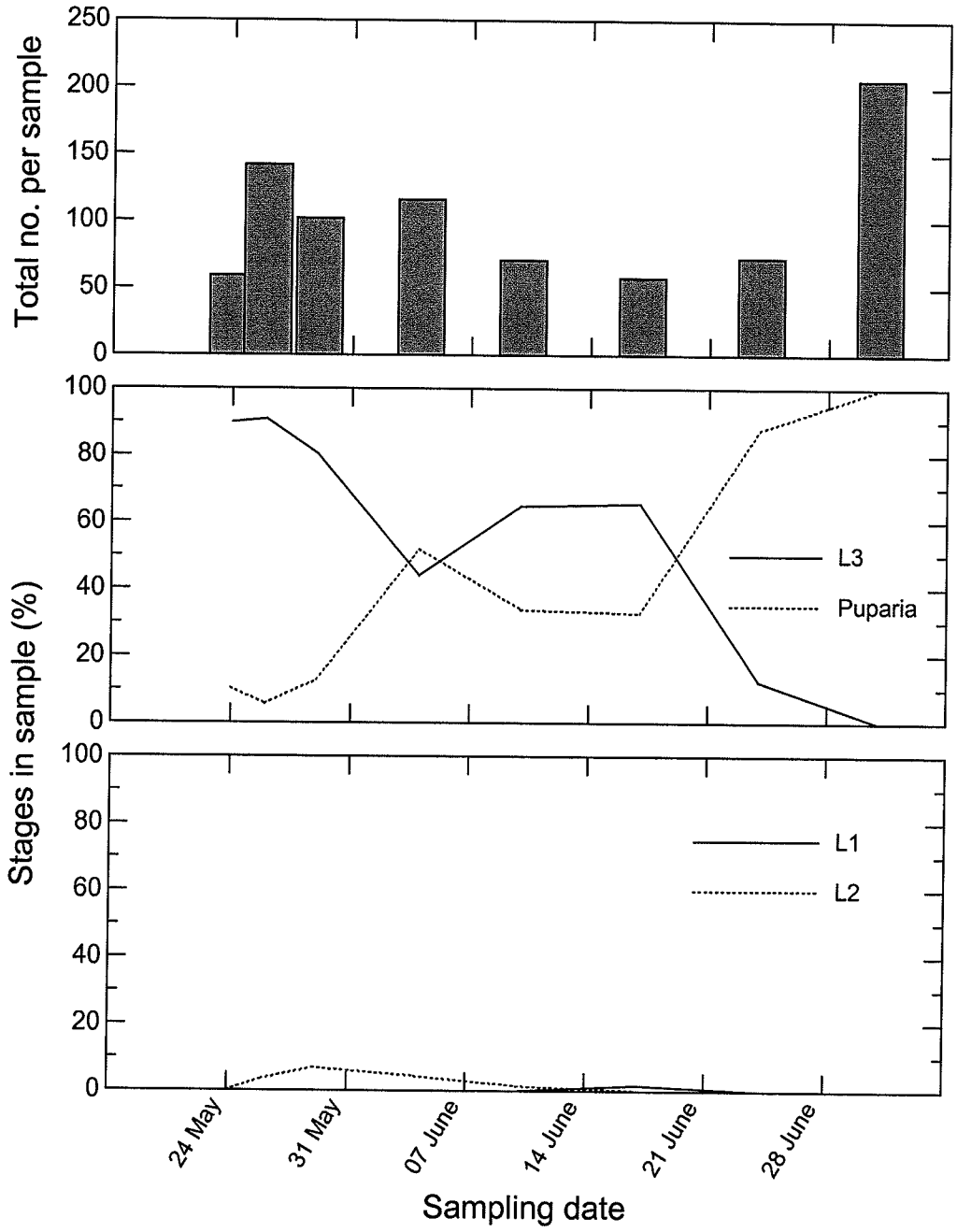

Figure 3.3 Number and stage composition of *Delia radicum* immatures in samples collected in volunteer winter canola at Fehmarn in 2001.

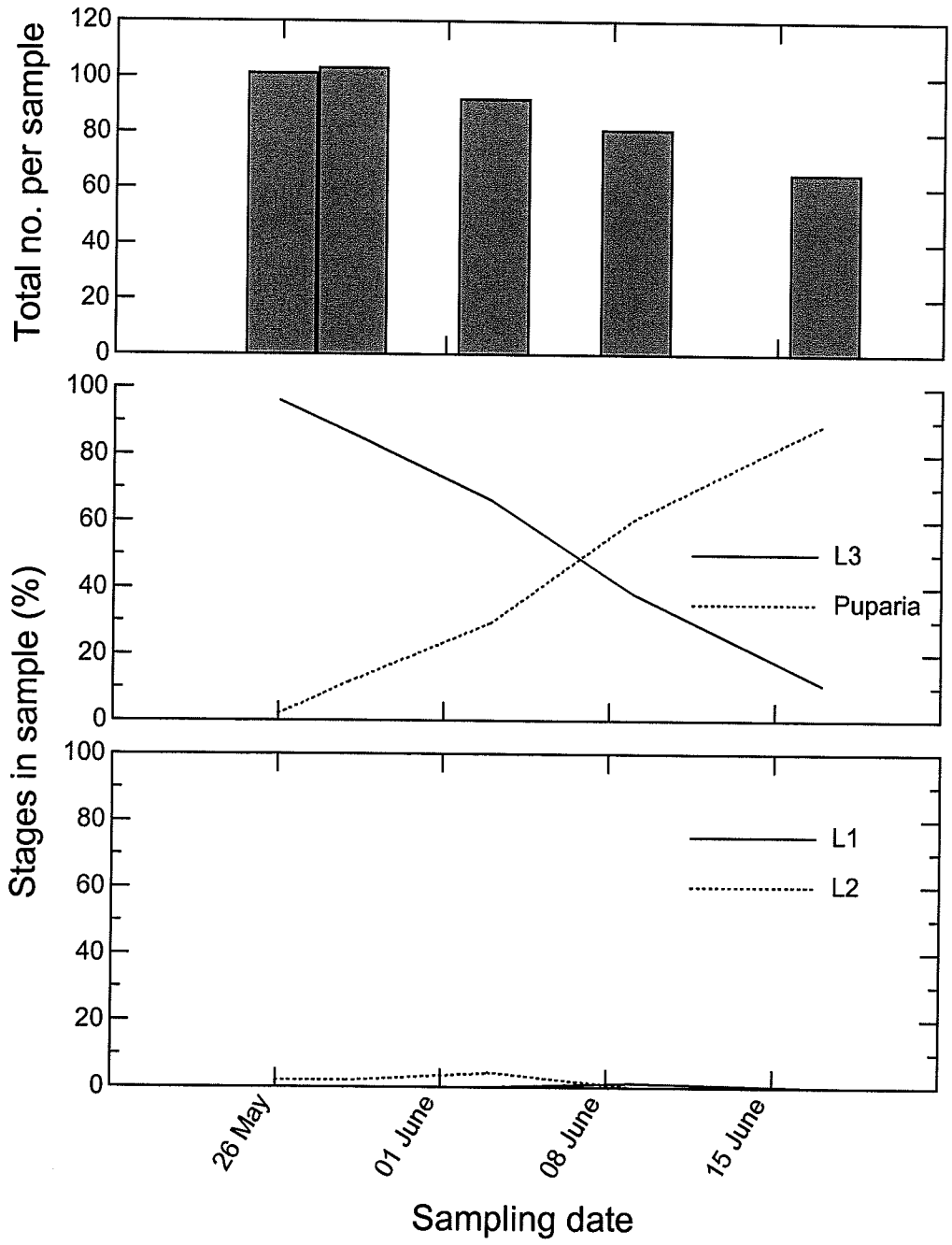

Figure 3.4 Number and stage composition of *Delia radicum* immatures in samples collected in volunteer winter canola at Rastorfer-Passau in 2001.

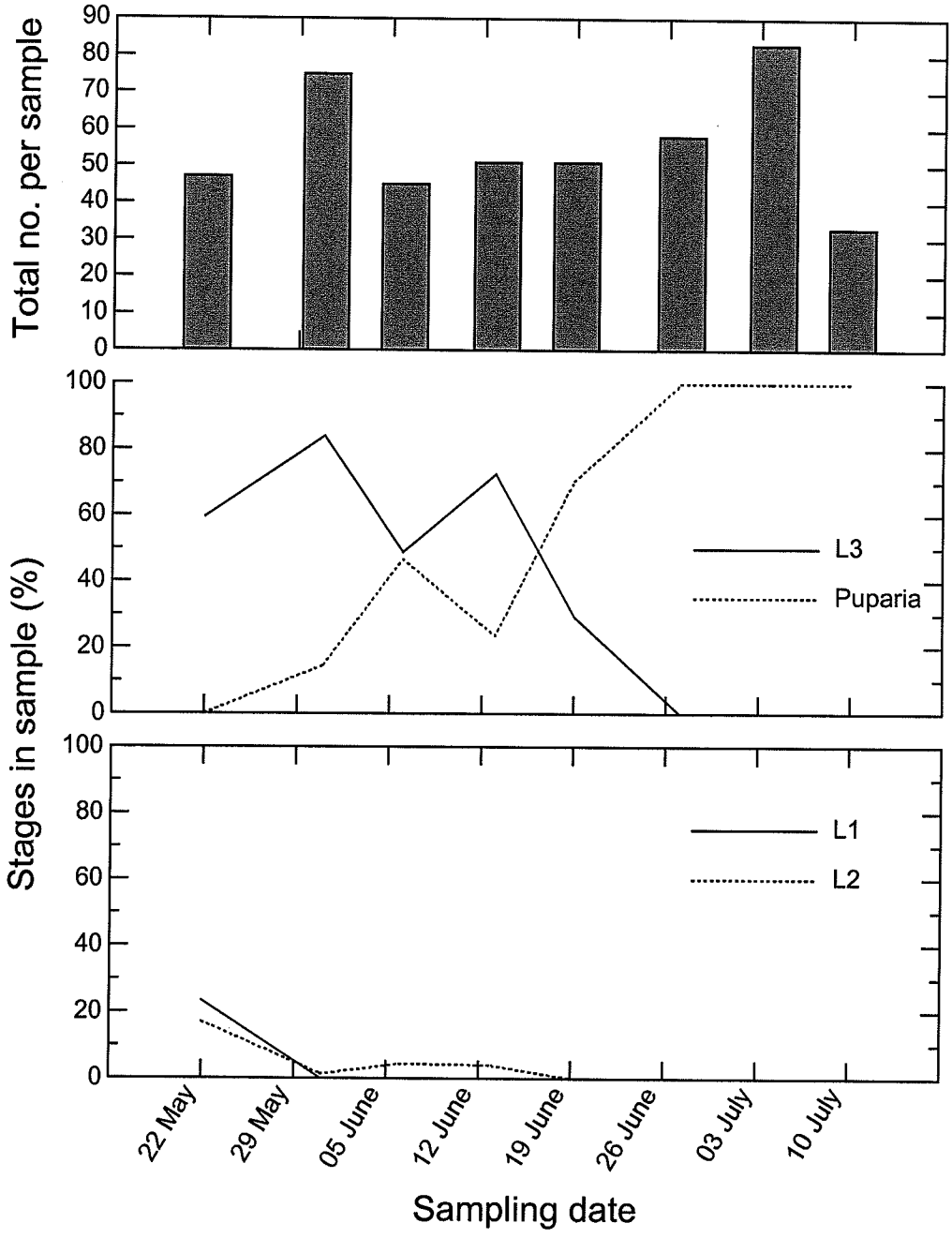

Figure 3.5 Number and stage composition of *Delia radicum* immatures in samples collected in winter canola at Neuenburg in 2001.

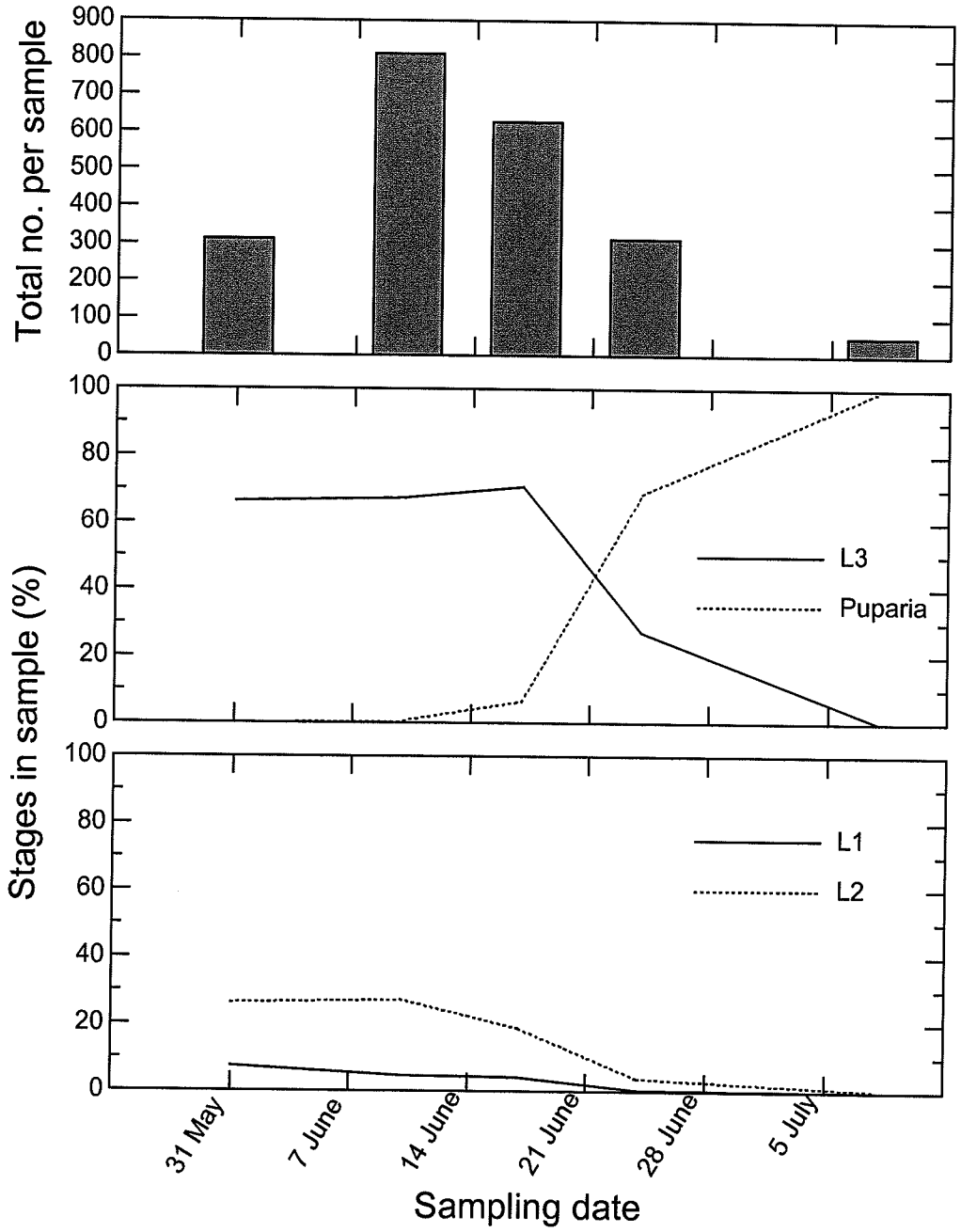

Figure 3.6 Number and stage composition of *Delia radicum* immatures in samples collected in summer canola at Birkenmoor in 2002.

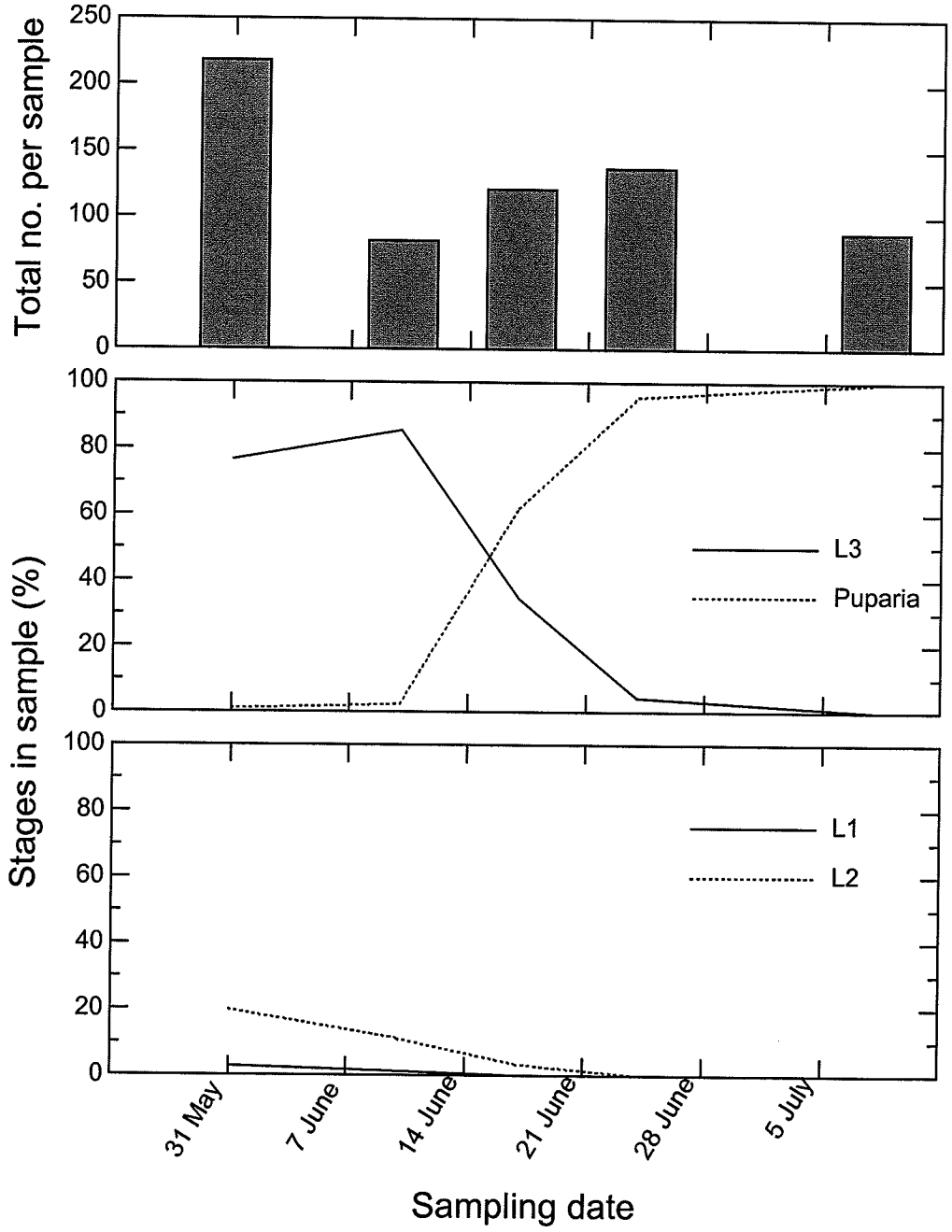

Figure 3.7 Number and stage composition of *Delia radicum* immatures in samples collected in summer canola at Schuby in 2002.

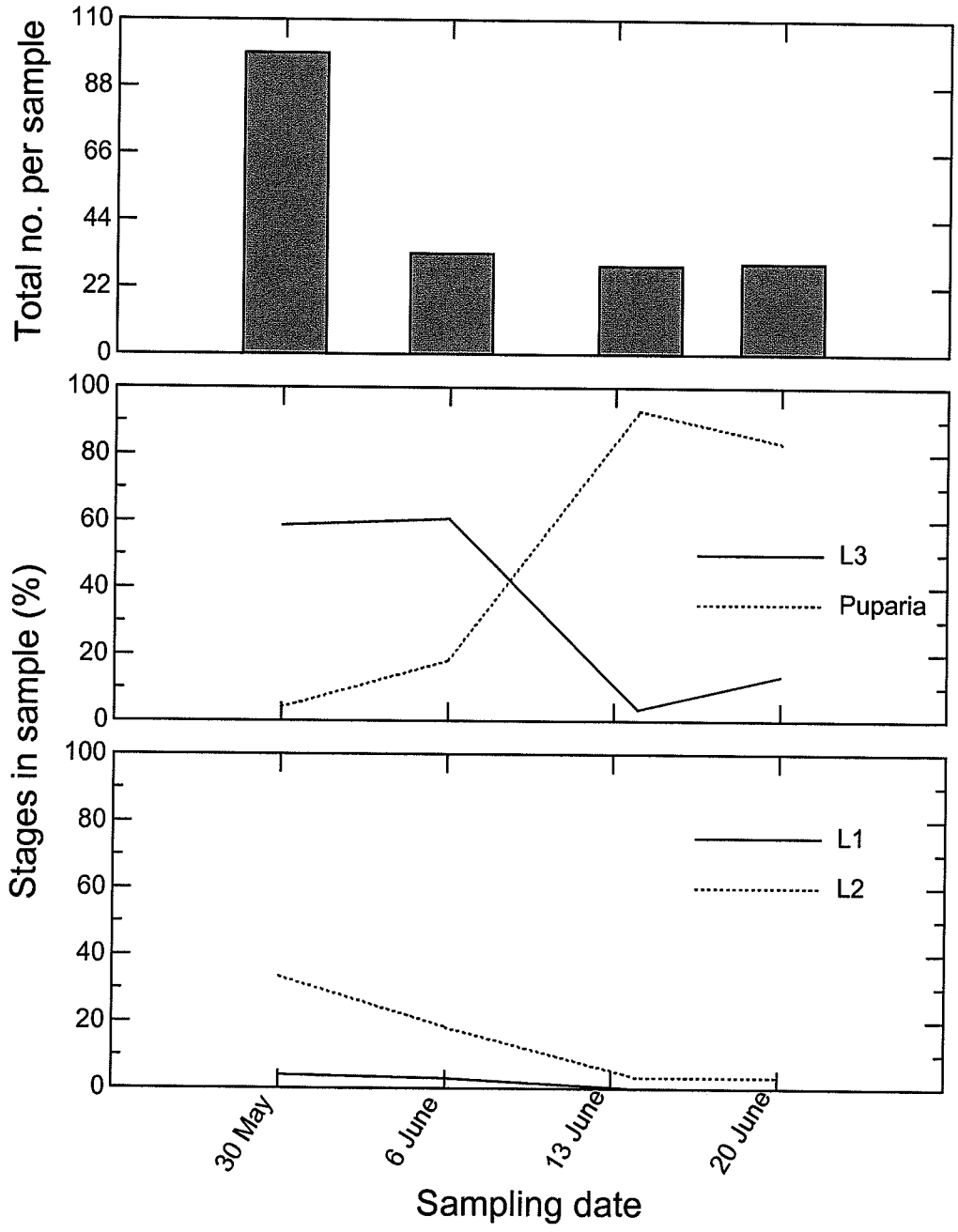

Figure 3.8 Number and stage composition of *Delia radicum* immatures in samples collected in summer canola at Rostock in 2002.

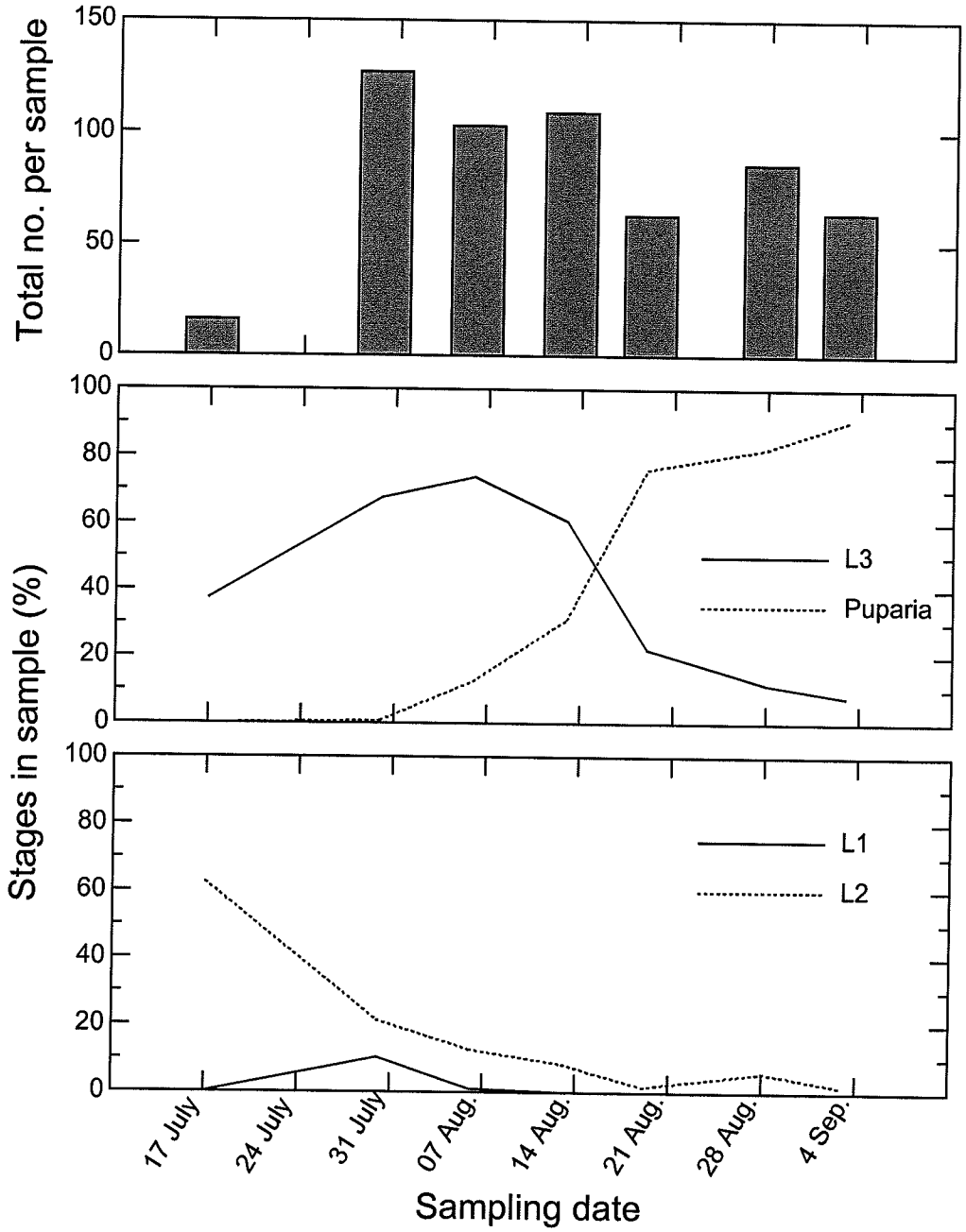

Figure 3.9 Number and stage composition of *Delia radicum* immatures in samples collected in late summer canola at Grundhof in 2001.

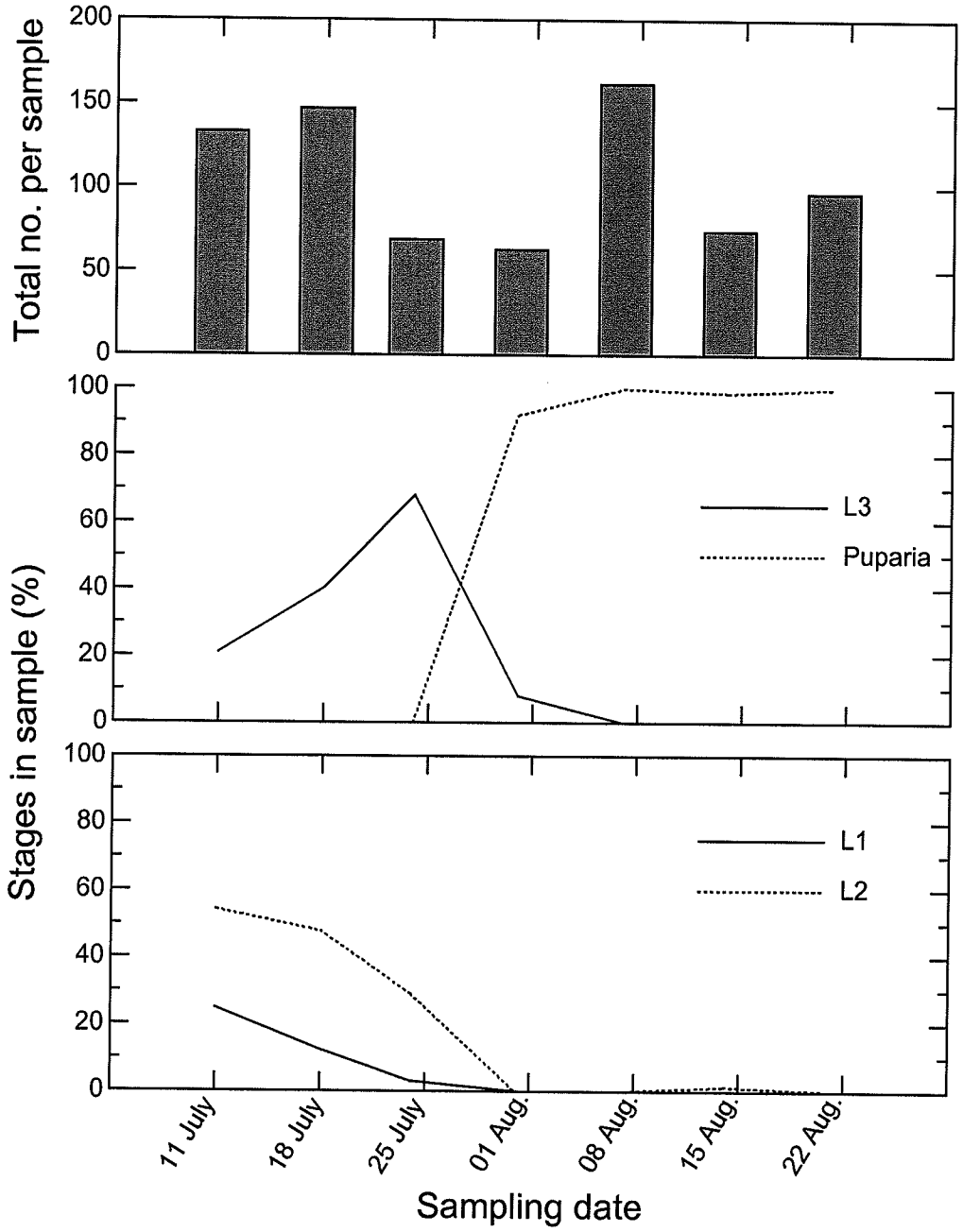

Figure 3.10 Number and stage composition of *Delia radicum* immatures in samples collected in late summer canola at Galmiz in 2001.

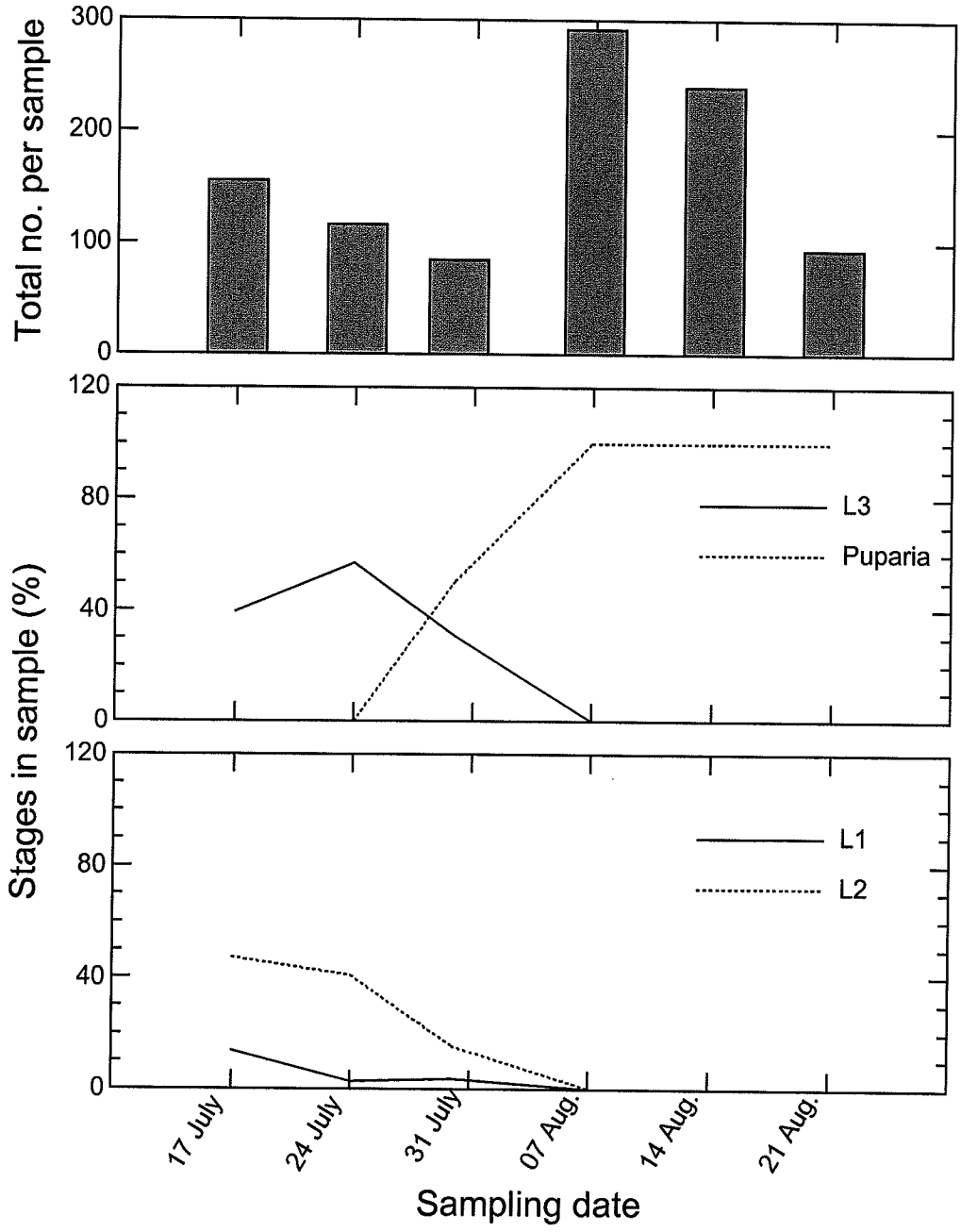

Figure 3.11 Number and stage composition of *Delia radicum* immatures in samples collected in late summer canola at Wünnewil in 2001.

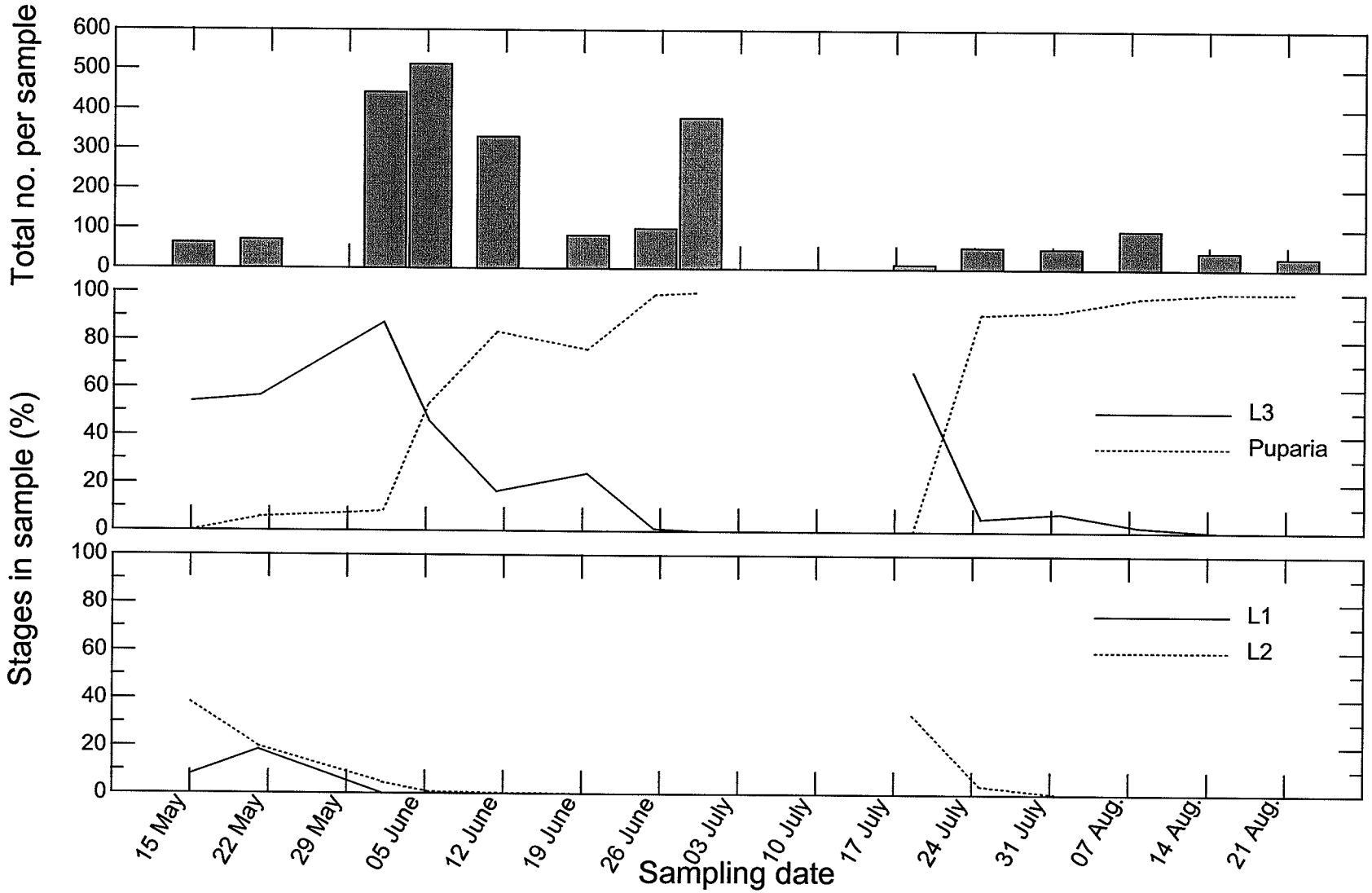

Figure 3.12 Number and stage composition of immature *Delia radicum* samples collected in brassica vegetables at Fraeschels in 2001.

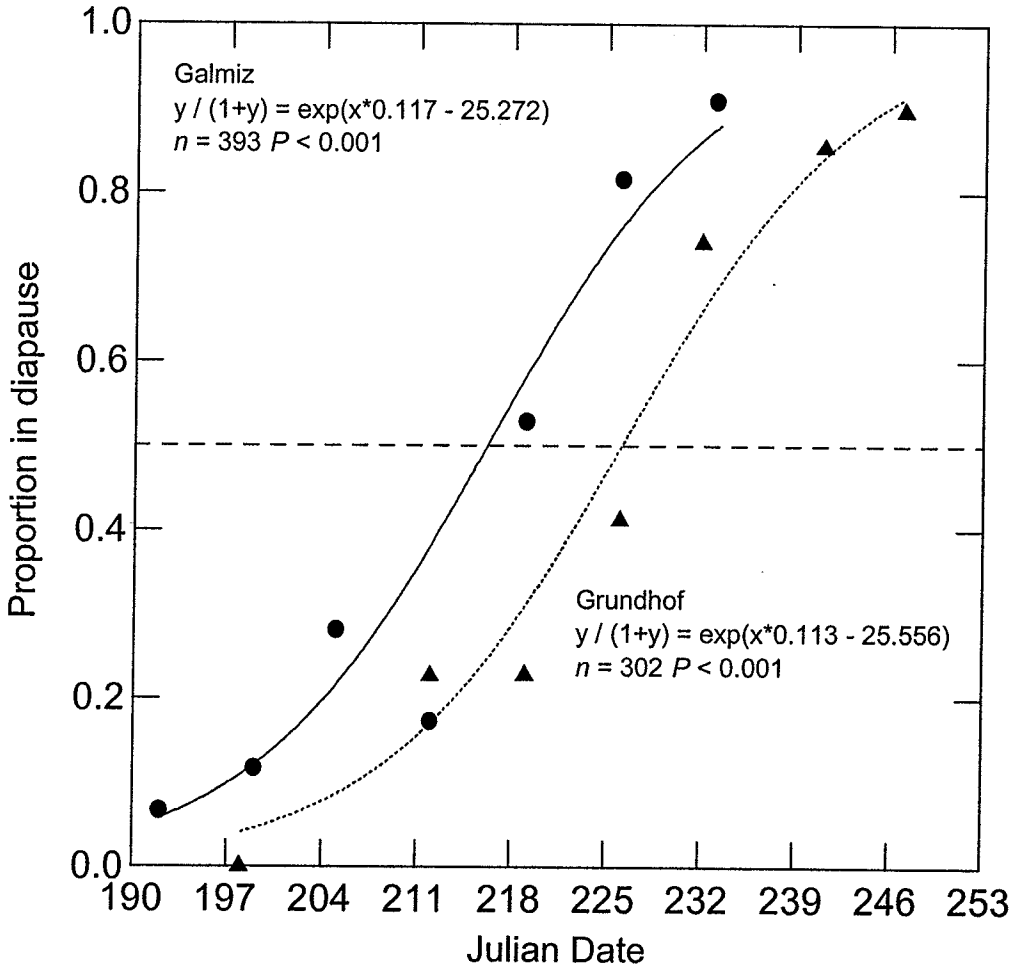

Figure 3.13 Probability of diapause of *Delia radicum* immatures in canola in Galmiz and Grundhof in relation to date of collection in summer 2001.

CHAPTER 3 SECTION 4

Effect of host distribution on parasitism of *Delia radicum* larvae by *Trybliographa rapae* in canola and cauliflower

Introduction

Trybliographa rapae (Westwood), a eucoilid parasitoid, plays an important role in suppression of *Delia radicum* (L.) populations in brassica vegetables (Finch and Collier, 1984). The parasitoid is present in North America and Europe and in brassica vegetables (Wishart and Monteith, 1954; Wishart, 1957) and canola habitats (Chapter 3 Section 1–2). Adult female parasitoids seeking hosts respond to chemical cues from host and host plants (Jones, 1986; Brown and Anderson, 1999), and to physical cues arising from larval movement (Vet and Alphen, 1985); visual cues are less important in host finding (Jones, 1986). Adult females follow the burrows of *D. radicum* larvae (Jones, 1986) or crawl down the infested root. *Trybliographa rapae* parasitizes all three larval instars of the host (Neveu *et al.*, 2000). The parasitoid adult emerges from a host puparium 54–60 days after oviposition (Kacem *et al.*, 1996). The adult female is pro-ovigenic, and oviposition starts within 2 days of emergence and continues for 10 days (James, 1928). Total fecundity averages 37.7 eggs per female (Jones, 1986).

The response of parasitoids to host patches affects the host's population dynamics. Parasitoids may aggregate in patches, producing a direct density dependent response. Alternatively, there may be an inverse density dependent or density independent responses to host patches (Godfray, 1994). Direct density dependent aggregation does not necessarily translate into direct density dependent parasitism (Hassell, 2000). Parasitism may be density independent or inversely density dependent due to limitations of parasitoids in exploitation of host patches (Hassell, 2000). Generally, long handling time (Hassell, 1982), constant giving up time (Hubbard and Cook, 1978), and egg limitation (Godfray, 1994) can lead to density independent

parasitism in host patches. Parasitism levels in host patches affect the level of suppression of the host population (Myers *et al.*, 1994).

Trybliographa rapae may have a physical limitation preventing searching females reaching *D. radicum* larvae that are feeding at deeper levels on brassica roots. This may produce refuges from parasitism. Physical refuges from parasitism are important in stabilizing host parasitoid interactions (Murdoch and Briggs, 1996), and the proportion of the host population in refuges from parasitism is a determinant of host population suppression (Hawkins *et al.*, 1993). Assessment of the role of refuges in the *D. radicum* population provides information on the potential of *T. rape* as a biocontrol agent.

The objectives of this study were to assess the spatial distribution of *T. rapae* in canola and cauliflower habitats and to assess the relationship between parasitism and host density. In addition, the feeding depth of *D. radicum* larvae on canola and cauliflower roots, and depth of penetration of adult *T. rapae* in search of host larvae were investigated in a model system.

Methods

Spatial pattern of host use by *Trybliographa rapae* in canola and cauliflower fields

Delia radicum larvae on canola and cauliflower roots were collected and reared until adult emergence to examine the relationship between larval density on the root and parasitism. *Delia radicum* larvae were sampled by collecting canola roots in fields of volunteer winter canola, commercial winter canola, summer canola and late summer canola in Germany and Switzerland. In addition, brassica vegetable roots were collected in Seeland, Switzerland. Volunteer winter canola fields at Fehmarn and Rastorfer-Passau, Germany and a commercial winter canola at Neuenburg, Germany were sampled.

Summer canola fields were at Birkenmoor, Schuby, and Rostock in Germany and late summer canola fields were at Galmiz and Wünnewil in Switzerland, and Grundhof in Germany. The brassica vegetable field was at Fraeschels, Seeland, Switzerland. Details of these fields were given in Chapter 3, Section 2.

At each site, two or three root samples of 30–100 roots per sample were considered in this study; these samples were collected when second- and third-instar larvae predominated in the field. The larvae were individually reared until adult emergence, and the parasitism by *T. rapae* was assessed as described in Chapter 3, Section 2. Parasitism was estimated as the number of *T. rapae* that developed to adulthood divided by the number of *T. rapae* and *D. radicum* that developed to adulthood. The number of larvae on each canola root and numbers of parasitized and unparasitized larvae on each root were recorded and the data were analysed using logistic regression in which probability of parasitism was the dependent variable and density (total number of larvae per root) was the independent variable. The relationship between parasitism and root diameter, and between probability of one or more hosts being parasitized and host density were also analysed using logistic regression.

Host patch exploitation by *Trybliographa rapae*

In caged plant pots, *D. radicum* larvae at different densities were exposed to *T. rapae* females and the larvae were reared until adult emergence to assess the parasitism. Eighty high-density polyethylene plastic pots, 13.9 cm diameter, 17.1 cm height and of 2 liter volume, were filled with a mixture (20:3.3:1) of commercial gardening soil, sand and fine grade vermiculite. Canola seedlings were planted in the pots and maintained in a greenhouse. When the plants were four weeks old, and the

diameter of the plant at soil level was 0.75–1 cm, the plants were infested with 1, 2, 4 or 6 *D. radicum* eggs per plant. Eggs were taken from a laboratory culture. There were 20 plants at each infestation level. After infestation, the plants were maintained for another 13 days then each plant was taken to the laboratory to expose the *D. radicum* larvae to gravid *T. rapae* female. A well fed and mated *T. rapae* female was introduced to each plant which was then covered with a 30 cm high and 15 cm diameter transparent crystal polystyrene cylinder with a fine mesh top for ventilation. The female *T. rapae* was allowed to stay in this system for 4 days, then the plants were dissected under a dissecting microscope (16 x) and the *D. radicum* larvae were recovered. The recovered larvae were reared individually in polystyrene vials (5 cm height, 2.2 cm diameter) on rutabaga cubes until pupation. Upon pupation, the puparia was placed in a new vial with moist fine vermiculite. Adult emergence from the puparia was recorded until December (four months after exposure to *T. rapae*) and the puparia from which adults had not eclosed were dissected to determine parasitization. Parasitism level was estimated as the number of *T. rapae* developed to adulthood divided by the number of *D. radicum* and *T. rapae* developed to adulthood. The data were analysed using logistic regression in which the probability of parasitism was the dependent variable and density was the independent variable.

Distribution of *Delia radicum* larvae on canola and cauliflower roots

Distribution of *D. radicum* larvae or their feeding damage on roots was examined using three samples of cauliflower, one sample of volunteer summer canola and two samples of summer canola. Three samples of cauliflower roots were collected at Galmiz, Seeland, Switzerland on 23, 26 and 30 July 2002. Each sample contained 30 cauliflower

roots, the head of which had been harvested a week or two earlier. Randomly chosen plants were uprooted, and excess soil and the aerial part of the plant were removed. Cauliflower roots were individually wrapped in plastic bags and brought to the laboratory for dissection. During the dissection of roots, the length of the root and the distance between the soil surface and *D. radicum* larvae or the site of their main feeding damage were recorded.

A sample of 75 volunteer summer canola roots was collected in a harvested wheat field, where canola plants had been growing for 5–6 weeks, in Delémont, Switzerland on 16 August 2002. Summer canola roots were sampled at Carman (150 plants) and Altamont (82 plants), Manitoba, Canada on 26 July 2003. The plants were randomly selected at the edge of each field. Some plants had more than one larva feeding at different depths on the roots so all depths were recorded. Frequency distribution of feeding depths of different crops were analysed using likelihood ratio chi-square analysis.

Effect of depth of *Delia radicum* larvae on parasitization of larvae by *Trybliographa rapae*

Delia radicum larvae at different depths in soil in pots were exposed to *T. rapae,* and the larvae were reared until adult emergence to estimate parasitization of larvae at different depths. Canola plants were grown in specially prepared high density polyethylene pots. The pots were 13 cm diameter, 15 cm high and 2 l in volume and were cut across at different depths from the top with an electric saw. Pots were cut at 2, 4 or 6 cm from the top. The two pieces of each pot were reattached using masking tape, and the cut pot was placed in an uncut pot of the same size. A 5 liter polyethylene bag was placed in between the two pots to enable the inner cut pot to be removed without breaking it apart. The inner cut pot was filled with a mixture (20: 3.3:1) of commercial

gardening soil, sand and fine grade vermiculite. The pot was filled right to the top and maintained at this level by adding extra potting medium when required during the experiment. Canola, *Brassica napus* variety "Express" was seeded at 3–4 seeds per pot at 1 cm depth in the soil. The pots were maintained in the garden at CABI Bioscience Switzerland Centre, Delémont, Switzerland, and watering, weeding etc. were carried out as required. When the plants were 10 days old, plants were thinned to leave only one healthy plant per pot.

When the plants were 40 days old, 10 day old *D. radicum* larvae were obtained from the culture maintained in the laboratory, and placed on a piece of rutabaga (3 x 3 cm and 1 cm thick), in a 10 cm diameter Petri dish. The larvae were then covered with a thin layer of fine, moist sand to facilitate establishment on the rutabaga. In this way, thirty pieces of rutabaga were prepared each containing 10 *D. radicum* larvae. Larvae were allowed to burrow into the rutabaga piece for 48 hours.

The rutabaga pieces with *D. radicum* larvae were introduced at different depths of canola roots without disturbing to the soil. The potted canola plants were prepared by removing their leaves with a sharp knife and cutting the stem at 15 cm height above the soil surface. The inner cut pot was taken out of the outer pot by lifting the polyethylene bag and through the previously made cut, the root of the canola plant and the soil were cut using a hacksaw blade. To ensure that the top ring of the pot with soil and canola plant were not disturbed, a hard polypropylene plastic sheet (30 x 30 cm, 2 mm thick) was inserted through the opening of the cut as the cutting progressed across the pot. Once the pot was cut across, the upper part of the pot with the plant and soil was on the plastic sheet. A rutabaga piece with *D. radicum* larvae was positioned on the root portion

in the bottom part of the pot. A small amount of soil and about 1 cm of taproot were removed from the bottom part of the pot to allow this. After installing the infested rutabaga piece, the cut pot was assembled and held together with masking tape, and the cut pot was placed in an uncut pot as before.

Adult female *T. rapae*, which had been reared from parasitized *D. radicum* puparia collected in brassica vegetable fields in Seeland, Switzerland, were maintained in small groups in clear polystyrene plastic cages, 12 cm diameter and 15 cm high. A piece of hard paper folded in the shape of a cup was placed inside the cage to provide shelter for the adult insects and 10% honey solution was supplied on filter papers. Each cage had 5–6 females and 4–5 males to ensure mating.

From these cages, *T. rapae* females, ≤9 days old, were removed and individually caged with an artificially infested canola plant in a cut pot. Cages were clear polystyrene cylinders (12 cm diameter and 45 cm high) with fine nylon mesh tops. The plastic cylinder was pushed into the soil in the cut pot and sealed around the edge with moist clay. One female parasitoid was caged with each plant for 4 days. At the end of this time, the system was examined and the location of the female parasitoid was recorded. The inner pot was lifted out and then the top part of the pot with the plant was removed. The rutabaga piece was removed and dissected under a binocular microscope (16 x) to recover the *D. radicum* larvae. Recovered larvae were reared individually in 5 cm high and 2.2 cm diameter polystyrene plastic vials, in which rutabaga was provided as larval food and moist, fine vermiculite was added to aid the establishment of larvae. The vials were examined regularly and food was replaced as necessary. Upon pupation, the puparia were placed in fresh vials with moist, fine vermiculite. Vials were maintained at

room temperature until January 2003 (five months after exposure to parasitoids) and the puparia from which there was no emergence were dissected and the contents examined to determine the parasitization. The parasitism at different soil depths was compared using contingency tables.

Results

Spatial pattern of host use by *Trybliographa rapae* in canola and cauliflower fields

Density of *D. radicum* larvae on brassica roots affected the probability of *T. rapae* finding a *D. radicum* infested root and parasitizing at least one larva (Fig. 4.1). There was a significant logistic regression between host density of the root and the proportion of plants at which parasitism occurred (Likelihood ratio (L.R.)$\chi^2 = 100.3$, df = 1 $P < 0.001$). The relationship was significantly different among crops (L.R.$\chi^2 = 56.7$, df = 4, $P < 0.001$), but the interaction of crop x host density was not significant (L.R.$\chi^2 = 5.5$, df = 4, $P = 0.237$). The relationship was common for volunteer winter canola, winter canola, late summer canola and brassica vegetables (L.R.$\chi^2 = 87.5$, df = 1, $P < 0.001$); among these crops, there was no significant effect of crop (L.R.$\chi^2 = 2.9$, df = 3, $P = 0.401$) or of the interaction of crop x host density of *D. radicum* (L.R.$\chi^2 = 1.8$, df = 3, $P = 0.621$) (Fig. 4.1). There was a significant location effect (L.R.$\chi^2 = 85.0$, df = 6, $P < 0.001$) within the crops, volunteer winter canola, winter canola, and late summer canola, but the location x host density interaction was not significant (L.R.$\chi^2 = 9.3$, df = 6, $P = 0.159$). Location effects within late summer canola (L.R.$\chi^2 = 31.4$, df = 2, $P < 0.001$) and within volunteer winter canola (L.R.$\chi^2 = 49.7$, df = 1, $P < 0.001$) were significant. The host density x location interaction within late summer canola (L.R.$\chi^2 = 8.5$, df = 2, $P = 0.014$) was significant, but the host density x

location interaction within volunteer winter canola (L.R.$\chi^2 = 0.006$, df = 1, $P = 0.938$) was not significant. The relationship for summer canola (L.R.$\chi^2 = 40.1$, df = 1, $P < 0.001$) was significantly different from the common relationship of volunteer winter canola, winter canola, late summer canola and brassica vegetables (L.R.$\chi^2 = 51.8$, df = 1, $P < 0.001$), and the interaction was also significant (L.R.$\chi^2 = 5.7$, df = 1, $P = 0.017$). Sampling location did not significantly affect the relationship for summer canola (L.R.$\chi^2 = 2.4$, df = 2, $P = 0.294$), nor was the interaction of location x depth significant (L.R.$\chi^2 = 1.2$, df = 2, $P = 0.546$) (Fig. 4.1).

Even though there was an increasing chance of finding ≥1 parasitized *D. radicum* on infested roots when larvae were at higher density on a root, there was no overall significant logistic relationship between the proportion of parasitized larvae on a root and host density on the root (L.R.$\chi^2 = 1.8$, df = 1, $P = 0.179$). When the data were examined separately for each crop, there was no significant logistic regression for volunteer winter canola (L.R.$\chi^2 = 1.9$, df = 1, $P = 0.164$), commercial winter canola (L.R.$\chi^2 = 0.1$, df = 1, $P = 0.715$) or brassica vegetables (L.R.$\chi^2 = 1.1$, df = 1, $P = 0.296$) (Fig. 4.2). In summer canola, the relationship between proportion of parasitized larvae per root and host density was significant (L.R.$\chi^2 = 4.6$, df = 1, $P = 0.031$); the location effect (L.R.$\chi^2 = 3.7$, df = 2, $P = 0.156$) and location x host density interaction (L.R.$\chi^2 = 0.05$, df = 2, $P = 0.977$) were not significant within this crop (Fig. 4.3). In late summer canola, the relationship between the proportion of parasitized larvae per plant and host density was positive and significant (L.R.$\chi^2 = 10.3$, df = 1, $P < 0.001$) and the location effect (L.R.$\chi^2 = 40.2$, df = 2, $P < 0.001$) and the location x density interaction (L.R.$\chi^2 = 6.2$, df = 2, $P = 0.045$) were also significant. Of the three late summer canola sites, the relationship was

significant only at Grundhof (L.R.$\chi^2 = 9.0$, df = 1, $P = 0.002$) (Fig. 4.4). The relationship between host density and proportion of parasitized larva in summer canola was significantly different from that in late summer canola (L.R.$\chi^2 = 73.1$, df = 1, $P < 0.001$), and the interaction between these two crops x host density was also significant (L.R.$\chi^2 = 14.0$, df = 1, $P < 0.001$).

In general, parasitism of *D. radicum* larvae per plant and diameter of root at soil level also followed a significant logistic regression (L.R.$\chi^2 = 17.6$, df = 1, $P < 0.001$); however, crop type significantly affected the relationship (L.R.$\chi^2 = 427.3$, df = 4, $P < 0.001$), and the interaction of root diameter x crop type was also significant (L.R.$\chi^2 = 58.7$, df = 4, $P < 0.001$). When the relationship was examined separately for each crop type, only volunteer winter canola (L.R.$\chi^2 = 19.3$, df = 1, $P < 0.001$) and late summer canola (L.R.$\chi^2 = 96.2$, df = 1, $P < 0.001$) had significant relationships of plant diameter with parasitism (Fig. 4.5). The relationship in those two crops was significantly different (L.R.$\chi^2 = 15.4$, df = 1, $P < 0.001$), but the interaction of crop x diameter was not significant (L.R.$\chi^2 = 3.0$, df = 1, $P = 0.08$). There was a significant location effect within late summer canola (L.R.$\chi^2 = 178.3$, df = 2, $P < 0.001$) and volunteer winter canola (L.R.$\chi^2 = 119.3$, df = 1, $P < 0.001$). The root diameter x sampling location interaction in volunteer winter canola (L.R.$\chi^2 = 0.6$, df = 1, $P = 0.45$) and late summer canola (L.R.$\chi^2 = 19.8$, df = 2, $P < 0.001$) was significant.

Host patch exploitation by *Trybliographa rapae*

The potted canola plants infested with *D. radicum* eggs had 1–17 larvae per root as a consequence of egg mortality and oviposition by wild *D. radicum* flies when plants were in the greenhouse. The probability of one or more hosts being parasitized per plant

and host density did not follow a significant logistic regression relationship (L.R.$\chi^2 = 0.06$, df = 1, $P = 0.799$). Since host densities above six had only one plant for each density, the relationship was re-examined excluding the densities above six but the relationship was not still significant. The overall relationship between probability of parasitism of a larva on a root and host density did not follow a significant logistic regression, but when the relationship was examined excluding the densities above six hosts per plant, the relationship was negative and significant (L.R.$\chi^2 = 4.3$, df = 1, $P = 0.038$) (Fig. 4.6). Examination of the possibility that the data fit a Holling type II functional response curve gave inconclusive results.

Distribution of *Delia radicum* larvae on canola and cauliflower roots

There was no difference in larval feeding depth between samples of summer canola from Carman and Altamont (L.R.$\chi^2 = 9.2$, df = 7, $P = 0.235$). However, distribution of feeding depth was significantly different among volunteer summer canola, summer canola and cauliflower crops (L.R.$\chi^2 = 28.0$, df = 14, $P = 0.014$) (Table 4.1). The distribution of larvae on volunteer summer canola roots and summer canola roots was not significantly different (L.R.$\chi^2 = 4.2$, df = 7, $P = 0.752$), but this distribution was significantly different from the larval distribution on cauliflower roots (L.R.$\chi^2 = 23.6$, df = 7, $P = 0.001$). In summer canola, about 60% of *D. radicum* larvae were in the depth range of 0–4 cm deep (Table 4.1).

Effect of depth of *Delia radicum* larvae on parasitization of larvae by *Trybliographa rapae*

In nine pots, the female parasitoid was found on the cage wall or on soil at the end of the experiment. In seven of these pots, five with larvae 6 cm deep and one each at

depths of 4 cm and 2 cm, no parasitism had occurred. In the remaining two of these pots, one each at 2 cm and 4 cm, parasitism had occurred. In two other pots, the female was found trapped in feeding tunnels in rutabaga at 2 cm deep; in one of these two, no parasitism had occurred.

The depth of rutabaga at which larvae were present significantly affected the proportion of plants that had at least one larva parasitized (L.R.$\chi^2 = 15.4$, df = 2, $P < 0.001$). There was no significant difference in proportions of plants with one or more parasitized larvae when rutabaga pieces with larvae were at 2 and 4 cm depths ($\chi^2 = 0.2$, df = 1, $P = 0.639$). The percentages of cages that had parasitized larvae were 70, 60 and 0% when the rutabaga pieces were at 2, 4 and 6 cm depths respectively. Similarly, the proportions of parasitized larvae per plant were significantly different with depths (L.R.$\chi^2 = 19.0$, df = 2, $P < 0.001$), as there were no parasitized larvae when the rutabaga was at 6 cm depth. The proportions of larvae parasitized were not significantly different when the larvae were at 2 and 4 cm deep (L.R.$\chi^2 = 1.2$, df = 1, $P = 0.278$). Mean (± SE) per cent of parasitism of larvae were 17.7 ± 5.5 and 12.5 ± 4.4 when the larvae were at 2 and 4 cm depths, respectively.

Discussion

In this study the probability of female *T. rapae* finding a plant and parasitizing at least one host increased with host density on a root (Fig. 4.1). This type of relationship occurred in all crop types and has previously been observed (Langer, 1996). This relationship is relatively consistent in cabbage monoculture and cabbage clover mix-culture (Langer, 1996).

The relationship between parasitism level per root and host density was inconsistent. In this study, the relationship was positively (Fig. 4.4), or negatively (Fig. 4.3) density dependent or density independent (Fig. 4.2). In previous studies, the same relationship has been density independent (Langer, 1996), directly density dependent (Jones, 1986; Jones and Hassell, 1988; Jones *et al.,* 1993; Langer, 1996), and inversely density dependent (Langer, 1996). Conditions of the previous studies were highly variable; therefore direct comparison of the relationships is difficult. For example, when host density ranges from 1 to 20 hosts per plant, a positive relationship has been observed in laboratory and field experiments (Jones, 1986; Jones and Hassell, 1988); however, within these data, a positive relationship is not apparent at host densities less than eight hosts per plant (Jones and Hassell, 1988). Further, the apparent density dependent relationship is not consistent over the years of study (Jones *et al.,* 1993), and varies among cropping systems and geographical locations (Langer, 1996). It appears that the relationship of *T. rapae* parasitism to host density is extremely sensitive to local conditions and is not a robust general phenomenon.

The relatively consistent relationship between probability of one or more hosts being parasitized and host density is probably associated with host searching behaviour. *Trybliographa rapae* use chemical cues, brassica odour, in host habitat location (Jones, 1986) in common with many other parasitoid species (Read *et al.,* 1970). In addition, *T. rapae* responds to volatile chemicals emanating from damaged tissues of host plants, host larvae and the frass of host larvae (Brown and Anderson, 1999). Greater numbers of larvae on roots would produce greater root damage, and consequently more volatile chemicals. In addition, the amount of host specific chemicals would be high on roots

with high host density. Thus, concentration of chemical cues could account for *T. rapae* finding plants with high host density more often than plants with low host density. It also appears that *T. rapae* female adults respond to root size (Fig. 4.5). The increased level of parasitism on bigger roots could be related to frequency of visits of females to bigger roots. This may result from a direct response of *T. rapae* females to root diameter.

Density independent parasitism of *T. rapae* would result if *T. rapae* leaves an infested root after a fixed time period. Leaving a host patch after a fixed time period has been observed in a eurytomid, *Eurytoma* sp. and a pteromalid, *Pteromalus caudiger* (Graham), that parasitize tephritid flies, *Tephritis conura* (Loew), feeding communally in thistle heads (Romstock-Volkl, 1990). The hosts are deeply buried in the thistle head and it seems unlikely that parasitoids can assess patch quality. *Trybliographa rapae* appears to use chemical cues and contact cues in host location, and it does not rely on visual cues (Jones, 1986). If *T. rapae* were unable to assess the patch quality, leaving the patch after a fixed time period would be an optimal search strategy (Godfray, 1994). When 15 readily accessible hosts were offered to individual *T. rapae* for 24 h in a laboratory trial, only 33% of them were parasitized (Neveu *et al.,* 2000). These results could indicate egg limitation or handling time limit parasitism of hosts in a patch. *Trybliographa rapae* may lay on average 3.7 eggs per day based on its fecundity and longevity (James, 1928; Jones, 1986). In this experiment, naïve females were used and initial fecundity is more relevant, but there are no data available on variation of daily fecundity with age. However, on occasions where density dependent parasitism has been seen, *T. rapae* has spent more time in patches with high host density (Jones and Hassell, 1988).

Larvae of *D. radicum* generally fed on roots at depths of 2–6 cm below the soil surface (Table 4.1) in summer canola and volunteer summer canola. No larvae were found on the first two centimeters of cauliflower root; however, mechanical weeding between rows adds soil around cauliflower roots so that at the time larvae started feeding, the feeding site could have been closer to the surface. Jones (1986) observed in a laboratory experiment that *T. rapae* follows *D. radicum* larvae penetrating up to 3 cm into the burrows made by host larvae in roots. In my study, *T. rapae* adults were capable of reaching host larvae 4 cm from the soil surface, but did not penetrate to 6 cm. This happened in the absence of host burrows in the root. Depending upon whether the limit of burrowing depth of a *T. rapae* female is nearer 4 cm or 6 cm, the proportion of *D. radicum* in canola in a refuge from parasitism could range from a maximum of about 40% to a minimum of about 10% (Table 4.1). The proportion in a physical refuge is important to stabilizing the host-parasitoid interaction (Murdoch and Briggs, 1996), and a relatively small refuge population still allows considerable suppression of the host population (Hawkins *et al.*, 1993).

Conclusions

The probability of *T. rapae* parasitizing at least one host on a plant was positively correlated with host density in brassica vegetables and canola fields. The proportion of hosts parasitized by *T. rape* on a root was not consistently related to host density. Generally, *D. radicum* feed on roots at 0–7 cm below the soil surface, and *T. rapae* is capable of reaching to 4 cm but not to 6 cm from soil surface.

Table 4.1. Distribution of depth between soil surface and feeding damage of *Delia radicum* on canola and cauliflower roots. Volunteer summer canola and cauliflower plants were collected at Delémont and Galmiz in Switzerland in 2002 whereas summer canola plants were collected at Carman and Altamont in Canada in 2003.

Depth from soil surface to major feeding place on root (cm)	Cumulative percentage of feeding depths from soil surface		
	Volunteer summer canola (N=101)	Summer canola (N=277)	Cauliflower (N=54)
0.0 - 0.9	2.0	0.7	0
1.0 - 1.9	9.9	11.2	0
2.0 - 2.9	30.7	30.3	9.3
3.0 - 3,9	58.4	62.5	37.1
4.0 - 4.9	77.2	80.9	77.8
5.0 - 5.9	90.1	93.5	96.3
6.0 - 6.9	97.0	96.4	100
≥7.0	100.0	100.0	0

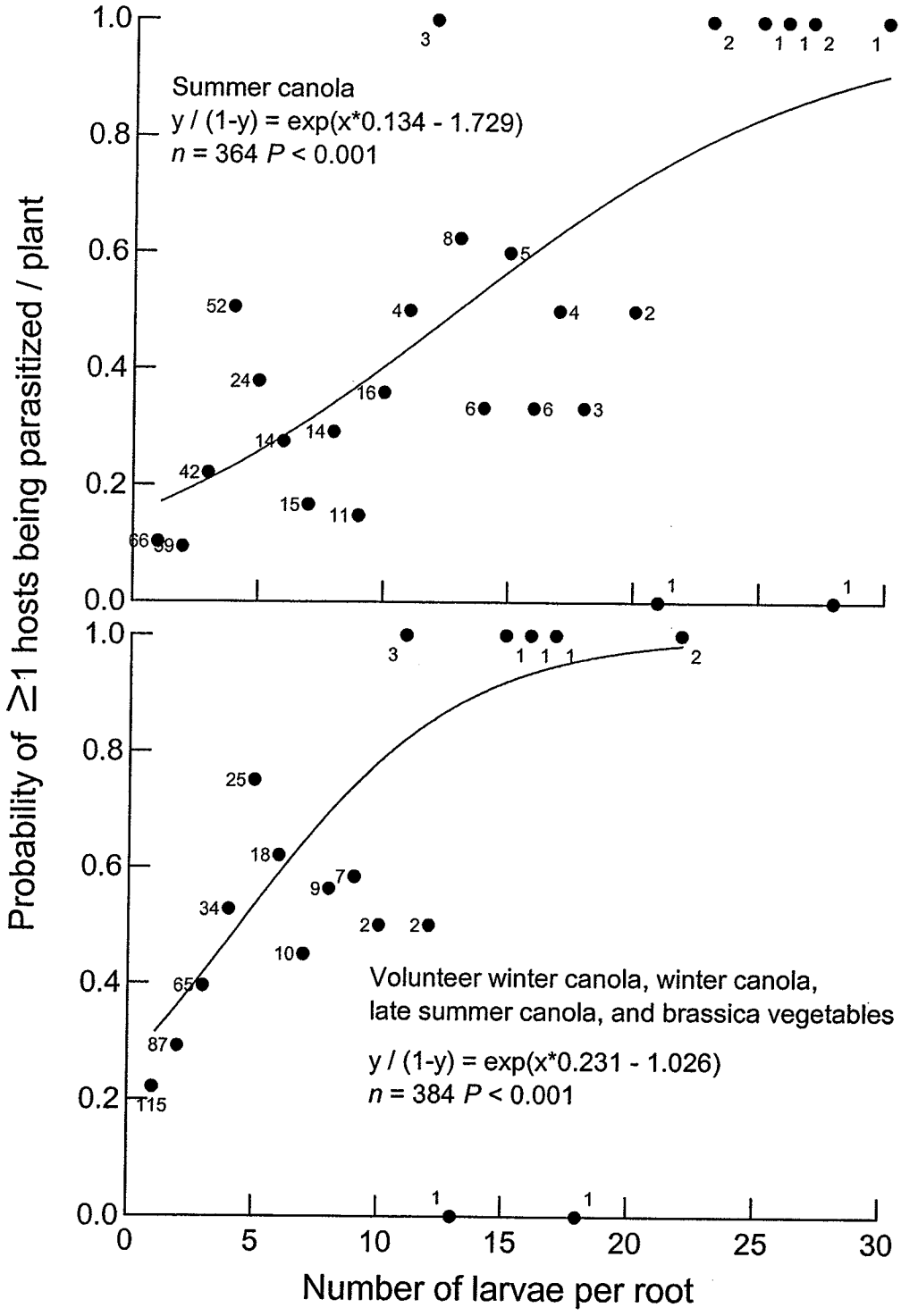

Figure 4.1 The probability of *Delia radicum* infested plants having at least one larva parasitized by *Trybliographa rapae* in relation to different infestation levels in volunteer winter canola, winter canola, summer canola, and brassica vegetables in Germany and Switzerland in 2001 and 2002. Number of plants studied at each larval density is indicated beside the plot symbol.

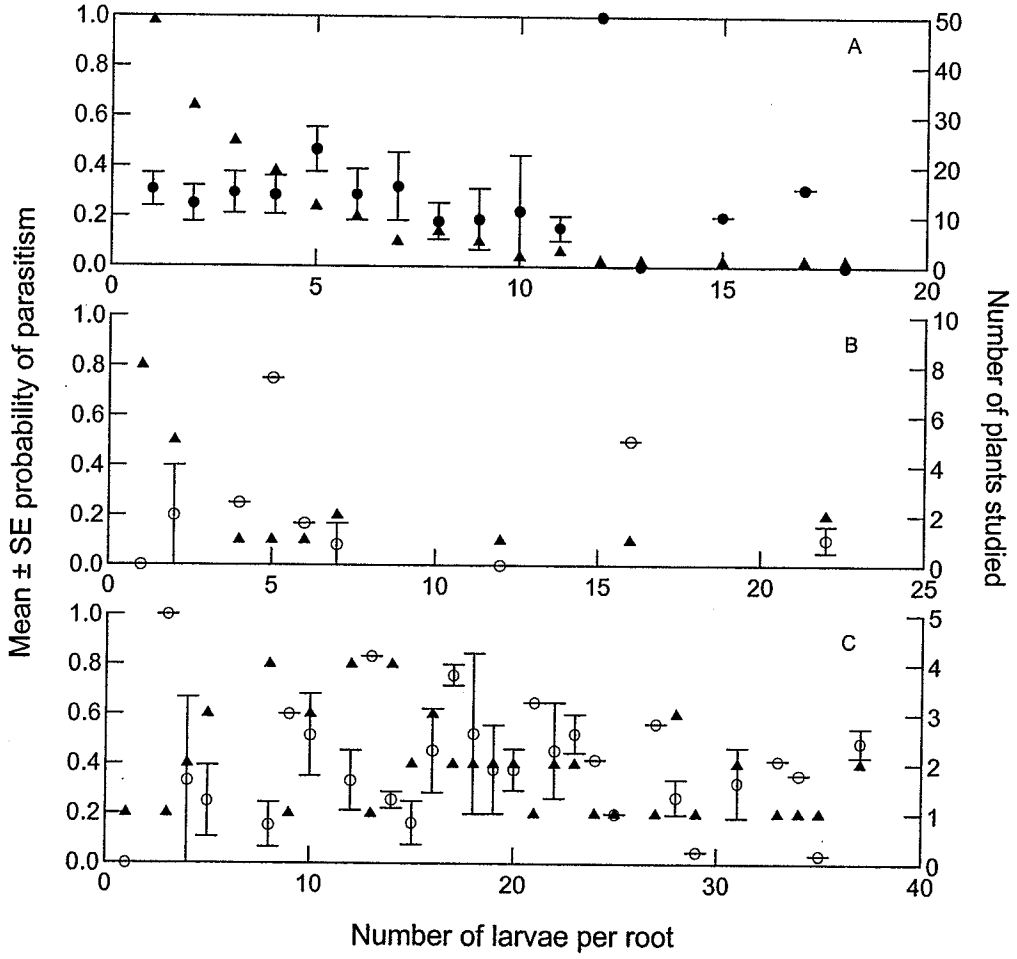

Figure 4.2 Probability of parasitism of *Delia radicum* larvae by *Trybliographa rapae* (O) in relation to host density in (A) volunteer winter canola, (B) winter canola, and (C) brassica vegetables. Numbers of plants used for probability assessment is indicated by ▲.

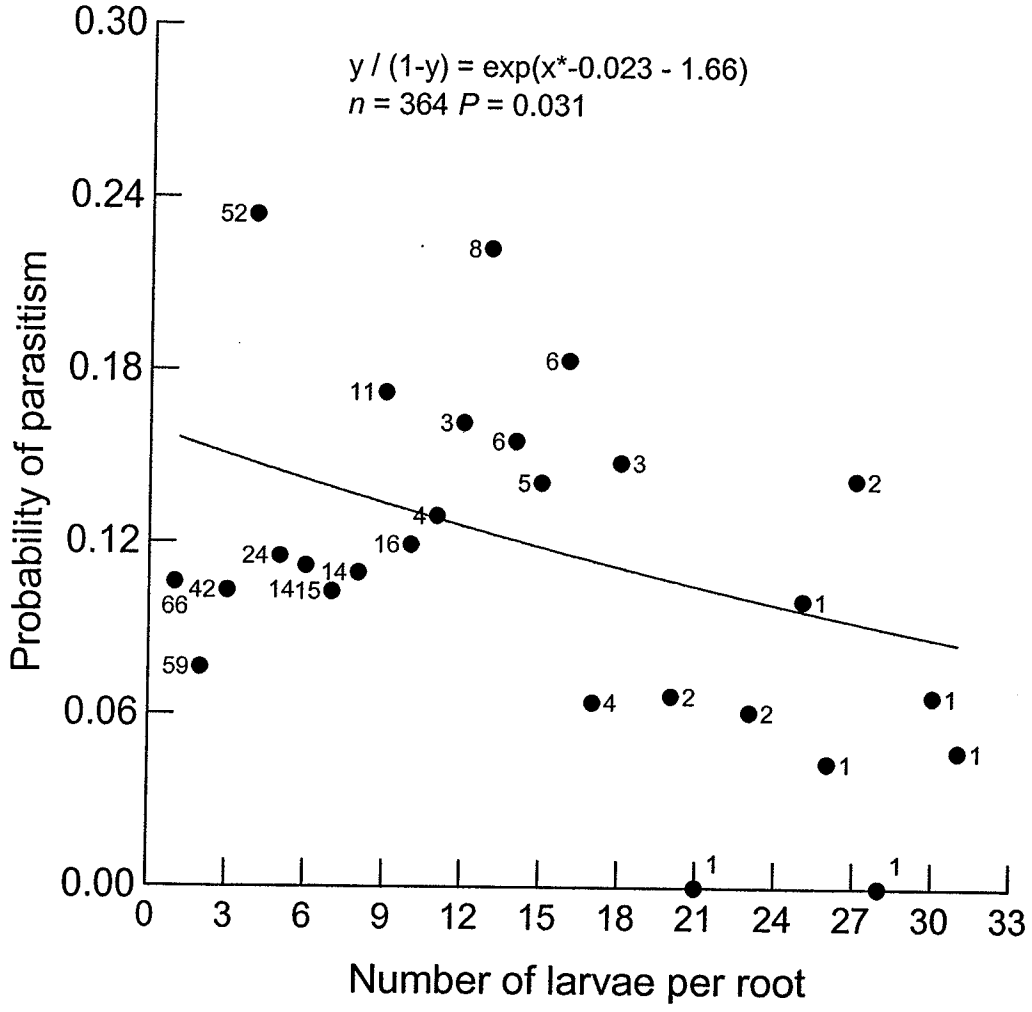

Figure 4.3 Probability of parasitism of *Delia radicum* larvae by *Trybliographa rapae* in summer canola in relation to host density. Summer canola was collected at Birkenmoor, Schuby, Rostock in 2002. Number of plants studied at each larval density is indicated beside the plot symbol.

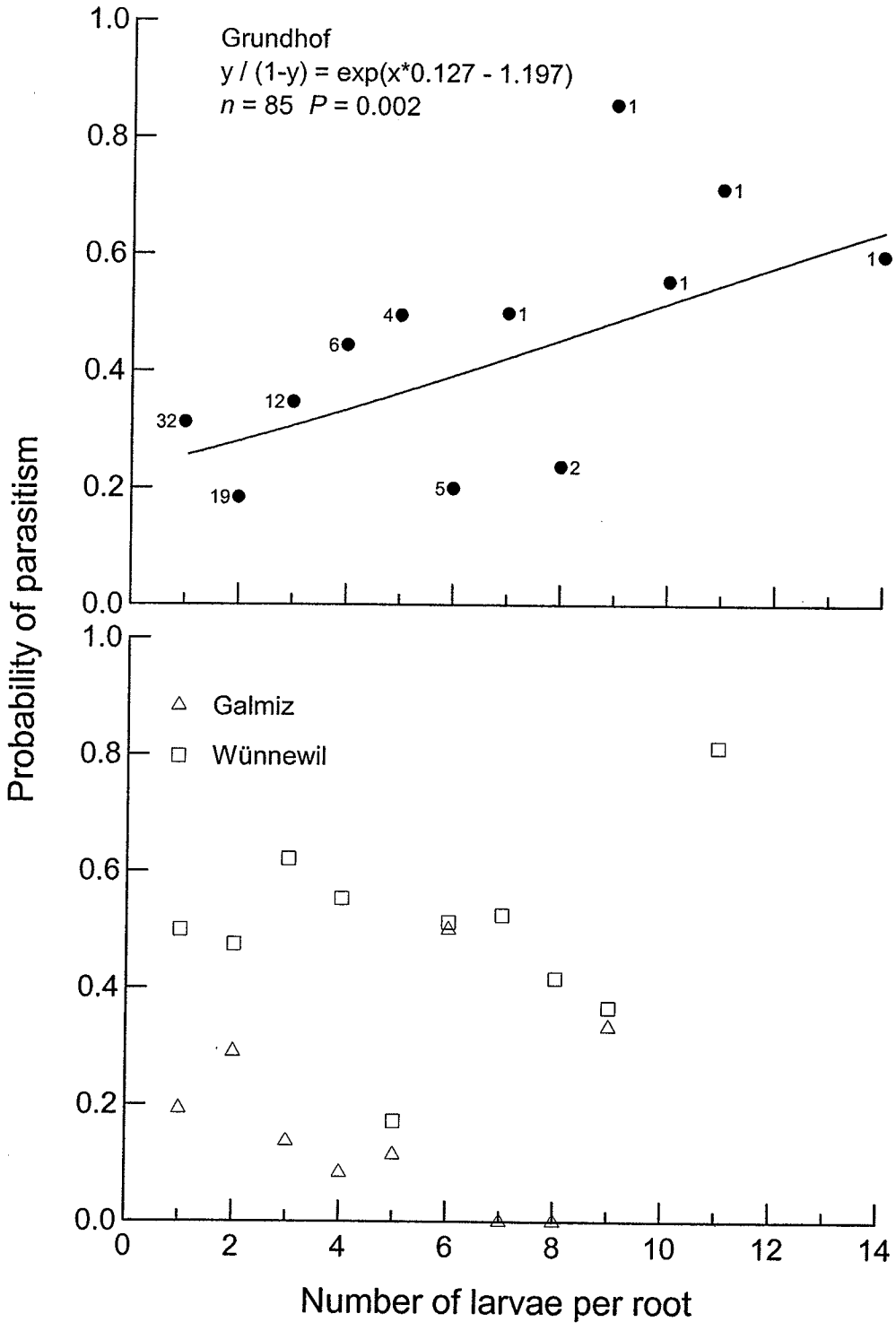

Figure 4.4 Probability of parasitism of *Delia radicum* larvae by *Trybliographa rapae* in late summer canola in relation to host density. Late summer canola was collected at Grundhof, Galmiz, Wünnewil in 2001. Number of plants studied at each larval density is indicated beside the plot symbol.

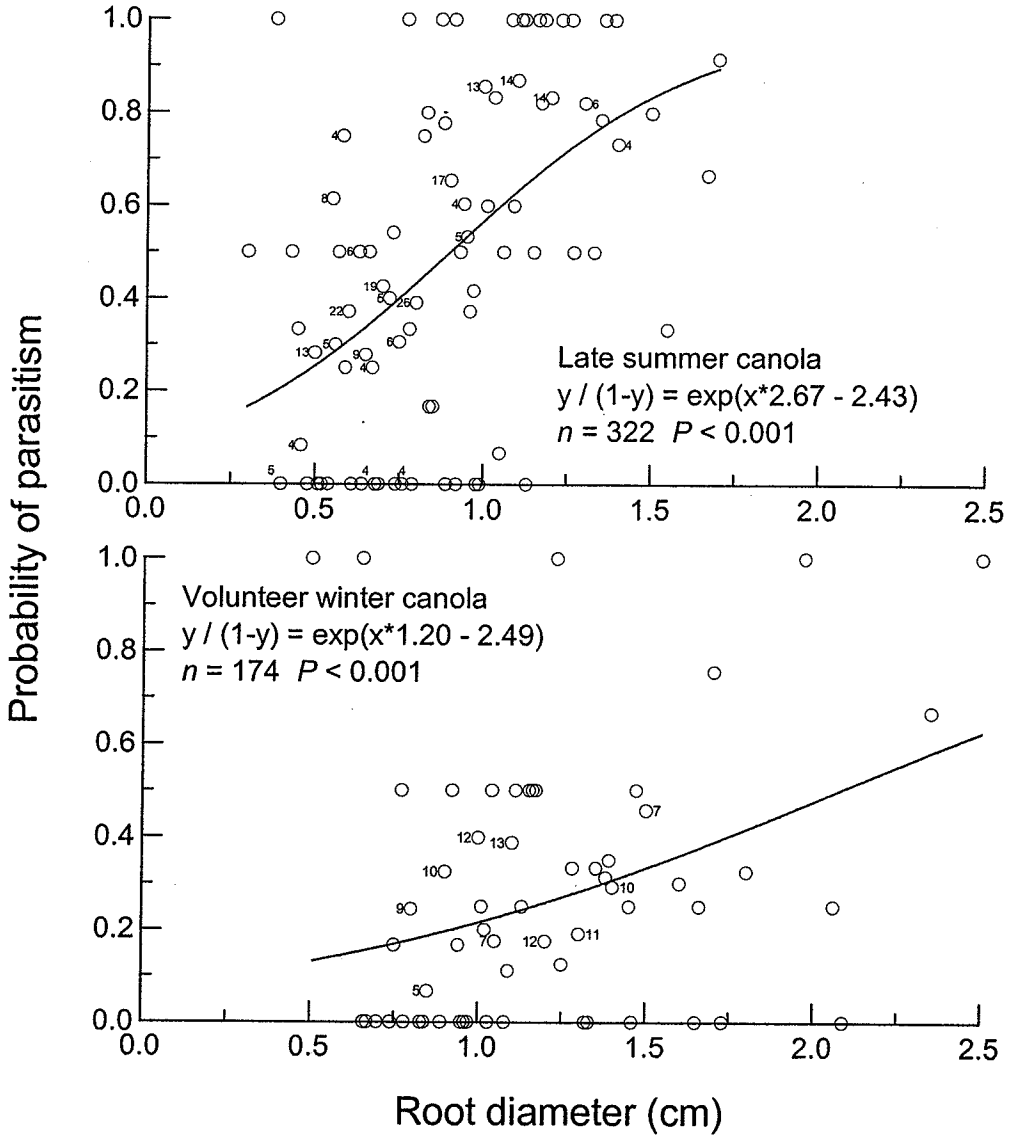

Figure 4.5 Probability of parasitism of *Delia radicum* larvae by *Trybliographa rapae* in relation to root diameter at soil level in late summer canola and volunteer winter canola. Number of plants studied at each level of root diameter is indicated beside plot symbol and unlabeled symbol represents ≤3.

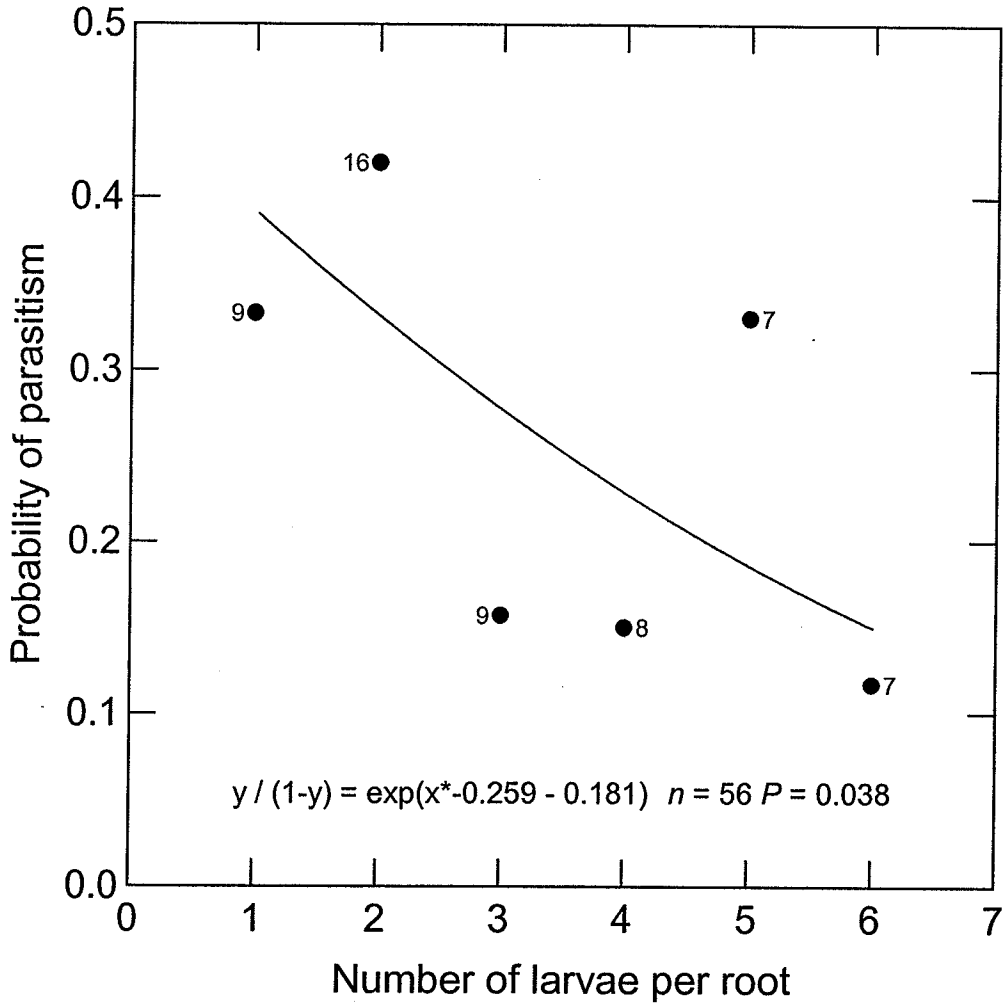

Figure 4.6 Probability of parasitism of *Delia radicum* larvae by *Trybliographa rapae* in relation to larval density on canola roots. Canola plants with larvae were exposed to parasitoid adults for four days. Number of plants studied at each host density is indicated beside plot symbol.

CHAPTER 3 SECTION 5

Relation of size of puparia of *Delia radicum* to host plants and to preference of *Aleochara* species for parasitism

Introduction

Aleochara bilineata Gyllenhal and *A. bipustulata* L. are predators of *D. radicum* (L.) eggs and larvae and are parasitoids of *D. radicum* pupae (Fuldner, 1960). Both species coexist in Europe, especially in northern Europe (Jonasson, 1994). *Aleochara bilineata* is present in North America and in Europe, but *A. bipustulata* is present only in Europe (Klimaszewski, 1984; Maus, 1996, 1998). *Aleochara bipustulata* becomes active earlier in the spring than *A. bilineata,* and is better synchronized with *D. radicum* eggs (Jonasson, 1994), hence *A. bipustulata* is more effective as a predator of *D. radicum* eggs than *A. bilineata* (Jonasson, 1994). *Aleochara bipustulata* is a potential candidate for biological control of *D. radicum* in Canada. As both species parasitize *D. radicum* puparia, there is a possibility that *A. bipustulata* might compete with *A. bilineata* after introduction. Competition among biocontrol agents may affect efficacy of suppression of the target pest (Debach and Rosen, 1991). From laboratory studies, Ahlström-Olsson (1994b) suggested that there is niche separation in relation to the size of *D. radicum* puparia. If this is the case in field conditions, then there would be little or no competition between *A. bilineata* and *A. bipustulata*. Therefore, the objective of this study was to examine the relationship between the size of puparia and the probability of parasitization by *Aleochara* species in the field.

Methods

Delia radicum puparia were measured from different crop habitats in 11 geographical locations (Table 5.1). Dead and deformed puparia were not measured, but other puparia were cleaned by rolling them on a moist paper towel, and then measured. Length, and maximum width were measured to the nearest 0.1 mm using an ocular scale

and a WILD M 38 dissecting microscope, at 16 x. Puparia were weighed using a METTLER AE 240 electronic balance. The puparia collected at Birkenmoor and Schuby were measured only for maximum width of puparia. Puparia that had been parasitized by *A. bilineata* or *A. bipustulata* collected at Birkenmoor, and Schuby were measured (maximum width) after eclosion of parasitoids. Parasitoids were identified using external anatomical characteristics and the identity was confirmed by subsequent examination of the aedeagus or spermatheca. Relationships between length, width and weight of puparia were established using linear regression. The relationship between the puparia size and the crop or the geographical locations was examined by analysis of variance. To allow use of all data for analysis, regression predictions were used to estimate unmeasured values. Frequency distributions (7 classes, each of class width of 0.2 mm) of width were compared using Likelihood ratio chi-squares in contingency tables.

Results

Measurements of *D. radicum* puparia collected in canola in 1999 and 2000 were strongly related to each other (Fig. 5.1). There was a significant linear regression between length and width ($F_{(1, 497)} = 1203.5$, $P < 0.001$), length and weight ($F_{(1, 497)} = 1255.6$, $P < 0.001$) and width and weight ($F_{(1, 497)} = 893.0$, $P < 0.001$) of the puparia.

Size of *D. radicum* puparia varied among the sampling locations (Table 5.1). Length ($F_{(4, 1484)} = 14.96$, $P < 0.001$) and width ($F_{(4, 1484)} = 8.65$, $P < 0.001$) of puparia varied among the Canadian sampling locations in canola. Similarly, width of puparia varied between European sampling locations in canola ($F_{(1, 257)} = 6.2$, $P = 0.013$), but length was not significantly different ($F_{(1, 257)} = 3.5$, $P = 0.063$) between sampling

locations. Width ($F_{(1, 376)} = 1.93$, $P = 0.166$) or length ($F_{(1, 376)} = 7.8$, $P = 0.005$) of puparia was not significantly different between years of sampling in the same location, e.g. Shellbrook.

In general the crop in which *D. radicum* larvae fed significantly affected the size of puparia. The effect of crop on length of puparia was significant ($F_{(2, 2011)} = 202.07$, $P < 0.001$); average length of puparia in canola, cauliflower and rutabaga was 5.87, 5.63 and 6.59 mm respectively. Similarly, the effect of crop on the width of puparia was significant ($F_{(2, 2011)} = 233.99$, $P < 0.001$); average width of puparia in canola, cauliflower and rutabaga was 2.12, 2.02 and 2.41 mm respectively. Length of puparia in European canola was not significantly different from that of in Canadian canola ($F_{(1, 1746)} = 0.58$, $P = 0.454$), but width was different ($F_{(1, 1746)} = 15.95$, $P < 0.001$). Length ($F_{(1, 390)} = 9.66$, $P = 0.002$) and width ($F_{(1, 390)} = 11.68$, $P = 0.002$) of puparia in European canola were significantly different from those of puparia in cauliflower. Similarly, length ($F_{(1, 1620)} = 86.0$, $P < 0.001$) and width ($F_{(1, 1620)} = 379.4$, $P < 0.001$) of puparia in Canadian canola were significantly different from those of puparia in rutabaga.

It appears that *A. bilineata* and *A. bipustulata* parasitize all sizes of puparia without discrimination (Table 5.2, Fig. 5.2). The frequency distribution of width of unparasitized puparia from European locations was significantly different from that for Canadian locations (L.R.$\chi^2 = 20.6$, df = 6, $P < 0.002$). The distributions significantly varied between Shellbrook and Saskatoon (L.R.$\chi^2 = 26.6$, df = 6, $P < 0.001$), but not between Birkenmoor and Schuby (L.R.$\chi^2 = 2.8$, df = 6, $P = 0.832$). Frequency distributions of width of unparasitized puparia and parasitized puparia by *A. bilineata* were not significantly different at Shellbrook (L.R.$\chi^2 = 1.8$, df = 6, $P = 0.936$) or

Saskatoon (L.R.$\chi^2 = 6.9$, df = 6, $P = 0.334$). Frequency distributions of width of unparasitized puparia and parasitized puparia by *A. bilineata* or *A. bipustulata* were not significantly different (L.R.$\chi^2 = 12.5$, df = 12, $P = 0.409$).

Discussion

The weight of *D. radicum* puparia is related to aspects of the nutritional composition of the root on which larvae feed, for example, the total sugar content, especially the ethanol soluble sugar (Hopkins *et al.*, 1999). Apparently the texture of roots that larvae fed on was different among rutabaga, canola and cauliflower, and might be associated with the quality of the food. These nutritional differences may account for differences in puparia size seen in this study. The weight of puparia from rutabaga (16.0 ± 0.26 mg) and canola (11.9 ± 0.06 mg) in my study was higher than the weights reported by Hopkins *et al.* (1999). Pupal weight was ≈12 mg in rutabaga, ≈10 mg in canola and ≈7 mg in kale when *D. radicum* were allowed to feed on plants in the laboratory (Hopkins *et al.*, 1999). The average weight of puparia is 16.6 mg when larvae feed on rutabaga (Harris and Svec, 1966). The weight of diapausing puparia is greater than of nondiapausing puparia (Johnsen and Gutierrez, 1997). Mean width (2.03 mm) of first generation puparia collected in rutabaga fields in Sweden (Jonasson, 1994) is less than the mean width of puparia collected in rutabaga in this study. The differences in size of puparia may be associated with the soil type, weather, physiological status of pupae, and generation of *D. radicum.*

In my data, there was no significant preference of *A. bilineata* larvae for a certain size class of *D. radicum* puparia. Similar results were reported by Jonasson (1994), who saw no preference among puparial width classes of 1.5–1.9, 2.0–2.3 and 2.3–2.5 mm.

When my data were analysed using theses size ranges no significant preference for any of the size classes for parasitization by *A. bilineata* was seen. In the laboratory, Ahlström-Olsson (1994b) saw no preference for particular puparial sizes within the range 9–25 mg, which corresponds to 2.0–2.5 mm wide. However, when 4–19 mg puparia were available for parasitism, 11–19 mg puparia were significantly preferred to 4–10 mg puparia for parasitization by *A. bilineata* (Ahlström-Olsson, 1994b). When I examined this with my data I did not see significantly higher parasitism of weight class 11–19 mg in puparia from Europe or at Shellbrook, but did so for puparia from Saskatoon. In this study, on average 13% parasitized puparia were approximately 4–10 mg size class. These results suggest that *A. bilineata* uses almost the full size range of puparia for parasitization and exhibits no marked host discrimination on size.

In my data, significant preferences of *A. bipustulata* for particular puparial sizes were not apparent. However, in a laboratory study, preference of *A. bipustulata* for small size puparia has been demonstrated (Ahlström-Olsson, 1994b). In addition, in field-collected puparia from Sweden, a greater proportion of smaller puparia (1.5–1.9 mm wide) had been parasitized by *A. bipustulata* than larger puparia (2–2.2 mm wide) (Jonasson, 1994). However, this apparent trend was based on only 25 puparia. When my data were analysed using these size ranges, no significant preference for any of the size classes for parasitization by *A. bipustulata* was seen.

First-instars of both *A. bilineata* and *A. bipustulata* search for host puparia randomly (Fuldner, 1960). *Aleochara bilineata* also responds to external puparial characteristics (Royer *et al.*, 1998) and chemical cues (Royer *et al.*, 1999). Therefore, *Aleochara* species may select among sizes of puparia; however, the short lifespan of the

first-instar larva and its limited mobility (Fuldner, 1960) may diminish the evolutionary advantage there might be from the avoidance of some puparia sizes that would produce niche separation between *A. bilineata* and *A. bipustulata.*

In summary, the crop that *D. radicum* larvae fed upon affected puparial length, width and weight. These size parameters are correlated to each other. *Aleochara bilineata* and *A. bipustulata* parasitized a similar size range of *D. radicum* puparia, and did not appear to select specific puparial sizes from among those that are available.

Table 5.1 Size of *Delia radicum* puparia (mean ± SE) collected in different geographical locations in Canada and Europe in brassica crops.

Geographical location	Date of collection	Number collected	Crop	Length (mm)	Width (mm)	Weight (mg)
Canada						
Portage La Prairie, Manitoba	October, 1999	133	Rutabaga	6.59 ± 0.04	2.41 ± 0.01	16.06 ± 0.26
Carman, Manitoba	7 October, 1999	18	Canola	5.80 ± 0.10	2.19 ± 0.04	12.13 ± 0.90
Vegreville, Alberta	3–4 October, 2000	100	Canola	5.72 ± 0.05	2.16 ± 0.02	11.70 ± 0.33
Shellbrook, Saskatchewan	6–7 October, 2000	148	Canola	5.87 ± 0.04	2.13 ± 0.02	12.42 ± 0.28
Altamont, Manitoba	11 October, 2000	50	Canola	5.61 ± 0.09	2.10 ± 0.04	11.31 ± 0.57
Carman, Manitoba	11 October, 2000	50	Canola	5.58 ± 0.08	2.04 ± 0.03	10.53 ± 0.52
Shellbrook, Saskatchewan[1]	16 October, 2001	230	Canola	5.95 ± 0.03	-	-
Saskatoon, Saskatchewan[1]	18, 25 October, 2001	893	Canola	5.73 ± 0.01	-	-
Europe						
Birkenmoor, North Germany	June, 2002	118	Canola	-	2.06 ± 0.02	-
Schuby, North Germany	June, 2002	141	Canola	-	2.11 ± 0.01	-
Galmiz, Seeland, Switzerland	June, 2002	133	Cauliflower	-	2.02 ± 0.02	-

[1]Sizes are for the pooled sample of parasitized and unparasitized puparia.

Table 5.2 Estimates of parameters of puparial size of *Delia radicum* in relation to status of parasitism. Puparia were collected at different geographical locations in the fall 2001 and the summer 2002.

Location and parasitoids	Number of puparia	Mean width ± SE (mm)	Maximum width (mm)	Minimum width (mm)
Shellbrook				
D. radicum	206	2.20 ± 0.01	2.66	1.59
A. bilineata	24	2.16 ± 0.03	2.54	1.83
Saskatoon				
D. radicum	819	2.12 ± 0.01	2.66	1.59
A. bilineata	74	2.06 ± 0.02	2.42	1.59
Schuby				
D. radicum	140	2.11 ± 0.01	2.43	1.50
A. bilineata	19	2.05 ± 0.23	2.56	1.52
A. bipustulata	33	2.12 ± 0.05	2.56	1.60
Birkenmoor				
D. radicum	118	2.06 ± 0.02	2.40	1.35
A. bilineata	6	2.04 ± 0.09	2.25	1.68
A. bipustulata	11	1.90 ± 0.13	2.25	0.88

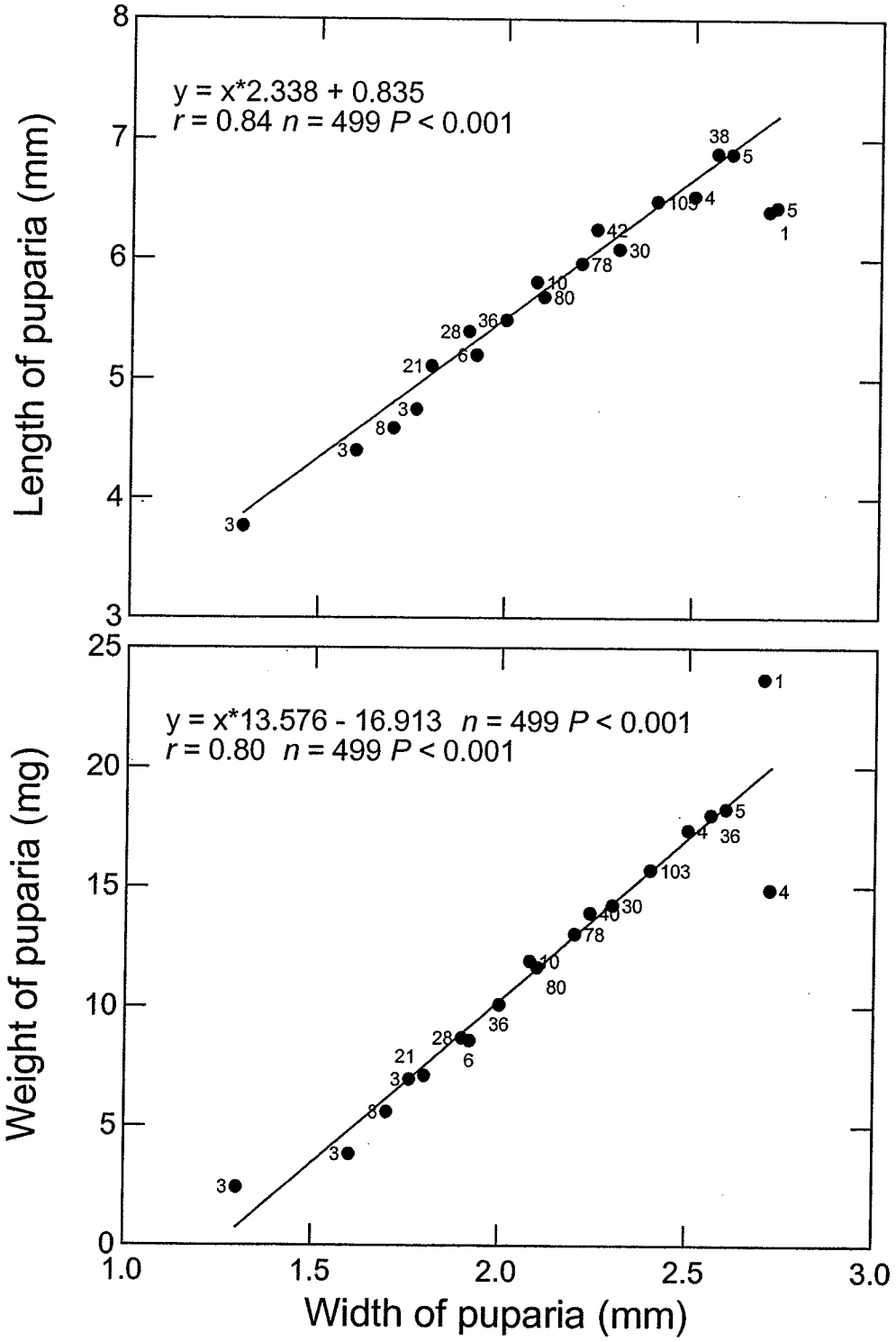

Figure 5.1. Relationship among width, length and weight of puparia of *Delia radicum* collected in canola fields in the Prairie Provinces of Canada. Number of puparia studied at each width is indicated beside the symbol.

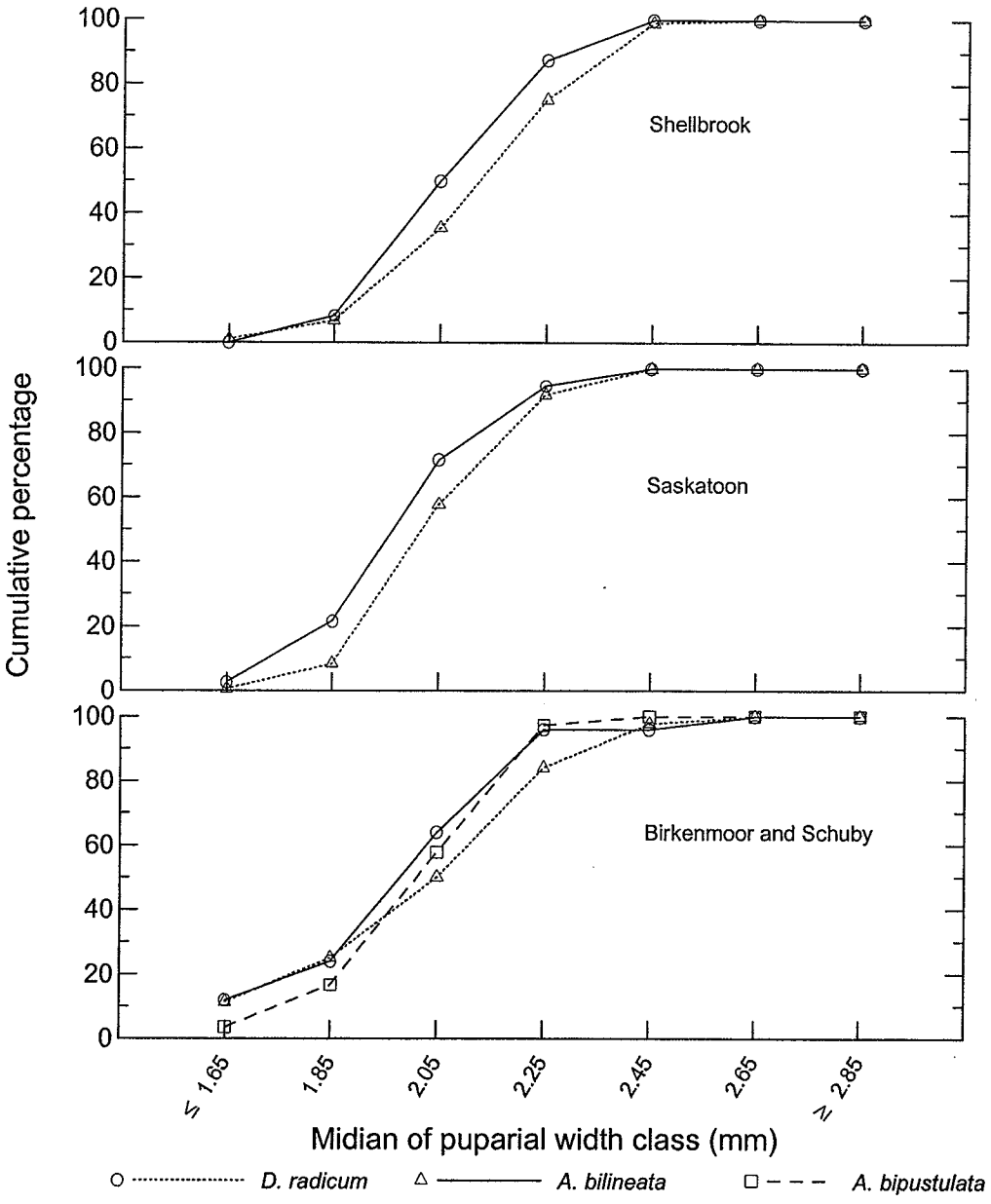

Figure 5.2 Width of *Delia radicum* puparia available and parasitized by *Aleochara bilineata* and *A. bipustulata.*

CHAPTER 3 SECTION 6

Status of occurrence of *Aleochara bipustulata* in North America

Introduction

Aleochara species have been the object of research in relation to biological control of *D. radicum* (L.) over the last 60 years. Among *Aleochara* species, *A. bilineata* Gyllenhal, *A. bipustulata* L. and *A. verna* Say are important species as predators and parasitoids of *D. radicum* (Fuldner, 1960; Klimaszewski, 1984; Jonasson, 1995; Maus *et al.*, 1998; Fournet *et al.*, 2000). In an attempt to achieve classical biological control of *D. radicum* in Canada, *A. bilineata* was introduced in the 1950s (McLeod, 1962; Soroka *et al.*, 2002). However, *A. bilineata* was in Canada even before the introduction (Soroka *et al.*, 2002) and had been identified as *Baryodma ontarionis* Casey (Casey, 1916; Colhoun, 1953). *Aleochara bilineata* was found in brassica vegetable habitats in Canada in subsequent studies (Wishart, 1957; Nair and McEwen, 1975; Turnock *et al.*, 1995). Other *Aleochara* species that have potential as biocontrol agents are *A. bipustulata* (Fournet *et al.*, 2000) and *A. verna* (Soroka *et al.*, 2002). In my research (Chapter 3 Section 1 and 2) comparing Canadian and European parasitoids, I have identified *A. bipustulata* as a promising candidate for introduction. However, to avoid repeating errors of the past, it is essential to ensure that this species does not already occur in North America.

Aleochara bipustulata and *A. verna* are similar in appearance and difficult to separate using external anatomical characteristics (Maus *et al.*, 1998). As a result, records of *A. bipustulata* and *A. verna* before 1986 are confusing. In European literature, "*A. bipustulata*" could refer to *A. bipustulata* or *A. verna,* and "*A. verna*" could refer to *A. verna* or *A. binotata* Kraatz (Maus *et al.*, 1998). The revision of Lohse (1986) established the status of *A. verna* and *A. bipustulata. Aleochara verna* and *A. bipustulata* can be reliably separated only on the basis of characteristics of aedeagus or spermetheca

(Klimaszewski, 1984; Maus, 1996, 1998). In a revision of the genus *Aleochara* in America north of Mexico, *A. bipustulata* was not found in North America (Klimaszewski, 1984), an opinion unaltered by Lohse's (1986) revision and shared by European taxonomists (Maus, 1996, 1998). However, there is published literature in which occurrence of *A. bipustulata* is reported in North America (Table 6.1). Hence, the objective of this study was to examine previous records of *A. bipustulata* in North America to determine their accuracy as a preparation for biological control of *D. radicum* in North America.

Methods

Museum specimens of *Aleochara* from North America that had been identified as *A. bipustulata* were examined to verify the identity, along with that of specimens collected in a field survey on the Canadian Prairie provinces. Research literature in which *A. bipustulata* was reported in North America was examined and attempts were made to trace and borrow voucher specimens related to the published work. Curators of insect collections were contacted and specimens that carried *A. bipustulata* labels were borrowed. In addition, a field survey was carried out in canola fields at Carman, and Altamont, Manitoba; Shellbrook, Saskatchewan and two fields at Vegreville, Alberta in summer and fall, 2000. *Delia radicum* puparia were collected in these fields, and puparia were reared in the laboratory until adult emergence. Emerged *Aleochara* beetles were compared with reference *Aleochara* specimens. Full details of the collection and rearing methods are given in Chapter 3 Section 1.

Museum specimens and field-collected specimens of *Aleochara* were initially keyed using Klimaszewski (1984), based on external anatomy. Specimens that were

thought to be *A. bipustulata* or *A. verna* were dissected and genitalia were mounted on microslides together with the abdominal segments separated from the body. The aedeagus and spermatheca were examined under the microscope (40 x) and compared with reference materials and drawings of Klimaszewski (1984) and Maus (1996, 1998).

Results and Discussion

All Nearctic *Aleochara* specimens from museum collections labeled as *A. bipustulata* were not *A. bipustulata* and most of them were in fact *A. verna*. These specimens had been collected in 45 different locations in North America and are now held in seven different museum collections (Table 6.2). These specimens represent all alleged North American *A. bipustulata* that I could trace, and correspond with several publications reporting *A. bipustulata* in North America (Table 6.1).

During the field survey, 4134 *D. radicum* puparia were reared to adulthood and 811 *Aleochara* beetles emerged during rearing. Of these beetles, 121 were *A. verna* and the 690 were *A. bilineata*. Both species were found at all sites and no *A. bipustulata* were found.

With these results, I conclude that the previous records of occurrence of *A. bipustulata* in North America are erroneous, and support the opinion of Klimaszewski (1984) and Maus (1996, 1998). Therefore, *A. bipustulata* is a potential candidate for introduction, provided that its biological characteristics meet the requirements of a potential biocontrol agent.

Table 6.1 Literature reporting occurrence of *Aleochara bipustulata* in North America.

Authors reporting *A. bipustulata* in North America	Year	Status of the specimens
Schoene, W.J.	1916	Contacted University of Cornell; voucher specimens were not found.
Wishart, G.	1957	Contacted Canadian National Collection, Ottawa; voucher specimens were not found.
McLeod, J.H.	1962	Review of biocontrol of *D. radicum*; refers to introductions made by Wishart and coworkers.
Moore, I., Legner, E.F.	1971	Specimens collected on different occasions by E.F. Legner and I. Moore were examined and found to be *A. verna.*
Thomas, G.D., Morgan, C.E.	1972	Attempted to contact authors without success; C. Wingo was a coworker in this study and specimens collected by C. Wingo were examined and found to be *A. verna.*
Nair, K.S.S., McEwen, F.L.	1975	Voucher specimens were examined and found to be *A. verna.*
Watts, K., Combs, R.L.	1975	Mississippi State University was contacted; no specimens were traced. Authors had acknowledged I. Moore for identification of specimens. Specimens collected on another occasion by I. Moore were examined and found to be *A. verna.*
Tomlin A.D., Miller, J.J. Harris, C.R., Tolman, J.H.	1985	Voucher specimens were examined and found to be *A. verna.*

Table 6.2 Specimens labeled *Aleochara bipustulata* that were examined and found to be *Aleochara verna.*

Location	No. of specimens	Date of collection	Collector	Location where specimens are held
Baja, California	1	28 May, 1950	I. Moore	University of California, Riverside, California
Berkeley, California	2	Aug.-Sep.,1919	H. Dietrich	Cornell University Insect collection, New York
Big Pine, California	1	June, 1971	D. Giuliani	University of California, Riverside, California
Bloomington Lake, Wasatch Mountains	1	7 July, 1952	B. Malkin	Field Museum of Natural History, Chicago
Brown's Valley	3	Oct., 1972	R.W. Merritt	University of California, Riverside, California
California	2	May-Aug.,1968		University of California, Riverside, California
Chiquito Creek, California	1	7 June, 1920	H. Dietrich	Cornell University Insect collection, New York
Columbia, Missouri	1	1 June, 1972	C. Wingo	University of California, Riverside, California
Columbia, Missouri	41	May-June, 1971	C. Wingo	Enns Entomology Museum, University of Missouri, Missouri
Coupeville, Washington	1	27 June, 1944	M.H. Hatch	Field Museum of Natural History, Chicago
Dalton Creek, California	1	15May, 1920	H. Dietrich	Cornell University Insect collection, New York
Dulzura, California	1	24 Apr., 1973	McErery	University of California, Riverside, California
Green Canyon, Hot. Spgs.	1	2 July, 1952	B. Malkin	Field Museum of Natural History, Chicago
Guelph, Ontario	3	Aug., 1951		Canadian National Collection, Ottawa
Ithaca, New York	2	20July, 1917	H. Dietrich	Cornell University Insect collection, New York
Kane Spgs, California	1	23 Feb., 1941	G.P. Mackenzie	University of California, Riverside, California
L. Arrowhead, California	1	24 Sep., 1939	G.P. Mackenzie	University of California, Riverside, California
Lake Hemet, California	1	30 June, 1965	R.E. Orth	University of California, Riverside, California
Linton Meadow	2	31 Aug., 1941	Deschufeb	Field Museum of Natural History, Chicago
Mount Falls Valley	3	25 May, 1935	Timberlake	University of California, Riverside, California
Mount Wilson, California	1	19 May, 1950	G.P. Mackenzie	University of California, Riverside, California
Northfolk, California	6	May-June, 1920	H. Dietrich	Cornell University Insect collection, New York
Pac. Grove, California	1		A. Fenyes	Field Museum of Natural History, Chicago

Continued

Table 6.2 Continued.

Location	No. of specimens	Date of collection	Collector	Location where specimens are held
Pawnee Grassland	6	7 July, 1971		University of California, Riverside, California
Peachland, British Columbia	3	July-Aug., 1912	J.B.Wallis	Canadian National Collection, Ottawa
Peachland, British Columbia	1	1918	J.B.Wallis	Canadian National Collection, Ottawa
Peachland, British Columbia	3	July, 1919	J.B. Wallis / Fenyes	Canadian National Collection, Ottawa
Phoenix Arizona	2	1Apr., 1934	R.H. Grandall	University of California, Riverside, California
Pistol River	1	7 July, 1951	B. Malkin	Field Museum of Natural History, Chicago
Preston, Ontario	5	July, 1973	K.S.S.Nair	University of Guelph, Ontario
Rock Creek R.S., Magic Mountain	2	19 July, 1952	B. Malkin / W.F. Barr	Field Museum of Natural History, Chicago
Saguva Beach, California	1	26 Dec., 1925		University of California, Riverside, California
San Francisco	1	29 Nov., 1919	H. Dietrich	Cornell University Insect collection, New York
Sant Jacinto, California	1	1 May, 1958	E.I. Schlinger	University of California, Riverside, California
Santa Lucia Mountain, California	1	8 Sep., 1962	R.V.d. Bosch	University of California, Riverside, California
Sebastopol, California	1	12 July, 1962	E.F. Legner	University of California, Riverside, California
Southwestern Ontario	7	1980-1981	A.D. Tomlin	Agriculture Agri-Food Canada, London, Ontario
Ames, Iowa	3	17 June, 1969		University of California, Riverside, California
St. Ana. River, California	1	3 Sep., 1953	A. Lander	University of California, Riverside, California
St. Jancinto Mountain, California	1	19 May, 1950	G.P. Mackenzie	University of California, Riverside, California
Steens Mountain	2	22-26 June, 1951	B. Malkin	Field Museum of Natural History, Chicago
Sunnymead, California	1	7 May, 1974	R.E. Orth	University of California, Riverside, California
Teel's Marsh	1	1 Aug., 1973	D. Giuliani	University of California, Riverside, California
Union, Ontario	1	1948		Canadian National Collection, Ottawa
Union, Ontario	2	23 May, 1949		Canadian National Collection, Ottawa
White Mount Park, California	1	31Aug., 1975	D. Giuliani	University of California, Riverside, California
White Mount Park, California	5	3 May, 1974	D. Giuliani	University of California, Riverside, California
Yosemite Valley, California	1	26-28 Sep., 1944	B. Malkin	Field Museum of Natural History, Chicago

CHAPTER 3 SECTION 7

Effect of tillage and seeding rate on occurrence of staphylinid beetles in canola

Introduction

Canola (*Brassica napus* L. or *Brassica rapa oleifera* (De Candolle) Metzger) is a popular, profitable crop grown on the Canadian Prairies, and on average 4.6 million ha of canola was grown annually over the period of 1994–2003 (Canola Council of Canada, 2004). Larvae of *Delia radicum* (L.) feed on canola roots, often causing economic damage (Liu and Butts, 1982; Griffiths, 1986a). There is no single effective strategy to control *D. radicum* in canola; hence, integration of all possible strategies has been proposed.

Tillage regime affects insect pests and their natural enemies living in soil or litter because tillage removes crop residues, exposes pests to adverse weather conditions and predators, and may separate insects from their food sources (Stinner and House, 1990; Kendall, 2003). For example, fall and spring tillage expose *D. radicum* puparia to predators, thus decreasing the population of *D. radicum* (Finch, 1989). Generalist predators feed on insect stages reducing the population levels (Stinner and House, 1990). Populations of some generalist predators increase under minimum tillage or no tillage, because weed and insect diversity increase, so providing food, nesting sites and refugia for predators under zero or minimum tillage (Altieri, 1994). Carabid and staphylinid beetles play an important role in lowering *D. radicum* pest population particularly through egg predation (Hughes, 1959; Coaker and Williams, 1963). In addition to predation, larvae of some staphylinid beetles parasitize *D. radicum* puparia, for example, *Aleochara bilineata* Gyllenhal (Fuldner, 1960; Jonasson, 1994) and *A. verna* Say (Nair and McEwen, 1975). Adults of these staphylinids consume immature *D. radicum,* and the first-instar larvae parasitize *D. radicum* puparia (Fuldner, 1960; Klimaszewski, 1984).

Therefore, it is important to understand the effects of tillage regime on the population dynamics of carabids and staphylinids in the canola production system.

Canola seed yield is relatively constant over a wide range of plant densities such as 95–760 plants per m^2 (Kondra, 1975; Dosdall *et al.,* 1996a); hence, plant density can be manipulated to manage pest populations. Plant density affects formation of plant canopy, through which its influence on the penetration of light affects weed growth and diversity (Altieri, 1994). It also affects the stem diameter of plants, and stem diameter is related to host plant selection for oviposition by *D. radicum* (Dosdall *et al.*, 1996a). Plant density also affects the formation of leaf litter through the accumulation of dead leaves on soil (Altieri, 1994). Moreover, elevated plant density reduces air circulation, creating a different microclimate under the canopy (Pimentel, 1961). Weed diversity and density, soil litter and microclimate affect the diversity and density of epigeic insects including carabids and staphylinids (Altieri and Letourneau, 1982). Hence the objective of this study was to examine the effects of tillage practices and plant density on staphylinid occurrence in canola. This study was a by-product of a study by A. Hawkins-Bowman, on the effects of tillage and plant density on *D. radicum* and carabids.

Methods

In 2000, diversity and abundance of staphylinid beetles were studied in a canola field plot in relation to plant density and tillage regime. The experimental field was established by A. Hawkins-Bowman, at the experimental farm of the University of Manitoba at Carman, Manitoba. The field plot was 60 x 240 m, and was divided into two blocks. Each block was divided into two plots (60 x 60 m), one of which received no tillage and one which received conventional tillage consisting of a fall tillage and spring

tillage. A deep till and tine harrow combination was used in the first week of October 1999 and a tine harrow and coil packer combination was used in the spring of 2000 to prepare seedbeds in the conventional tillage plots. Each tillage treatment plot was subdivided into two (30 x 60 m) sub-plots, one of which was seeded at 4 kg per ha and the other at 8 kg per ha. Seeding rate treatments were randomly assigned to sub plots. The canola variety, LG 3235 Roundup Ready, was seeded on 16 May 2000 using a 3 m wide Amazone zero till drill with 17.5 cm row spacing. The recommended agronomic practices for canola, other than seed density and tillage, were followed, but no insecticides were applied. The crop was swathed in mid August, and harvested on 30 August.

In each of the eight sub-plots, two pitfall traps were set up, one at the centre of the east half and one at the centre of the west half. The traps were plastic beer cups (Polar® 445 ml) buried in soil, with another similar cup placed within the buried cup. The inner cup of the trap was filled with 300 ml of salt solution and its lip was at the level of the soil surface. To protect the trap from rain and small vertebrates, the trap was covered with a 15 x 15 cm plywood sheet, which was suspended about 2.5 cm above the trap rim using 10 cm nails at the four corners.

The traps were set up in the field on 20 April 2000 and sampling continued until 10 August 2000. Traps were not in the field between 10 May and 24 May when seeding and crop emergence were in progress. The traps were emptied weekly starting 3 May 2000 by draining the salt solution through a plastic strainer; the trap was then reset by adding fresh salt solution. The trap catch was stored in 70% ethanol in 200 ml glass bottles in the laboratory until the contents were sorted.

Populations of *D. radicum* larvae and pupae were assessed by taking root samples and, counting the number of larvae or puparia per root. Two plants were sampled per plot per week until 27 June, and very few larvae and no puparia were found. On 27 June and each week thereafter until 1 September, six plants were sampled per plot. Plants were sampled by taking 10 cm diameter cores to a depth of 17 cm. Cores were centered on the selected plant's root, and the root and core were brought to the laboratory for hand sorting to remove *D. radicum.* Root damage was assessed using on the root rating scale of Dosdall *et al.* (1994).

Ms. A. Hawkins-Bowman set up the field trial and the collection of beetles using pitfall traps. She studied the carabids in the samples and I removed the staphylinid beetles from the samples for identification and analysis. I identified the staphylinids using taxonomic keys and comparing them with previously identified specimens in the J.B. Wallis Museum of Entomology at the University of Manitoba. Representative specimens were sent to J. Klimaszewski, Laurentian Forestry Centre, Canadian Forestry Service, Sainte-Foy (Québec), Canada and A. Smetana, for verification. The data were analysed using analysis of variance. Data were $\log_{10}(x+1)$ transformed when necessary to stabilize variance.

Results

In total, 508 adult staphylinids belonging to 11 species were caught during the entire sampling period; larval staphylinids were not caught. *Philonthus cognatus* Stephens represented 34.8% of the catch and *Aleochara bilineata* Gyllenhal represented 31.7% (Table 7.1). Tillage regime significantly influenced catches of two species: *P. cognatus* ($F_{(1,3)} = 10.6$, $P = 0.04$) and *P. occidentalis* ($F_{(1,3)} = 17.5$, $P = 0.03$). The total

catch over the entire sampling period of *P. cognatus* in zero tillage plots was higher than that for conventional tillage. In contrast, the catch of *P. occidentalis* was higher in the conventional tillage than in the zero tillage (Table 7.1). Plant density had no significant effect on catches of any staphylinid species. However, the tillage x plant density interaction for *A. gracilicornis* catches was significant ($F_{(1,3)} = 17.5$, $P = 0.03$) (Fig. 7.1 A). Similarly, the tillage x plant density interaction for *A. verna* catches was almost significant ($F_{(1,3)} = 9.0$, $P = 0.058$) (Fig. 7.1 B).

The staphylinid species caught were active at different time periods during the sampling period, 3 May–10 August 2000 (Figure 7.2). *Neohypnus obscurus* was caught only in the early period of sampling, whereas other species were caught later in the season. *Tachyporus nitidulus* and *Dinarea* sp. were caught both early and late in the season. The peak activity of *A. bilineata* and *A. verna* was around August 3, 2000 (Fig. 7.2).

It appears that peak catches of pitfall traps of a few staphylinid species coincided with peak catches of immature *D. radicum* in samples. The peak of *P. occidentalis* coincided with the peak of *D. radicum* larvae whereas the peak of *P. cognatus* appeared at the beginning of the peak of puparia. *Aleochara bilineata, A. verna, A. gracilicornis,* and *Philhygra* species were caught in highest numbers during the peak of puparial abundance (Fig 7.2).

Discussion

There are no biological data to suggest that active density of these stphylinid species were related. Therefore, treatment effects on each species were examined separately. The

effect of interactions of treatments was examined even though the total catch of *A. verna* and *A. gracilicornis* was low.

Aleochara bilineata occurs frequently in brassica habitats where *D. radicum* is available (Wilkes and Wishart, 1953; Wishart *et al.*, 1956, 1957; Read, 1962; Coaker and Williams, 1963; Bromand, 1980; Andersen, 1982; Jonasson *et al.*, 1995). The adults feed on *D. radicum* eggs (Read, 1962) and larvae of *D. radicum, Drosophila melanogaster,* and *Musca domestica* (Colhoun, 1953). In this study, the majority of pitfall catches of adult *A. bilineata* occurred later than the period of presence of *D. radicum* eggs (Fig. 7.2). *Aleochara bilineata* overwinters as a first-instar larva within the *Delia* puparium and takes 25 days to develop from the second-instar larva to adult eclosion in laboratory conditions (Fuldner, 1960). In addition, *A. bilineata* may need time to move from overwintering sites in last year's brassica crops to current brassica crops. Consequently, *A. bilineata* is too late to prey upon *D. radicum* eggs and its role as an egg predator of *D. radicum* is limited (Read, 1962; Ahlström-Olsson and Jonasson, 1992).

First-instar larvae of *A. bilineata* parasitize puparia of *D. radicum, D. platura* (Meigen), *D. antiqua* Meigen, *D. floralis* Fall., *D. florilegia* Zett., *D. planipalpis* Stein, *D. coarctata* Fall., *Pegomya betae* Curtis and *Muscina stabulans* Fall. (Colhoun, 1953; Fuldner, 1960; Maus *et al.*, 1998). *Aleochara bilineata* generally lay eggs over about 45 days (Read, 1962), at a rate of 5–15 eggs per day (Read, 1962; Bromand, 1980; Fournet *et al.*, 2000). Eggs hatch within 5 days at 22°C (Bromand, 1980) and first-instar larva can be free living for about 5–6 days (Fuldner, 1960; Royer *et al.*, 1999). During the free-living stage, the first-instar larva seeks a host puparium and enters it (Fuldner, 1960). The first-instar larvae use puparia of any age (Fuldner, 1960). Parasitization of

puparia is a significant pupal mortality factor in brassica vegetables (Mukerji, 1971; Benson, 1973). In this study, the seasonal pattern of pitfall catches of *A. bilineata* was synchronized with the numbers of *D. radicum* puparia caught in the samples; consequently, host puparia were available for first-instar *A. bilineata* for parasitism.

Aleochara bilineata is little affected by the change of microhabitats such as in monoculture and intercropping (Tukahirwa and Coaker, 1982), and the results in this study are in accord with this; there was no significant effect of tillage regime or seeding rate on catches of *A. bilineata.* Thus there is an opportunity to manipulate tillage and seeding rate to control *D. radicum* without negatively affecting one of the important parasitoids of *D. radicum.*

Aleochara verna is less common in brassica vegetables than *A. bilineata* (Andersen, 1982) and it inhabits a diverse range of habitats such as forest litter, decaying organic matter, wet mosses in a seepage area (Klimaszewski, 1984) and vegetable fields (Rämert *et al.*, 2002). Like *A. bilineata,* it preys upon fly eggs and parasitizes the puparia of *Delia* species (Maus *et al.*, 1998). In this study, pitfall catches of *A. verna* (Table 7.1) did not respond to the treatments, although catches were too small for subtle responses to be detectable. Despite the small numbers caught, it is clear that catches were synchronized with the numbers of *D. radicum* puparia caught. *Aleochara verna* larvae parasitize *D. radicum* puparia, and adult beetles were in the field at right time to oviposit for parasitism to occur.

Philonthus cognatus was caught more frequently in zero or minimum tillage in spring cereal crops in Norway (Andersen, 1999), as it was in this study. *Philonthus cognatus* exists in agricultural fields (Smetana, 1995) and preys upon nematodes, snails

and small arthropods including maggots (Smetana, 1995; Kendall, 2003) and *D. radicum* eggs (Wishart *et al.,* 1956). *Philonthus cognatus* is one of the most abundant staphylinid species in both summer canola and winter canola in Europe (Büchs and Alford, 2003) *Philonthus cognatus* is a spring breeder in Europe (D'Hulster and Desender, 1982) and active from May to October in raspberry fields in Québec (Levesque and Levesque, 1996). In this study, pitfall catches of *P. cognatus* were high at the time *D. radicum* larvae were abundant (Fig. 7.2) and were synchronized with the numbers of larvae and puparia of *D. radicum.* Thus, *P. cognatus* is active at times and places when prey densities are high. High catches in zero till treatments corresponded with low densities of *D. radicum* larvae and reduced root damage, even though *D. radicum* egg abundance was unaffected by tillage regime (Hawkins-Bowman personal communication). It may be that the influence of tillage regime on *D. radicum* is the result of predation by the greater number of *P. cognatus* in the zero till plots.

Philonthus occidentalis is caught more frequently in conventional tillage in spring cereals in Norway (Andersen, 1999), which agrees with the finding of this study. *Philonthus occidentalis* has similar habitats to *P. cognatus* and preys on nematodes, snails and arthropods including maggots (Smetana, 1995) and *D. radicum* eggs (Wishart *et al.,* 1956). The small number of beetles caught in the early part of the sampling period could have been ovewintered beetles. Peak catches of *P. occidentalis* were about 10 days earlier than those of *P. cognatus* (Fig 7.2). Consequently, *P. occidentalis* was quite closely synchronized with the *D. radicum* larval population, better so than *P. cognatus.* Synchronization indicates the potential of *P. occidentalis* to be a predator of *D. radicum.*

Neohypnus obscurus occurs in decaying organic matter, forest floor, under bark and in dung and carrion and feeds on small arthropods (Smetana, 1982). This species is generally active from May–October, with two peaks of activity (Levesque and Levesque, 1996). One of the peaks of activity-density in raspberry fields in Québec is in October when the new generation emerges (Levesque and Levesque, 1996). Our sampling continued only mid August, so only the first peak of activity density was seen in canola at Carman (Fig. 7.2). Synchronization of immature *D. radicum* and *N. obscurus* pitfall catches was poor, hence its values as a predator of *D. radicum* may be limited.

The other staphylinid species (Table 7.1) were caught in small numbers, hence those numbers were too small to provide evident temporal patterns or correlations with immature *D. radicum* or treatments. Since they were rarely caught in the canola field, their value as predators of *D. radicum* may be limited.

In summary, 11 species of staphylinids were caught in the experimental canola system and *P. cognatus, P. occidentalis, A. bilineata* and *N. obscurus* were caught in relatively high numbers in pitfall traps. *Philonthus* species responded differently to tillage regime and none of the staphylinid species responded to seeding treatment. Activity density of staphylinids was variable across the sampling time. Catches of *Philonthus* species were the greatest at the time of *D. radicum* larval development. Peak activity density of *A. bilineata* and *A. verna* occurred at a similar time, a time when *D. radicum* puparia were abundant in the field.

Table 7.1 Total number of adult staphylinid beetles collected from 20 April to 10 August, 2000 in canola in Carman. Data are seasonal totals averaged over the eight pitfall traps operated in each tillage or seeding treatment

Species	Total	Mean number of staphylinids ± SE per trap			
		Tillage Regime		Seeding rate (kg / ha)	
		Conventional	Zero	4	8
Aleocharinae					
Aleochara bilineata Gyllenhal	161	10.0 ± 3.2	10.1 ± 3.1	8.1 ± 2.5	12.0 ± 3.5
Aleochara gracilicornis Bernhauer	24	1.8 ± 0.7	1.3 ± 0.5	1.9 ± 0.7	1.1 ± 0.5
Aleochara verna Say	15	1.1 ± 0.5	0.8 ± 0.4	1.0 ± 0.5	0.9 ± 0.4
Dinaraea sp.	14	1.0 ± 0.4	0.8 ± 0.3	0.8 ± 0.3	1.0 ± 0.4
Philhygra sp	5	0.5 ± 0.3	0.1 ± 0.1	0.0 ± 0.0	0.6 ± 0.3
Oxytelinae					
Anotylus sp.	3	0.4 ± 0.2	0.0 ± 0.0	0.3 ± 0.2	0.1 ± 0.1
Staphylininae					
Neohypnus obscurus (Erichson)	35	2.0 ± 0.5	2.4 ± 0.6	2.6 ± 0.6	1.8 ± 0.5
Ontholestes sp.	2	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.0 ± 0.0
Philonthus cognatus Stephens	177	7.8 ± 1.2	14.4 ± 2.4	12.6 ± 2.6	9.5 ± 1.8
Philonthus occidentalis Horn	57	6.4 ± 1.4	0.8 ± 0.4	3.4 ± 1.1	3.8 ± 1.8
Tachyporinae					
Tachyporus nitidulus (Fabricius)	15	1.0 ± 0.5	0.9 ± 0.2	1.1 ± 0.5	0.3 ± 0.3

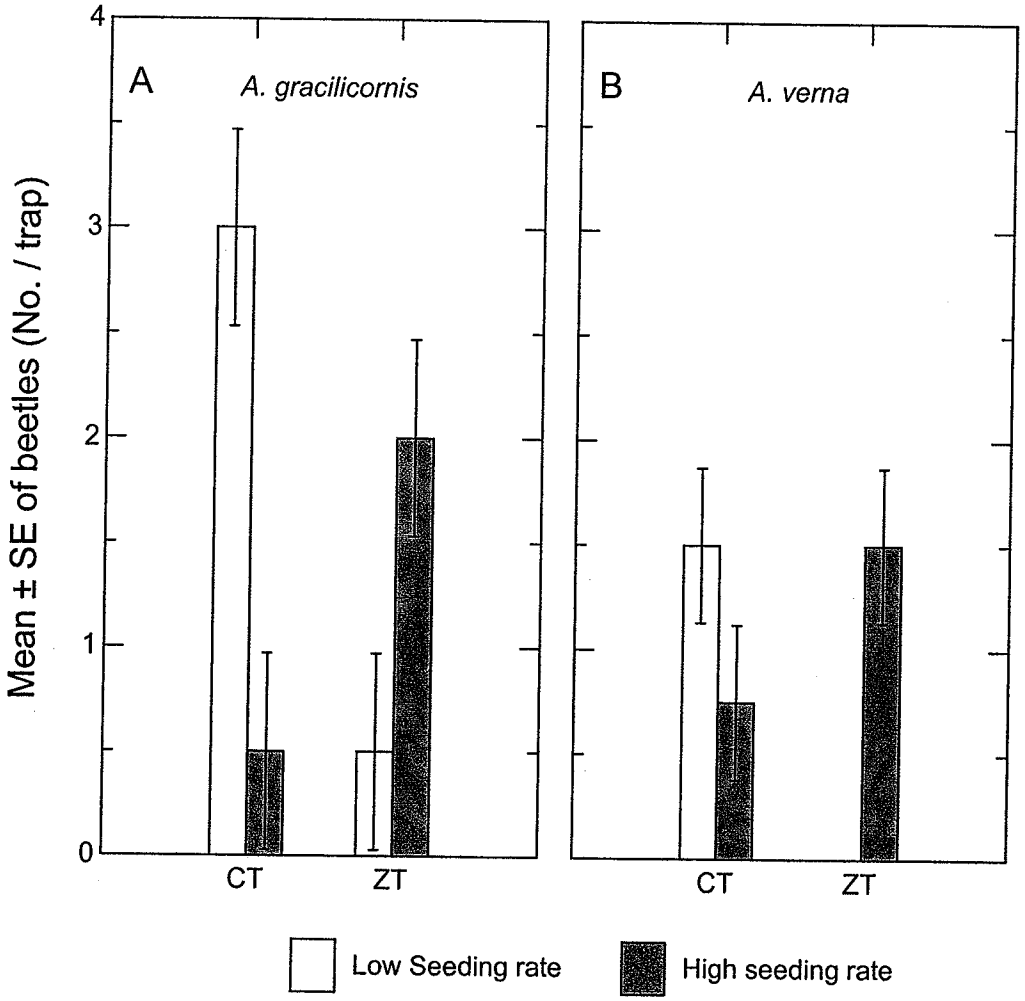

Figure 7.1 Mean numbers of *Aleochara gracilicornis* and *Aleochara verna* caught in conventional tillage (CT) and zero tillage (ZT) at low and high seeding rates of canola at Carman in summer 2000.

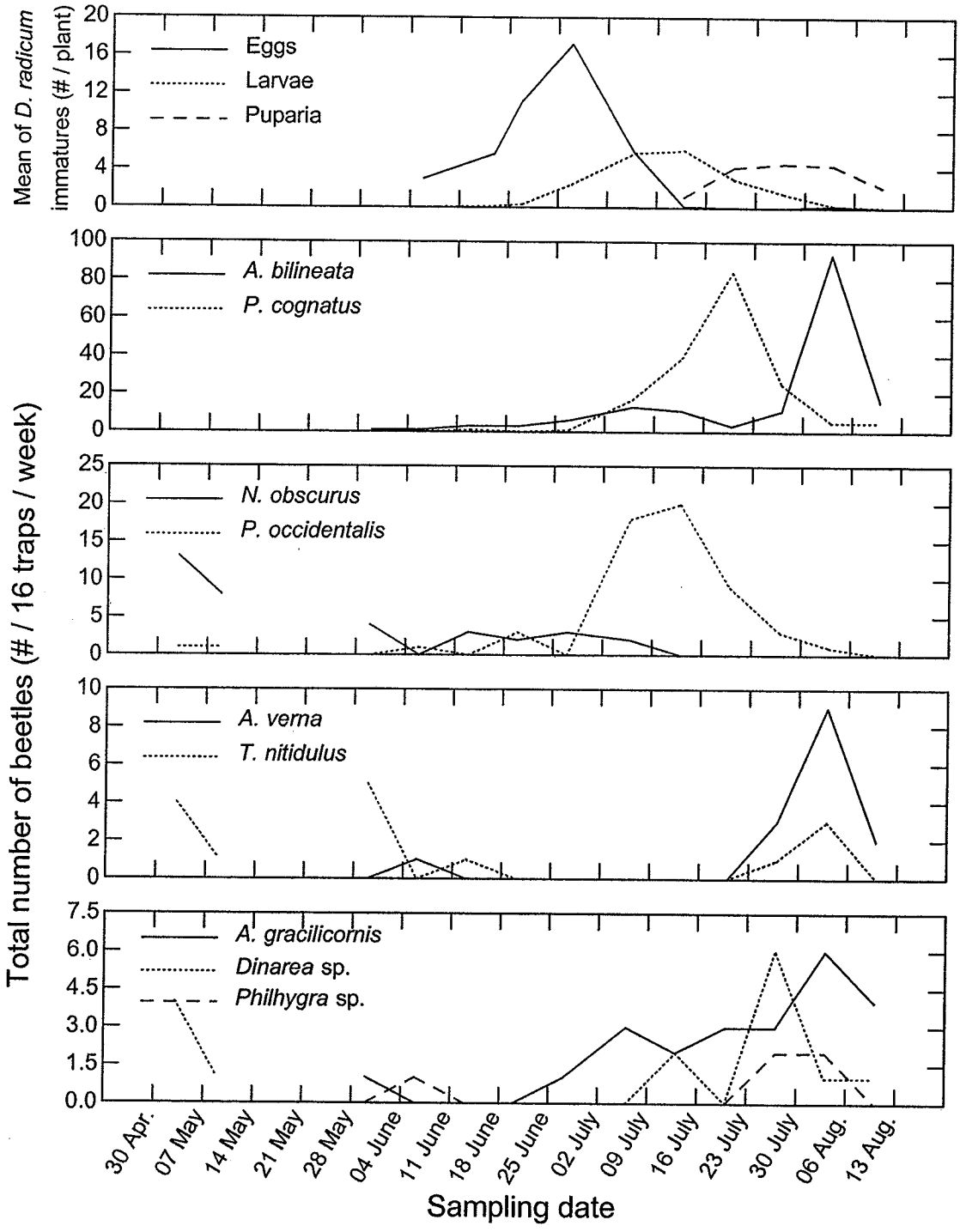

Figure 7.2 Numbers of staphylinid beetles caught in pitfall traps in relation to prevalence of *Delia radicum* immatures in canola fields in Carman in summer 2000. Data for *D. radicum* abundance are from Hawkins-Bowman (personal communication).

CHAPTER 3 SECTION 8

Effect of duration of cold exposure and warming rate after cold exposure on adult emergence of *Delia radicum*

Introduction

Delia radicum (L.) is an important pest insect in Europe and North America (Finch, 1989). *Delia radicum* undergoes facultative diapause, and can be reared without diapause in the laboratory for use in experiments (Read, 1969; Whistlecraft *et al.*, 1985b). In studies of the ecology of *D. radicum*, rearing of field-collected puparia is necessary. Puparia collected in diapause in the field require a cold period (<10°C) for diapause development (Coaker and Wright, 1963; Collier and Finch, 1983a, 1983b) and the necessary duration of the required cold exposure varies with geographic location of puparia population (Collier and Finch, 1983b). The required cold period for *D. radicum* puparia has not been documented for Western Canada.

Upon completion of diapause development, *D. radicum* requires a period of warm temperature for post-diapause development; optimal conditions for this development are 20°C and 16:8 L:D (Collier and Finch, 1983a, 1983b). The rate of transition from cold temperature to warm temperature may have an effect on survival of *D. radicum*; rapid transfer of puparia from 1°C to 20°C could be a thermal shock for *D. radicum*. Hence information on warming of diapausing *D. radicum* puparia would be useful for laboratory experiments.

The objectives of this study were to assess the minimum cold period required for diapause development in *D. radicum* and to identify appropriate procedures for raising puparia from 1 to 20°C after diapause development for *D. radicum* collected in canola in Saskatchewan.

Methods

Effect of duration of cold exposure

To examine the effect of duration of cold period on adult eclosion, field collected *D. radicum* puparia were exposed to 1°C for different durations, followed by a period of 20°C until adult emergence. *Delia radicum* puparia were collected in experimental canola plots at the Saskatoon Research Center on 18 and 25 October 2001 and in a commercial canola field at Shellbrook on 16 October 2001. The puparia collected on 16 and 18 October were delivered by hand to Winnipeg whereas the puparia collected on 25 October were mailed to Winnipeg. The puparia were stored as batches in 500 ml plastic containers with moist soil during transport and kept at 4°C at all possible times.

Upon receipt of the puparia at the University of Manitoba, Winnipeg, the puparia were cleaned by rolling them on a moist paper towel, and were examined under a dissecting microscope (25 x) for the presence of parasitoid larvae. Unparasitized puparia were used in this experiment. The puparia collected on each date were assigned randomly to five treatments. The treatments were 16, 17, 19, 20 and 21 weeks of cold exposure at 1°C. The puparia were individually placed with moist medium grade vermiculite in vials, (5 cm height, 2.2 cm diameter) (Premo®, BC, Canada). All the puparia were kept in continuous darkness at 1°C from 3 November 2001 onwards in an incubator raised to 50–60% relative humidity by means of an open water pan. The cold period was terminated on 23 February, 2, 16, 23 and 30 March 2002 by warming the puparia to 20°C within two days. At 20°C the puparia were exposed to a light regime of 16:8 h L:D.

After the vials were transferred to 20°C, the puparia were checked several times for adult eclosion. Puparia, from which no eclosion of adults had occurred after three

months, were dissected to determine the status of development. From the dissection, it was determined whether pupae had died without developing to the adult stage, termed early death, or whether pupae had developed to adult but had not emerged, termed late death. The data were analyzed using log linear modeling of contingency tables.

Effect of warming rate

Field collected *D. radicum* puparia were warmed at different rates after a fixed chilling period and examined for adult eclosion. *Delia radicum* puparia were collected in a commercial canola field on 6 October 2000 at Shellbrook, Saskatchewan. The collected puparia were mixed with 300 ml of moist soil and stored in 500 ml plastic cups. Each cup contained about 250 puparia. The puparia were exposed to 1°C in continuous darkness for a period of 21 weeks from 10 October 2000 to 5 March 2001.

During the last week of the cold exposure period, the apparently healthy puparia were packed in Falcon® ELISA micro-well plates so they could be handled easily. Two sets of 40 puparia each were packed in one micro-well plate, a process that took <30 min and was performed at room temperature. Each plate had 96 wells, and the two sets of puparia were separated by leaving 16 empty wells. A thin sheet of sponge was placed between the lid and plate, and the plate was tightly closed using masking tape. The sponge sheet prevented escape from micro-wells of the emerged adults. Upon the completion of 21 weeks of cold exposure at 1°C, eight micro-well plates were randomly assigned to four different warming rates. Hence, 160 puparia in four sets in two micro-well plates were exposed in each warming rate treatment. In each treatment, the temperature was raised from 1°C to 20°C through steps at 5°C, 10°C and 15°C. The four warming rate treatments were provided by keeping puparia at each of the three

temperature steps for 1, 2, 4 or 6 days. After proceeding through the three temperature steps, puparia were held at 20°C until emergence. Thus the four warming rates resulted in puparia changing from 1°C to 20°C in 3, 6, 12 or 18 days. A 16:8 h L:D photoperiod was provided during warming and at 20°C until adult emergence.

Adult eclosion was recorded daily from the first eclosion of adults until no further eclosion of adults occurred. Puparia from which there was no emergence were dissected to determine whether pupae had died without developing to adult, termed early death, or had developed to adult but had not emerged, termed late death. The data for total eclosion were analysed using contingency tables, and the relation of emergence patterns to time were compared using logistic regression.

Results

Effect of duration of cold exposure

The duration of the cold period to which puparia were exposed did not significantly affect the frequency of adult eclosion, early death or late death (Likelihood Ratio (L.R.) $\chi^2 = 2.0$, df = 8, $P = 0.981$) (Fig. 8.1). On average, the percentage of adult eclosion in all the treatments was 54.5 ± 6.2. Per cent of early death puparia was 41.3 ± 0.6 and late death puparia was 4.3 ± 0.6%. Location of the puparial collection significantly affected adult eclosion and pupal mortalities (L.R.$\chi^2 = 76.9$, df = 2, $P < 0.001$). On average, 82.0 ± 2.3% of puparia collected at Shellbrook in commercial canola fields survived to adult eclosion. In contrast, adult eclosion was low in the puparia collected in Saskatoon, and adult eclosion on average was 40.7 ± 4.9%.

Percentage of early death in puparia which were collected in Saskatoon was higher, 54.9 ± 4.9%, than the early death of Shellbrook puparia which was 14 ± 1.7%.

Per cent of late death of puparia which were collected in Saskatoon and Shellbrook were 4.4 ± 06 and 4.0 ± 1.3 respectively. The method of transportation did not significantly affect adult emergence, early death or late death (L.R.$\chi^2 = 0.5$, df = 2, $P = 0.763$).

Effect of warming rate

Flies emerged from 78.9% of the puparia used in the experiment. Of all puparia, 66.4% produced *D. radicum,* 9.1% produced *T. rapae,* 3.4% produced *Aleochara* and 10.8% were classified after dissection as "early death". From dissection, 7.2% of puparia were late death *D. radicum* and late death *T. rapae* and *Aleochara* sp. were found in 2.8% and 0.3% respectively. Only naturally emerged flies were considered to examine the effect of warming period on adult emergence.

The speed of warming did not significantly affect fly emergence (L.R.$\chi^2 = 2.3$, df = 3, $P = 0.508$) (Fig. 8.2). The relation between emergence of flies and time at 20°C for all four warming periods followed a sigmoid curve, fitted by a logistic regression, and warming rate affected the pattern of fly emergence (L.R.$\chi^2 = 222.6$, df = 3, $P < 0.001$) (Fig. 8.3). The interaction of regression slope with warming period was significant (L.R.$\chi^2 = 76.7$, df = 3, $P < 0.001$). Thermal accumulation of puparia after post-diapause development was calculated using 4°C as the lower threshold temperature for post-diapause development of *D. radicum* pupae (Collier and Finch, 1985). Hence, when puparia reached 20°C within 3, 6, 12 and 18 day warming periods they had accumulated 18, 36, 72 and 108 DDC respectively. The warming rate significantly affected the relationship between fly emergence and degree day accumulation (L.R.$\chi^2 = 64.0$, df = 3, $P < 0.001$) and also the interaction between warming period and degree day accumulation was significant (L.R.$\chi^2 = 76.2$, df = 3, $P < 0.001$) (Fig. 8.4). The thermal

accumulation at the 50th percentile of fly emergence was greatest at the longest period of warming rate, and it ranged from 517–555 DDC above 4°C.

Discussion

The minimum cold period required for diapause development of *D. radicum* pupae appeared to be ≤16 weeks, and longer cold exposures did not affect the percentage of adult emergence. The minimum cold exposure required for diapause development was variable in previous studies (Coaker and Wright, 1963; Collier and Finch, 1983a, 1983b). For example, in a population of *D. radicum* from Wellesbourne, U.K. a minimum of 15 weeks cold period (5°C) was required for termination of diapause, and less than 15 weeks cold period resulted in a low percentage of adult emergence (Coaker and Wright, 1963). Collier and Finch (1983b) confirmed that the minimum cold period required for diapause development was 15 weeks for a population at Wellesbourne. Nevertheless, flies emerged within a period of 40 days from 70% of puparia which had been exposed to a 12 week cold period (Collier and Finch, 1983b). Whistlecraft *et al.* (1985b) suggested that the minimum cold period required for diapause development was 16 weeks. Johnsen *et al.* (1997) estimated that the minimum cold period required for diapause development was 17 weeks for a *D. radicum* population in Denmark. From my study, field collected *D. radicum* puparia from Saskatchewan can be used in laboratory experiments after a minimum of 16 weeks cold period.

It appears that rapid post-diapause warming does not increase mortality of *D. radicum* or fly emergence. Warming rate affects the pattern of fly emergence. The time required for post-diapause development decreases with increasing temperature (Collier *et al.*, 1989), although temperatures above 21°C delay fly emergence (Finch and

Collier, 1985). In this study, 50% of flies emerged after accumulation of 517–555 DDC, which was higher than the estimations of Eckenrode and Chapman (1971), Collier and Finch (1985), Walgenbach *et al.* (1993), and Biron *et al.* (1998) using *D. radicum* from brassica vegetables (Fig. 8.5). These studies are like mine in which diapaused puparia were incubated at 20°C in the laboratory; studies using field emergence in relation to air or soil temperatures (Eckenrode and Chapman, 1972; Nair and McEwen, 1975; Wyman *et al.,* 1977; Bracken, 1988) are not directly comparable. Generally, there are early, intermediate and late emerging flies in a *D. radicum* population (Finch and Collier, 1983). Early emerging flies emerge within 14 days at 20°C after completion of diapause development, and represent about 67% of the population in Europe (Finch and Collier, 1983). However, the proportion of an early emerging population is variable with geographic locations (Walgenbach *et al.,* 1993; Turnock and Boivin, 1997). Per cent of early emerging fly population varies among years and it raged from 31 to 90% among nine years in a population in rutabaga at Winnipeg (Turnock and Boivin, 1997). Close inspection of Fig. 8.3 shows that 4–12% of the population in my study would conform to the definition of early emerging flies, and that this group is somewhat separated from the main body of emergence. When the early emergence per cent was 23% in a *D. radicum* population in rutabaga at Winnipeg, 50% of fly emerged at the accumulation of about 500 DDC (base at 4°C) (Turnock and Boivin, 1997).

The much higher thermal requirements of the *D. radicum* population in this study compared with those from brassica vegetables implies a delay, compared with other populations, in emergence of the order of one month under average conditions in Saskatchewan canola growing regions (Fig. 8.5). The emergence pattern of insects is

influenced by availability of resources, mates, predictability of resources (Waldbauer, 1978) and agricultural practices in the area (Walgenbach *et al.,* 1993; Turnock and Boivin, 1997). Canola on the Canadian Prairies is suitable for *D. radicum* oviposition generally later than brassica vegetables, so *D. radicum* might have been selected for late emergence. In addition, climate is less variable in European locations than on the Canadian Prairies and climatic variability may have an effect on time of fly emergence.

In summary, the proportion of adult emergence from *D. radicum* puparia collected in Western Canada does not change with increasing cold period (1°C) above 16 weeks. After a cold period, puparia can be warmed to 20°C within 3 days without affecting the proportion of adult emergence. The post-diapause thermal requirements for adult emergence in this study were much greater than in previous studies using *D. radicum* from brassica vegetables, likely an adaptation to host plant availability.

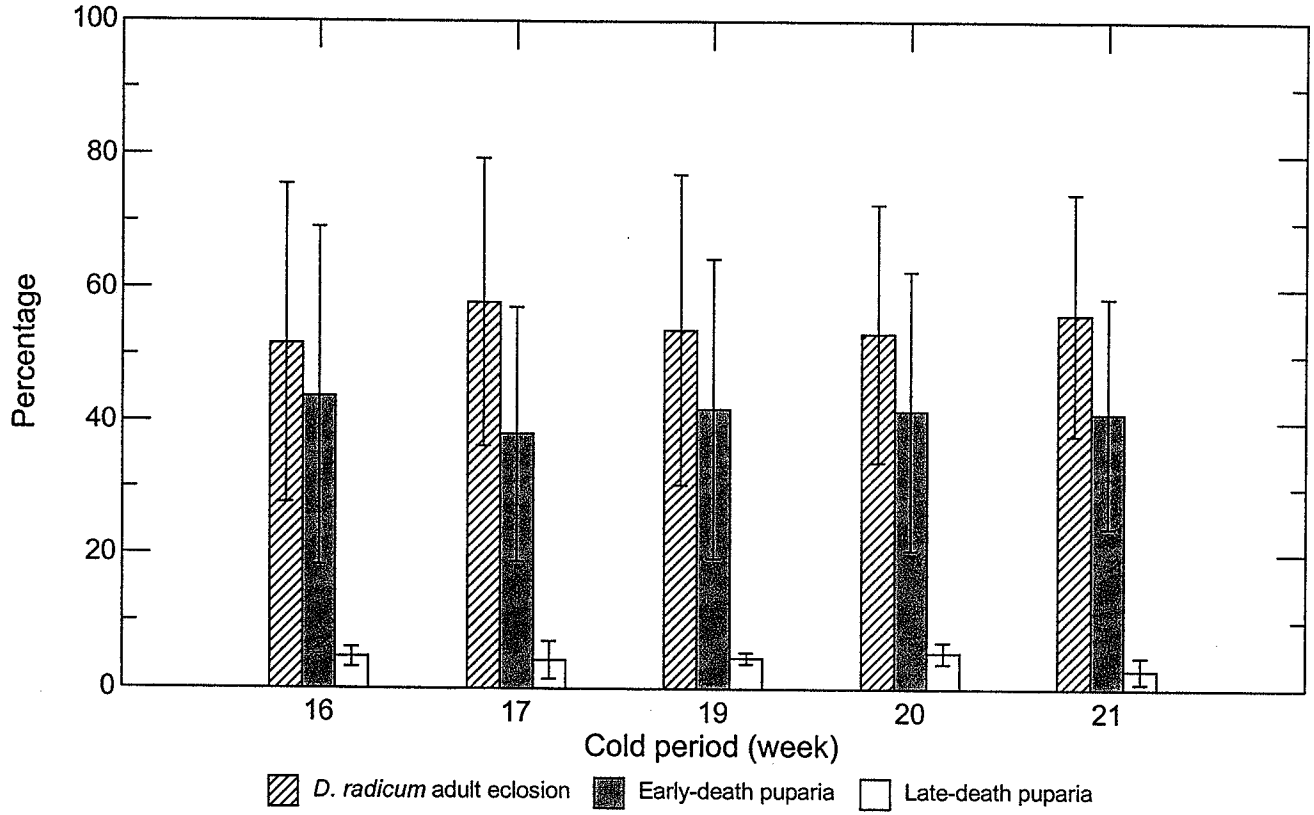

Figure 8.1 Fate of *Delia radicum* puparia when they were exposed to different durations of cold period for diapause development.

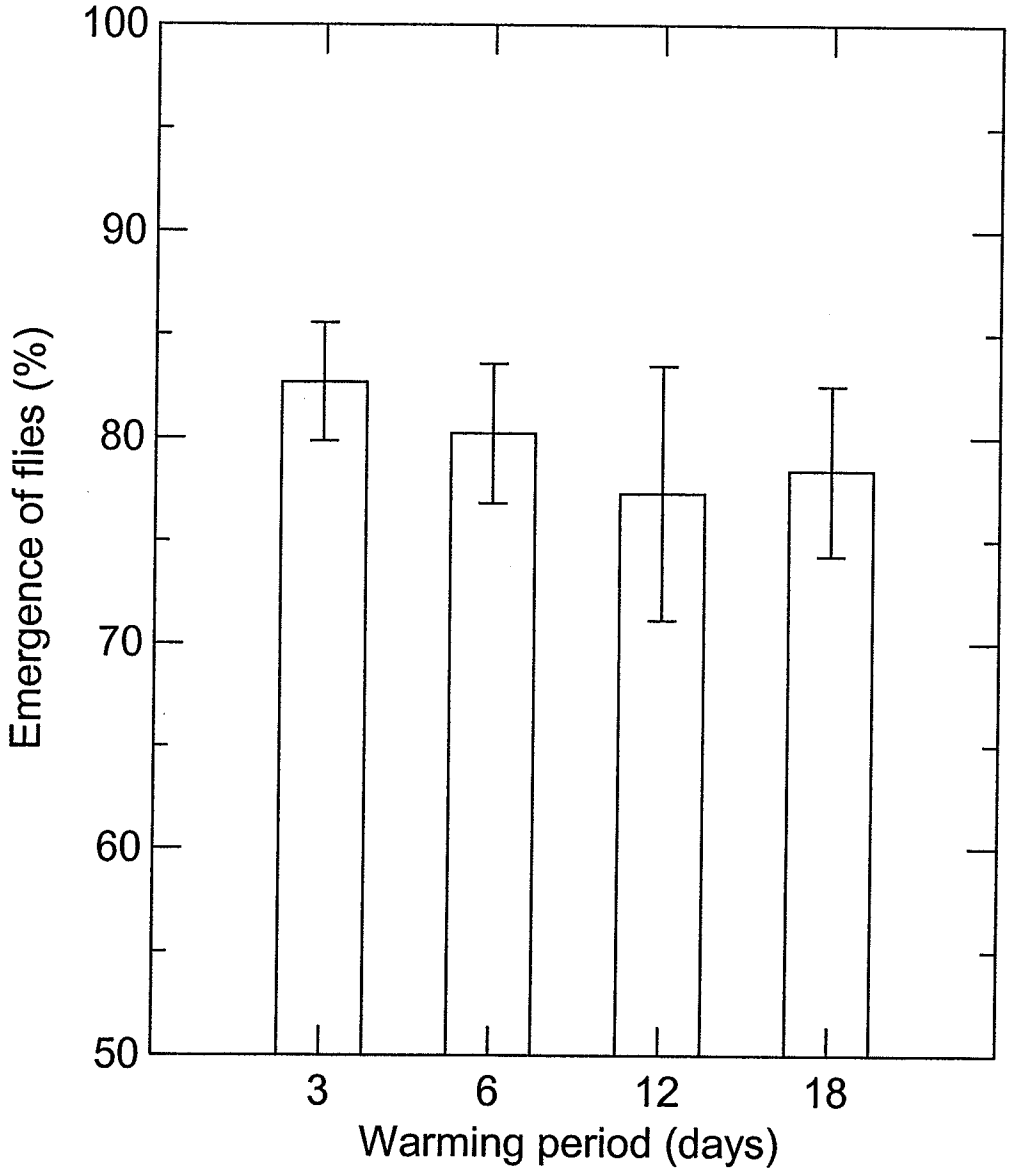

Figure 8.2 Per cent of adult *Delia radicum* emerged from pupae, when pupae were warmed from 1°C to 20°C at different rates after 21 weeks of cold exposure for diapause development.

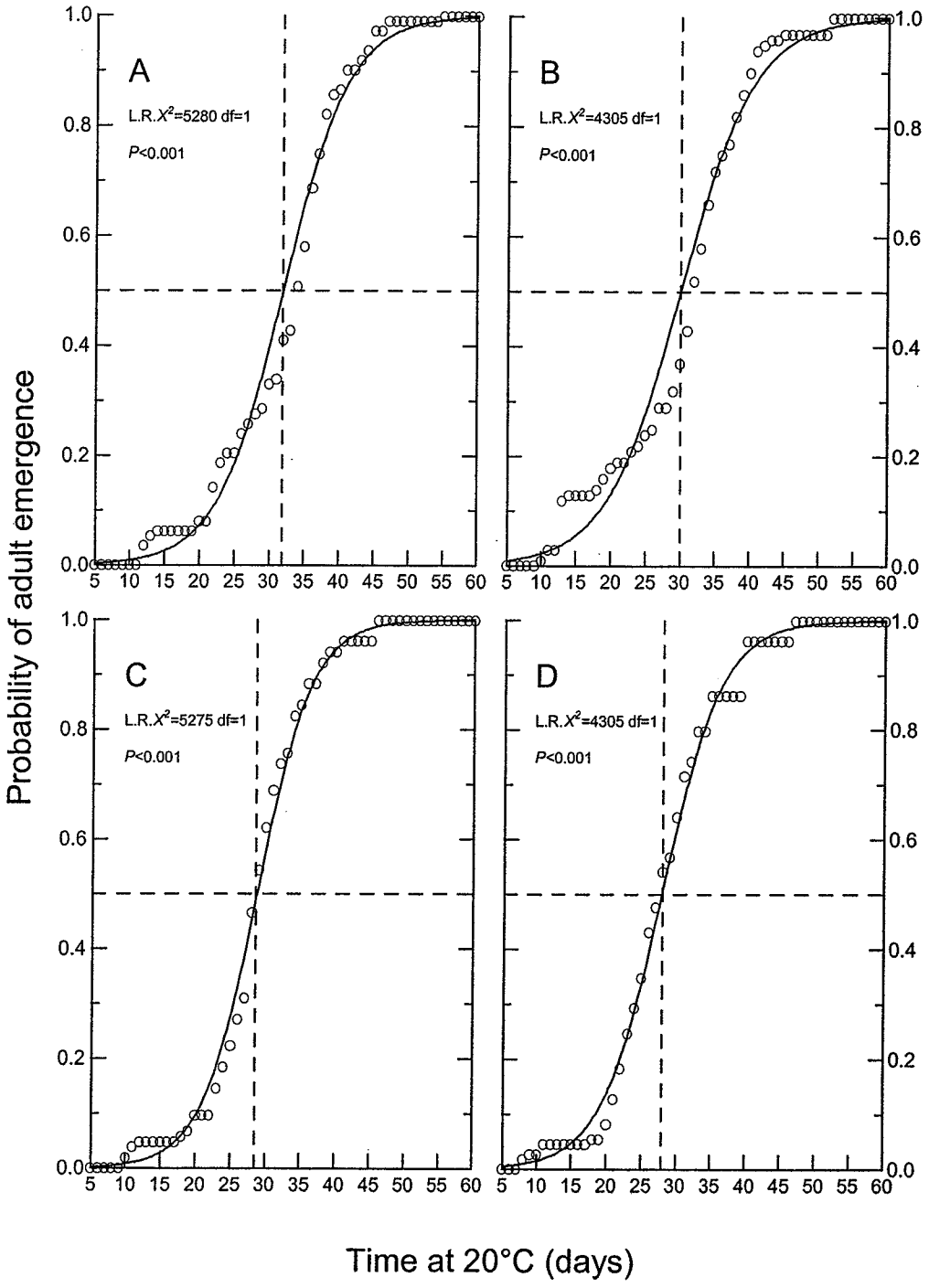

Figure 8.3 Time of emergence of adult *Delia radicum* at 20°C when puparia were brought to 20°C from 1°C within (A) 3, (B) 6, (C) 12 and (D) 18 days after 21 weeks of cold exposure for diapause development.

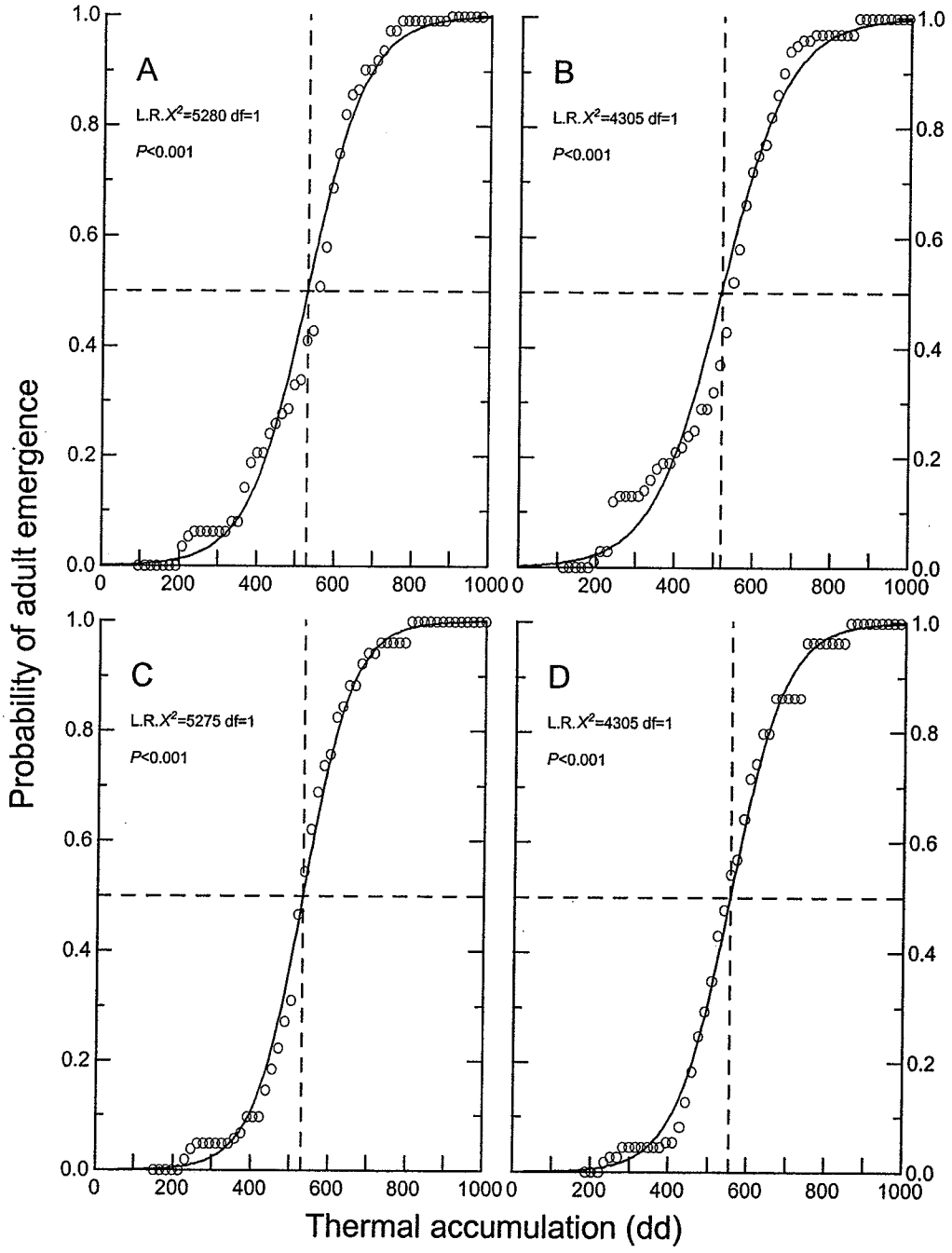

Figure 8.4 Emergence of adult *Delia radicum* in relation to thermal accumulations above 4°C when puparia were brought to 20°C from 1°C within (A) 3, (B) 6, (C) 12 and (D) 18 days after a 21 week cold exposure for diapause development.

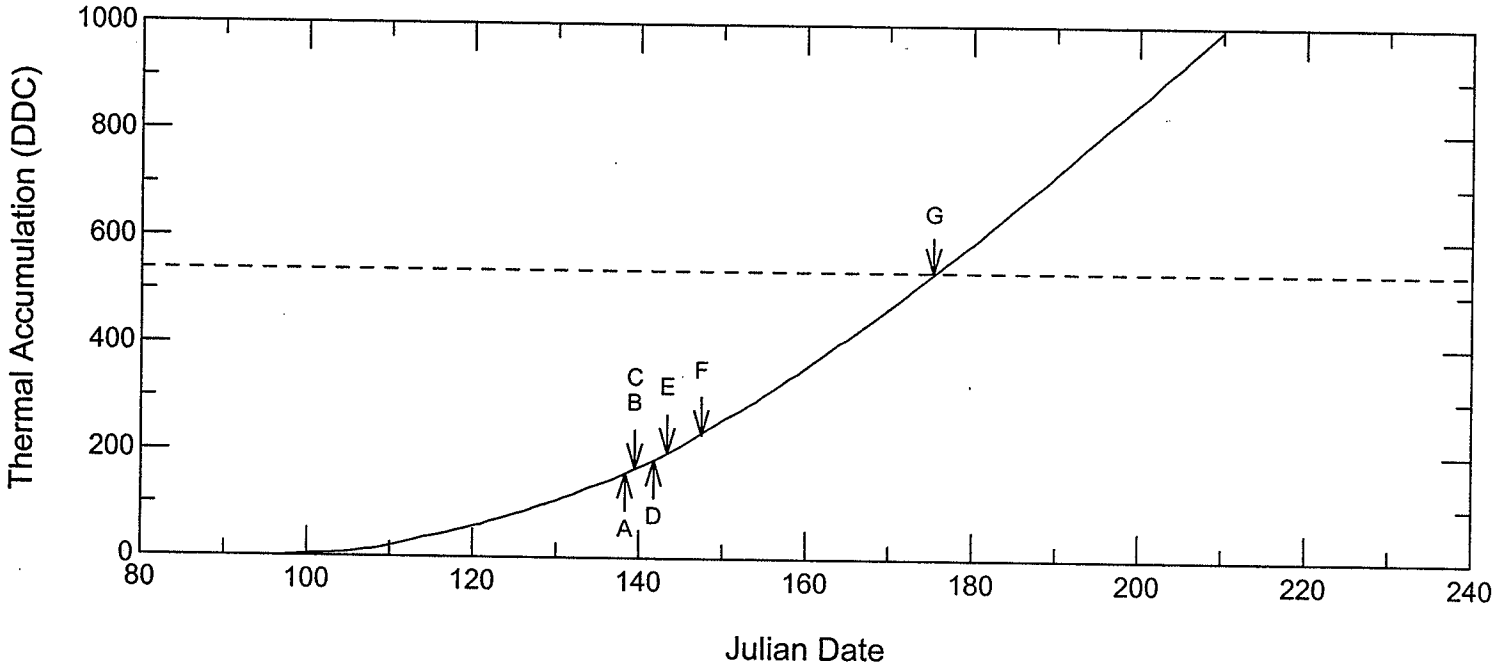

Figure 8.5 Emergence of 50% *Delia radicum* fly population from overwintered puparia in the laboratory in relation to Julian date, based upon thermal accumulation provided by the 30-year average daily maxima and minima at Prince Albert, Saskatchewan. Thermal accumulation was calculated according to Arnold (1960). Base temperature is 4°C, and populations are from (A) Quebec 160 DDC (Biron *et al.*, 1998); (B) Wellesbourne, UK 168 DDC (Collier and Finch, 1985); (C) New York 169 DDC (D) Fletcher, North Carolina 184 DDC (Walgenbach *et al.,* 1993); (E) Wisconsin 197 DDC (Eckenrode and Chapman, 1971); (F) Scaly Mountain, North Carolina 232 DDC (Walgenbach *et al.,* 1993) in brassica vegetables and (G) Saskatchewan in canola 538 DDC.

CHAPTER 4

General Discussion

Comparison of the parasitoid community of *D. radicum* in canola on the Canadian Prairies and in Europe provides a means of choosing potential parasitoids for introduction to canola on the Canadian Prairies. The importance of *D. radicum* in canola may differ among canola systems on the Canadian Prairies and Europe. Varieties of *Brassica napus* are extensively grown on the Canadian Prairies as a summer crop (Canola Council of Canada, 2004), but those varieties are mainly grown as a winter crop in Europe (Bromand, 1990). Varieties of *B. rapa* are seeded as a summer crop where the growing season is short such as in northern Alberta (Canola Council of Canada, 2004), Finland, Norway and Sweden (Bromand, 1990). *Delia radicum* is an injurious insect in summer canola on the Canadian Prairies (Soroka *et al.*, 2002), but in European summer canola, *D. radicum* is regarded as not injurious (Bromand, 1990), or as an occasional pest in summer canola in Europe (Alford *et al.*, 2003). In my study, *D. radicum* caused root injury in winter canola in Europe, but does not get the attention of canola growers due to lack of visible symptoms on aerial parts of the plant.

The parasitoid community of *D. radicum* in canola on the Canadian Prairies was not very different from that of brassica vegetables in North America. Major or abundant parasitoids in canola on the Canadian Prairies included *T. rapae, A. bilineata* and *A. verna.* Minor or less abundant parasitoids included two species of *Phygadeuon, Aphaereta minuta* and *Trichopria* species. The parasitoid community of *D. radicum* in brassica vegetables in North America includes *T. rapae* (Wishart and Monteith, 1954; Wishart, 1957; Nair and McEwen, 1975; Turnock *et al.,* 1995), *A. bilineata* (Schoene,

1916; Colhoun, 1953; Wishart, 1957; Read, 1962; Nair and McEwen, 1975; Turnock *et al.*, 1995), and *A. verna* (as *A. bipustulata* in Schoene, 1916; Wishart, 1957; Nair and McEwen, 1975). In addition, *Aphaereta pallipes* (Say) (as *auripes* (Prov.)) has been reported (Wishart, 1957; Turnock *et al.*, 1995). Hence, the major parasitoid species were present in both canola and brassica vegetables. Occurrence of minor parasitoids was not consistent between canola and brassica vegetables, probably because of differences in sampling time, sample size, and geographic location. For example, in my study, samples were taken throughout the growing season. Hence, there was a high probability of getting minor parasitoids in samples. In many of the previous studies, single puparial samples were taken in fall and the timing of this collection may exclude some parasitoid species. For example, *Phygadeuon* spp. tend to parasitize host puparia in a narrow window of time and adults emerge in the same summer. Hence, the probability of collecting a *D. radicum* puparium parasitized by a *Phygadeuon* sp. is low.

Generally, when a parasitoid species is rare in a host or in a habitat, it has a preferred host or habitat elsewhere (Wishart and Monteith, 1954). I found *A. verna* in canola but it was not found in rutabaga in a collection of 24650 puparia in five locations over several years in Manitoba, Ontario, Québec and Newfoundland (Turnock *et al.*, 1995). From my examination of museum specimens of *A. verna* (labeled as *A. bipustulata*), label information showed that *A. verna* occurred in very diverse habitats including beaches, grassland, marshland, carrion and cattle dung. In addition, *A. verna* has been collected in wet moss, forest litter, muddy soil and rotting mushrooms (Klimaszewski, 1984). Therefore, it could be suggested that either *A. verna* prefers the canola habitat to the brassica vegetable habitat or that collection of *A. verna* in canola

was related to greater sampling efficiency. In addition, the preference of *A. verna* in diverse habitats suggests that *A. verna* could be an opportunistic generalist that concentrates on available hosts. In western Canada, *D. radicum* in canola represents an enormous host resource. Vegetable brassicas tend to be in small areas and, so *A. verna* may rely on hosts in dung, carrion etc. in localities where the only *D. radicum* are in small patches. This may explain the finding of *A. verna* in canola but not in brassica vegetables in Western Canada.

The parasitoid community of *D. radicum* in canola in Europe was not very different from that of brassica vegetables in Europe. The parasitoid community of *D. radicum* in my European study in canola included *T. rapae, A. bilineata,* and *A. bipustulata* as major parasitoids. Minor parasitoids included *Phygadeuon trichops,* an undescribed *Phygadeuon* species, *A. brevipennis* and a *Trichopria* species. Major parasitoids in brassica vegetables included *T. rapae, A. bilineata* and *A. bipustulata* and minor parasitoids included *Phygadeuon* sp. In previous studies, a few other minor parasitoids species have been reported in brassica vegetables, including *Phygadeuon fumator* (Grav.) (Wadsworth, 1915a; Wishart *et al.,* 1957), *Aphaereta difficilis* Nees, *Aphaereta tennuicornis* Nix (Wishart *et al.,* 1957); *Dacnusa stramineipes* Halid (Smith, 1927), *Loxotropa tritoma* (Thoms.) (Wishart *et al.,* 1957), *Trichopria cilipes* Kieff, (Adashkevich, 1983), *Aleochara binotata* Kraatz (Jonasson, 1994), *A. brundini* Bernh (Jonasson *et al.,* 1995) and *A. curtula* (Goeze) (Peschke and Fuldner, 1977). As with the Canadian parasitoid community, differences in species composition of the parasitoid community of *D. radicum* in canola and brassica vegetables in Europe may be related to sampling time, sample size and sampling location.

The parasitoid community of *D. radicum* in canola on the Canadian Prairies was different to that of canola in Europe. Two undescribed *Phygadeuon* species and *A. verna* were found on the Canadian Prairies but not in Europe. One undescribed species of *Phygadeuon, P. trichops* and *A. bipustulata* were found in Europe but not on the Canadian Prairies. *Aleochara verna* has been found in Europe (Rämert *et al.*, 2002), but I did not find *A. verna* in my samples in canola or brassica vegetables. This leads to the speculation that in the large areas of canola in the Prairies *A. verna* has shifted hosts to exploit the availability of *D. radicum,* but that in the smaller cropping systems of brassica vegetables and European scale canola production this shift has not occurred.

Biological characteristics of *T. rapae* suggest that it is an important biocontrol agent of *D. radicum*. The host search behaviour of *T. rapae* is highly specialized and leads to high levels of parasitism of *D. radicum* larvae. *Trybliographa rapae* responds to chemical cues from host larvae, frass and damage tissues of host plants (Brown and Anderson, 1999). Visual cues are less important in the host search process (Jones, 1986). Furthermore, *T. rapae* did not limit the host search to a particular habitat. In this study, parasitism was found in brassica vegetables and in canola. Hence, it appears that the habitat structure of theses two crops does not inhibit host searching, and *T. rapae* is able to follow the host species. Female *T. rapae* crawl through the soil to find host larvae for oviposition (Jones, 1986). I found that *T. rapae* females were not capable of reaching depths $\geq$6 cm from the soil surface. *Delia radicum* larvae feed on summer canola roots at 0–7 cm area from soil surface. Therefore, a portion (10–40%) of the population of *D. radicum* larvae is in a refuge from *T. rapae* parasitism. *Trybliographa rapae* responds to host density in the search for hosts for oviposition. The probability of having at least

one parasitized host per plant increases with host density (Langer, 1996) (Chapter 3 Section 4), but there is no consistent relationship between parasitism and host density (Langer, 1996) (Chapter 3 Section 4). Lack of a positive relationship between host density and parasitism may be related to egg limitation, or to a fixed giving up time for search on a single plant (Godfray, 1994). Diameter of brassica roots at soil level was positively correlated with number of *D. radicum* larvae on the root. Parasitism of *D. radicum* larvae on a root was positively correlated with the root diameter at soil level. Even though, the parasitism level was inconsistent with host density, the positive relation between root diameter and parasitism suggests that *T. rapae* visits more frequently large root brassica plants than small root brassica plants.

Temporal synchronization of host and parasitoid is important for survival of a parasitoid population (Godfray, 1994). Time of emergence of parasitoid adults after diapause compared to the time of host emergence, longevity of adult females and duration of the oviposition period all affect host-parasitoid synchronization. In this study, *T. rapae* was synchronized in five locations and was not synchronized in five other locations with parasitism being a few days early or late. A few days early or late would probably not affect the parasitism because adult *T. rapae* live on average 21 days (Wishart and Monteith, 1954) and lay eggs over 10 days (James, 1928). In Europe, *D. radicum* emerges in April (Miles, 1956) or early May (Finch *et al.*, 1975) depending on geographical location and *T. rapae* were available in the field to parasitize the *D. radicum* larvae. On the Canadian Prairies, *D. radicum* emerged in June and *T. rapae* were available in the field to parasitize *D. radicum* larvae although at both sites with adequate numbers for study, parasitism was slightly delayed. Therefore, it can be

concluded that the mechanisms of temporal synchronization of *T. rapae* with *D. radicum* are quite well adapted in both Europe and the Canadian Prairies.

Generally hosts and parasitoid populations are synchronized in the spring as a result of their responses to diapause induction and post-diapause development. In some parasitoid species, diapause status of the host dictates the diapause status of the parasitoid (Schoonhoven, 1962; Tauber *et al.*, 1983). Wishart and Monteith (1954) suggested that diapause status of *D. radicum* dictates the diapause status of *T. rapae*; however, my results from canola in Canada did not support this. In my study, most *D. radicum* from the Prairies diapaused but about 50% of *T. rapae* emerged in the same summer. The emergence of *T. rapae* in the laboratory might be the effect of reversal of diapause induction by the unusual exposure to warm temperatures and long days in the laboratory. If *T. rapae* had not diapaused in the field, they would have emerged in the third week of August or later. Fitness of emerged adults would be low because there were no *Delia* larvae in canola by the end of August. On the other hand, it could be that *T. rapae* has characteristics that are adaptive in brassica vegetables in which two or more generations of *D. radicum* are possible per year. Even though host and parasitoid may have shifted from brassica vegetables to canola, perhaps *T. rapae* has not yet responded to selection for synchrony with the host in the canola system. Further examination of emergence patterns is needed to confirm the diapause behaviour of *D. radicum* and *T. rapae* in the field.

Diapause induction of *D. radicum* and parasitoids was not examined in Europe because there were not enough diapausing insects in any of the sampling sites. *Trybliographa rapae* may emerge in the same summer and complete at least two

generations. *Delia radicum* completes two or three generations in Europe (Finch, 1989); hence, there will not be a shortage of *D. radicum* larvae for parasitization. For example, *D. radicum* larvae collected in August at Grundhof were parasitized by *T. rapae*, and this indicated that parasitoids were active in the latter part of summer.

The biological characteristics of *A. bilineata* suggest that it is an important biocontrol agent of *D. radicum*. Adult females respond to chemical cues originating from *D. radicum* larvae, frass and brassica host plants (Royer and Boivin, 1999; Fournet *et al.*, 2000). The parasitoid also responds to host density (Langer, 1996), probably as a result of responses to the semiochemicals of the host. I found a positive relationship between host density and the probability of at least one host being parasitized per plant, as did Langer (1996), but I did not find a positive relationship between the parasitism and host density. Response to chemical cues and host density by adult beetles increases the probability of the first-instar *Aleochara* larvae finding host puparia. *Aleochara bilineata* does not limit its host search to a particular habitat. I found *A. bilineata* parasitism in brassica vegetables and canola. Hence, it appears that the structure of the habitat in which hosts live does not greatly influence host search, and *A. bilineata* is able to follow the host species.

The diapause behaviour of *A. bilineata* affects voltinism and synchrony with host puparia in the following generation. *Aleochara bilineata* diapause as a first-instar larva and, subsequent larval development takes place in the spring (Colhoun, 1953). Hence, it is important to have living hosts until the end of winter. The parasitoid does not survive within a puparium with a dead host pupa (Jonasson, 1994). Non-diapausing host puparia do not survive more than eight weeks at low temperatures (Whistlecraft *et al.*, 1985a).

Therefore, *A. bilineata* cannot diapause within a non-diapausing host puparia. In this study, *A. bilineata* collected in early summer in parasitized host puparial, emerged in late summer in the laboratory. If they had emerged in the field, peak emergence would be in the second week of September because development time from egg to adult is one month at 22°C (Read, 1962; Bromand, 1980). In mid September, the canola crop had been harvested, and there were no canola roots with fresh *D. radicum* damage. Hence, fitness of emerged beetles in mid September would be low because the probability of finding a host plant with host puparia around it is low. In this study, the population of *A. bilineata* in the canola field at Carman reached a peak in late August, as indicated by pitfall catches. A certain proportion of *A. bilineata* emerge in the same summer, probably from the parasitized non-diapausing host puparia. At this time, first-instar larvae may find diapausing host puparia in the field for parasitization. The first-instar larvae are capable of parasitizing puparia of any age (Bromand, 1980). Therefore, unlike in *T. rapae*, *A. bilineata* may contribute progeny to the next generation. Even though *D. radicum* and *A. bilineata* responded differently to diapause induction cues, *A. bilineata* may survive in canola. It is plausible, that observed emergence of beetles in the laboratory could be an effect of warm rearing temperatures and long days reversing diapause induction that had occurred during exposure in the field. Further research is needed to confirm the pattern of adult emergence of *A. bilineata* in the field on the Canadian Prairies.

Generally, adult *A. bilineata* emerge later than *D. radicum* in spring in Prince Edward Island (Read, 1962). As a result, *A. bilineata* may not reach its full potential as a *D. radicum* egg predator (Read, 1962; Jonasson, 1994). Therefore, inundative release of *A. bilineata* in synchrony of *D. radicum* eggs in the field has been suggested

(Whistlecraft *et al* 1985a; Bromand, 1980). Difficulties of mass production to meet the rate of release, 20000–65000 beetles per ha, distribution of beetles in the field and effect of inundative release of beetles on existing predatory beetles makes it less practicable (Finch, 1996). Late emergence of *A. bilineata* adults leads to synchrony of its first-instar larvae with *D. radicum* puparia in the field (Ahlström-Olsson and Jonasson, 1992).

Generally, *D. radicum* in brassica vegetable fields emerge earlier in the spring than I observed in canola in Canada. Post-diapause thermal accumulations of 230 DDC (base 4°C) were required for emergence of 50% of population in brassica vegetable fields in European populations (Collier and Finch, 1985). In the laboratory, 50% of flies emerge upon the accumulation of 160–197 DDC (base 4°C) (Eckenrode and Chapman, 1971; Collier and Finch, 1985; Biron *et al.*, 1998). In my laboratory study, 50% of *D. radicum* flies emerged after accumulation of 517–550 DDC (base 4°C) for the puparia collected in Saskatchewan. In European locations the climate is less variable than in Canada. Brassica crops are available and suitable for oviposition earlier in spring than in canola. Early emergence of flies allows *D. radicum* to complete several generations in brassica vegetables. Canola plants suitable for *D. radicum* oviposition are not available in early spring; hence, there is no advantage to *D. radicum* emerging early in the spring on the Canadian Prairies. Therefore *D. radicum* may have been selected to emerge late in canola the Canadian Prairies. In this study, there was a 3–9 day gap between occurrence of 50% parasitism and 50% of unparasitized puparia. Moreover, parasitized puparia were found in the first sample of puparia. Early occurrence of *A. bilineata* affects potential parasitism of *D. radicum*.

Occurrence of *A. bilineata* larvae earlier than occurrence of *D. radicum* puparia may be possible if the *A. bilineata* population has not been selected for the conditions on the Canadian Prairies in canola. This raises an important issue with respect to introduction of parasitoids from Europe. Parasitoids taken from European *D. radicum* requiring 197 or fewer DDC may not survive because of the delay in appearance of host stages for parasitism in canola on the Canadian Prairies.

As the population of *D. radicum* in the Prairies appears to be increasing (Soroka *et al.*, 2002), *T. rapae, A. bilineata,* and other mortality factors are insufficient to suppress *D. radicum* populations and there is a need for additional biocontrol agents. In comparing the parasitoid community of *D. radicum* on the Canadian Prairies with that of Europe, it appears that *A. bipustulata* is the most promising candidate. *Aleochara bipustulata* is one of the parasitoids found only in Europe. The previous records of *A. bipustulata* in North America are erroneous, which was confirmed by the examination of museum specimens collected in North America that were alleged to be *A. bipustulata.* North American and European *Aleochara* taxonomists agree that *A. bipustulata* has been found only in Europe (Klimaszewski, 1984; Maus, 1996, 1998).

From biological characteristics of *A. bipustulata,* it appears to have a potential as a biocontrol agent of *D. radicum* (Fuldner, 1960; Fournet *et al.*, 2000). *Aleochara bipustulata* overwinters as an adult (Fuldner, 1960); therefore, it is active in the spring earlier than *A. bilineata* (Jonasson, 1994). As a result, adult *A. bipustulata* may be better synchronized with the occurrence of *D. radicum* eggs in the field, though there is a high *D. radicum* egg predation by other general predators (Mukerji, 1971). Fecundity, longevity and intrinsic rate of increase of *A. bipustulata* reveal that *A. bipustulata* has a

high potential as a biocontrol agent (Fournet *et al.*, 2000). *Aleochara bipustulata* coexists with *A. bilineata* (Rämert *et al.*, 2002) and appears to be more abundant in more northerly areas e.g. Sweden (Jonasson, 1994) than in lower latitudes e.g. Switzerland. In addition, Ahlström-Olsson (1994b) suggested that *A. bilineata* and *A. bipustulata* respond to the size of host puparia leading to possible niche separation. However, I was unable to show a similar trend of host size discrimination. There may be niche separation of *A. bilineata* and *A. bipustulata* related to differences of temporal occurrence.

In this study, *A. verna* was found only in Canada, but *A. verna* also exists in Europe and coexists there with *A. bipustulata* (Klimaszewski, 1984; Whitehead, 1993; Rämert *et al.*, 2002). It has been recorded in brassica vegetables in Canada and occupies diverse habitats (Klimaszewski, 1984; Whitehead, 1993). *Aleochara verna* parasitizes *Delia* species associated with brassica plants and several other host insect species (Maus *et al.*, 1998). Previous records on host range and occurrence should be used with caution because records of *A. verna* before Lohse (1986) could refer to *A. binotata* Kraatz or *A. bipustulata* (Maus *et al.*, 1998).

Two species of *Phygadeuon* were found on the Canadian Prairies whereas one undescribed species was found in Europe. If the undescribed species in Europe was different from the Canadian species, then the European species may be considered for introduction. However, *Phygadeuon* species are a taxonomically difficult group, and are generally polyphagous and opportunistic (Horstmann, personal communication). Polyphagous parasitoids may shift among hosts depending on host availability, and frequently the resulting parasitism level is low (Huffaker *et al.*, 1976). In addition, polyphagous parasitoids pose a potential risk for non-target organisms in the target

introduction area (Mason and Kuhlmann, 2002). Therefore, *Phygadeuon* spp. are not suitable candidates for introduction.

From comparisons of the parasitoid community of *D. radicum* in canola on the Canadian Prairies and in Europe, two parasitoid species were identified as potential biocontrol agents. After assessing the characteristics of these two species, it is recommended that *A. bipustulata* be considered the most promising candidate for introduction to canola on the Canadian Prairies to impose added mortality on *D. radicum.*

Directions for future research

In the proposed system, *A. bilineata, A. bipustulata, A. verna* and *T. rapae* would parasitize *D. radicum* in canola on the Canadian Prairies. Potential interactions among parasitoid species could affect the level of *D. radicum* control in canola. I found that all three *Aleochara* species are capable of surviving in the canola system. Furthermore, *A. verna* coexists with *A. bipustulata* (Rämert *et al.*, 2002), and *A. bipustulata* coexists with *A. bilineata* in European fields that I studied. I did not find *A. verna* and *A. bipustulata* together with *A. bilineata* in the canola system in Europe. Therefore, the interaction of all three species together and the resulting level of control of *D. radicum* should be examined in detail before the introduction. Potential displacement of already established parasitoid species is a major concern and competition among congeneric species is quite probable and therefore, needs further investigation. In addition, the effect of *Aleochara* species on *T. rapae* needs to be investigated in the canola system. The effect of introducing parasitoid species on non-target hosts is a concern of researchers and the general public, hence additional work on non-target hosts is required, particularly given the taxonomic confusion before Lohse (1986).

CONCLUSIONS

- *Trybliographa rapae* and *A. bilineata* were present on the Canadian Prairies in canola and Europe in canola and brassica vegetables.
- *Aleochara bipustulata* was present in canola and brassica vegetables only in Europe; it does not exist in North America.
- *Aleochara verna* was present in canola on the Canadian Prairies.
- *Aleochara bipustulata* is the most promising candidate for introduction to suppress *D. radicum* in canola on the Canadian Prairies.
- *Trybliographa rapae* was the most common parasitoid of *D. radicum* in canola and brassica vegetables.
- *Trybliographa rapae* was generally synchronized with *D. radicum* larvae and poor synchronization did not affect parasitism.
- Adult female *T. rapae* are capable of crawling through soil to at least 4 cm deep in search of *D. radicum* larvae.
- *Trybliographa rapae* responded positively to host density in search of host-infested plants, but the parasitism was not density dependent.
- *Aleochara bilineata* responds positively to host density in search of host-infested plants, but the parasitism was not density dependent.
- *Aleochara bilineata* and *A. bipustulata* do not discriminate among *D. radicum* puparia on the basis of size in Switzerland.
- *Aleochara bilineata* occurs several days earlier than the occurrence of *D. radicum* puparia in canola on the Canadian Prairies.

- *Delia radicum* infests volunteer winter canola, winter canola, summer canola, late summer canola, and brassica vegetables.
- *Delia radicum* populations in canola on the Canadian Prairies emerge later in the spring in canola than all other populations studied.
- *Delia radicum* puparia in rutabaga fields are bigger than puparia in canola fields.

SUMMARY

Delia radicum is an important insect in canola on the Canadian Prairies and there is no single effective method of control of *D. radicum.* Hence, classical biological control has been proposed as a means of suppressing this pest. Assessment of the parasitoid community on the Canadian Prairies is a prerequisite to biological control, so that introduction of pre-existing parasitoids is avoided. The primary objective of this study was to assess the parasitoid community in canola on the Canadian Prairies and in Europe to identify potential candidates for introduction. In addition, related aspects of the biology of *D. radicum* and its parasitoids were examined.

In summer 2000, at least 100 immature *D. radicum* per field were collected each week in two canola fields in each of the Prairie Provinces. When there were <100 puparia in the regular samples, a mass collection of puparia was made in fall 2000. Sampled immatures were individually reared until adult hosts or parasitoids emerged and parasitoids were identified and counted. The abundant parasitoid species included *Trybliographa rapae* (Westwood), *Aleochara bilineata* Gyllenhal, and *Aleochara verna* Say. Minor parasitoids included two undescribed species of *Phygadeuon, Aphaereta minuta* (Nees) and *Trichopria* sp. Total parasitism of *D. radicum* puparia in fall varied from 23% to 48%. *Trybliographa rapae* was synchronized with the occurrence of *D. radicum* larvae in some locations whereas in other locations, *T. rapae* was delayed relative to its host. *Trybliographa rapae* and *D. radicum* responded to diapause induction cues differently. *Aleochara bilineata* was not synchronized with the occurrence of *D. radicum* puparia and *A. bilineata* occurred early relative to its host. *Aleochara bilineata* and *D. radicum* responded to diapause induction cues differently. At Carman,

Manitoba *Phygadeuon* species were delayed relative to the vulnerable stage of *D. radicum* puparia but this parasitoid invariably emerged without diapausing. The short period during which *Phygadeuon* was in the puparia may account for its absence from mass puparial collections.

In the summers 2001 and 2002, immature *D. radicum* were sampled at 12 locations in Germany and Switzerland in volunteer winter canola, winter canola, summer canola, late summer canola and brassica vegetables. Immature *D. radicum* were collected weekly and reared until adult emergence. Upon emergence of parasitoids, species were identified and counted. *Delia radicum* was found in each crop examined, and all types of canola crop had a similar level of *D. radicum* infestation. The number of *D. radicum* larvae on a root was associated with root diameter. Infestation levels were related to locality among canola crops. Abundant parasitoids included *T. rapae, A. bilineata,* and *A. bipustulata* L. Less abundant parasitoids included an undescribed species of *Phygadeuon, Phygadeuon trichops* (Thomson), *Trichopria* sp. and *Aleochara brevipennis* Gravenhörst. *Trybliographa rapae* was synchronized with the vulnerable stages of *D. radicum* in some locations, but was inconsistently early or delayed in other locations.

The probability of having at least one host per plant parasitized by *T. rapae* was positively correlated with the number of hosts on a root, but the percentage of larvae parasitized was not consistently correlated with the number of hosts per root. In a laboratory experiment, a negative correlation was found between host density and parasitism. In a laboratory experiment, *T. rapae* was capable of parasitizing hosts 4 cm deep, but not 6 cm. In the field, 40% of *D. radicum* larvae on roots of summer canola fed

>4 cm and 8% fed >6 cm below from soil surface. The probability of having at least one host on a plant parasitized by *A. bilineata* was positively correlated with host density on the root, but the percentage of puparia parasitized was not associated with host density. Similar trends were found for *A. bipustulata*.

Size of *D. radicum* puparia was examined in relation to crop and parasitoids. Puparia from rutabaga fields were bigger than those from canola. Puparia in canola in the prairies and in Europe were not different in size. *Aleochara bilineata* used puparia of all sizes, and there was no difference in puparial sizes parasitized by *A. bilineata* and *A. bipustulata*.

Staphylinid catches in canola in relation to tillage and seeding rate were examined using pitfall traps in canola at Carman in 2000. Eleven species of staphylinids were found and *Philonthus cognatus* Stephens, *Philonthus occidentalis* Horn, *Aleochara bilineata* Gyllenhal, *Aleochara gracilicornis* Bernhauer, and *Neohypnus obscurus* (Erichson) were the abundant species. Only *Philonthus* species responded to tillage regime and none of the species responded to seeding rate. Pitfall catches of *Philonthus* species were temporally correlated with the occurrence of *D. radicum* larvae in the field. No species exhibited positive temporal correlation with the number of *D. radicum* eggs.

In laboratory experiments on assessment of minimum cold period required for diapause development of a *D. radicum* population in Saskatchewan, 16 weeks at 1°C at 0:24 L:D was sufficient. Upon diapause development, puparia can be warmed within 3 days to 20°C without sacrificing per cent of adult emergence. The thermal requirement for post-diapause development of puparia was 517–555 degree day Celsius above 4°C.

By comparing the parasitoid community on the Canadian Prairies, two species of parasitoids were preliminarily identified as potential candidates for introduction to prairie canola. They were *A. bipustulata* and an unidentified species of *Phygadeuon*. *Phygadeuon* is a taxonomically difficult genus, and *Phygadeuon* spp. are generally polyphagous and opportunistic. These characteristics do not match with the desirable characteristics of a potential biocontrol agent. *Aleochara bipustulata* was found only in Europe. Previously published reports of *A. bipustulata* in North America were proved erroneous upon the examination of voucher specimens and other museum specimens previously identified as *A. bipustulata*. Characteristics of *A. bipustulata* suggest that *A. bipustulata* is a potential candidate biocontrol agent, and it is recommended that further studies be conducted on *A. bipustulata* with the objective of introducing it for biological control of *D. radicum* in canola on the Canadian Prairies.

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