AGAPETA ZOEGANA (L.) (LEPIDOPTERA: COCHYLIDAE), A SUITABLE PROSPECT FOR BIOLOGICAL CONTROL OF SPOTTED AND DIFFUSE KNAPWEED, CENTAUREA MACULOSA MONNET DE LA MARCK AND CENTAUREA DIFFUSA MONNET DE LA MARCK (COMPOSITAE) IN NORTH AMERICA

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Abstract

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The taxonomy, distribution, life history, and host plant relationships of the cochylid moth *Agapeta zoegana* (L.), an oligophagous, facultatively multivoltine root feeder, are discussed. The results of oviposition and larval feeding tests with 56 plant species in five families are presented and show that *A. zoegana* is restricted to a few closely related species of *Centaurea*. In Europe the moth is widely distributed and abundant in the majority of the root-feeding guilds of *Centaurea maculosa* Monnet de la Marck studied, with densities of 23.6 larvae per 100 roots in eastern Austria/northwestern Hungary and less than 8 larvae per 100 roots in central Hungary and the Alsace. The acceptance of target North American species (the tetraploid form of *C. maculosa* and the diploid *Centaurea diffusa* Monnet de la Marck), the damage caused, and the active searching ability rate *A. zoegana* as a potentially effective natural enemy of spotted and diffuse knapweed in North America. *Agapeta zoegana* will be especially promising as it predominantly attacks the rosette, which is, according to a recently developed population model for diffuse knapweed in Canada, the most sensitive stage determining equilibrium knapweed density. *Agapeta zoegana* is compatible with *Pelochrista medullana* Staudinger (Lepidoptera: Cochylidae), another knapweed root feeder recently introduced into North America, and will complement the seed-feeding species already established. The moth was approved for release in Canada and the USA and has been established in British Columbia since 1984 on *C. diffusa*.

Résumé

Cette contribution porte sur la taxonomie, la distribution, le cycle vital et les relations avec les plantes-hôtes du papillon cochylide *Agapeta zoegana* (L.), une espèce radicicole oligophage facultativement multivoltine. Les résultats de tests de ponte et d'alimentation des larves avec 56 espèces de plantes appartenant à cinq familles sont rapportés, et montrent que *A. zoegana* est spécifique de quelques espèces apparentées de *Centaurea*. En Europe le papillon est largement distribué et abondant dans la majorité des communautés radicicoles associées à *Centaurea maculosa* Monnet de la Marck qui ont été étudiées, avec des densités de 23,6 larves par 100 racines dans l'est de l'Autriche–nord de la Hongrie, et moins de 8 larves par 100 racines en Hongrie centrale et en Alsace. L'acceptation d'espèces nord-américaines visées, la forme tétraploïde de *C. maculosa* et l'espèce diploïde *C. diffusa* Monnet de la Marck, les dommages infligés, de même que la capacité de recherche élevée de *A. zoegana* en font un auxiliaire naturel de lutte contre la centaurée maculée et la centaurée diffuse en Amérique du Nord. *Agapeta zoegana* sera d'autant plus efficace qu'il attaque la rosette, soit le stade critique pour la détermination de la densité d'équilibre de la centaurée d'après un modèle démographique de la centaurée diffuse récemment mis au point au Canada. *Agapeta zoegana* est compatible avec *Pelochrista medullana* Staudinger (Lepidoptera: Cochylidae), une autre espèce radicicole associée à la centaurée qui a été récemment introduite en Amérique du Nord, et s'ajoutera donc aux espèces déjà établies. Le relâchement du papillon a été approuvé au Canada et aux USA, et il est établi en Colombie-Britannique depuis 1984 sur *C. diffusa*.

Introduction

Spotted knapweed, *Centaurea maculosa* Monnet de la Marck, a short-lived perennial, and diffuse knapweed, *Centaurea diffusa* Monnet de la Marck, typically a biennial, both

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of European origin, were accidently introduced into Canada and the northern United States with seed grain (apparently alfalfa) from southeastern Europe. *Centaurea maculosa* was first discovered in Victoria, B.C., in 1893 (Groh 1943), and *C. diffusa* was first recorded in Washington State in 1907 (Howell 1959). Several factors, including suitable ecological conditions, extensive overgrazing of the natural vegetation, the allelopathic properties of the *Centaurea* spp. (Fletcher and Renney 1963), and prolific seed production, enhanced their establishment and spread. Today, spotted knapweed is most abundant in Montana, where approximately 800 000 ha are infested (Maddox 1979). In British Columbia the weed occurs on some 4000 ha and is most abundant in the forest steppe region (Harris and Cranston 1979). In 1972, *C. diffusa* infested 25 952 ha of dry grassland in British Columbia and small areas in Alberta (Watson and Renney 1974) and Harris and Cranston (1979) expect that it will continue to spread; some 7.5 million ha of open uncultivated sites are susceptible for infestation.

Both species tend to dominate the natural vegetation where they become established. Losses of available forage on natural pastures may attain 88% (Harris and Cranston 1979). Chemical control with picloram is possible but not economic for most of the infested area, and cultivation is often not possible because of the topography and other adverse factors. Harris and Cranston (1979) concluded that an increased investment in biological control should be made as it would be expected to give a superior return to alternative methods of control.

Between 1970 and 1972, three seed-feeding species (two tephritids (*Urophora affinis* Frauenfeld and *U. quadrifasciata* Meigen) and a gelechiid (*Metzneria paucipunctella* Zeller)) were released and established in British Columbia (Harris and Myers 1984). A root-feeding buprestid beetle (*Sphenoptera jugoslavica* Obenberger) was first released in 1976 and became established at White Lake, B.C. (Harris and Myers 1984). Despite the establishment of these natural enemies, which resulted in a drastic decline of seed production in both knapweed species, no change in plant density has occurred (Harris and Myers 1984). The investigation of additional biocontrol agents was proposed in 1977 by the Canadian Department of Agriculture. A second faunistic survey was initiated by the Commonwealth Institute of Biological Control, Delémont (CIBC) in 1979 to investigate the species of insects associated with the roots of the two knapweed species in their native range in Europe.

The objective of this study was to investigate the life history, ecology, and host specificity of the root-mining moth *Agapeta zoegana* (L.). The impact of the moth on host and target plants was also studied to determine its potential for the biological control of the two knapweed species in North America.

Materials and Methods

Field Studies. The general survey carried out between 1979 and 1983 comprised 4 sites in France, 4 sites in Germany, 15 sites in Austria, 7 sites in Hungary, 6 sites in Czechoslovakia, and 15 sites in Rumania for *C. maculosa* (110 samples), 7 sites in Rumania for *C. diffusa* (41 samples), and 11 sites in Switzerland and 2 sites in Italy for *C. vallesiaca* (de Candolle) Jordan (41 samples) (Fig. 1). Most localities were sampled several times and in different seasons. Each sample contained 50–100 randomly sampled plants. These were dissected in the laboratory to assess the root-feeding entomofauna. This also provided information on interspecific associations of the root-feeding insects. To determine voltinism, additional root samples were collected at 2-week intervals from late May to late August at Dürnstein in Lower Austria (1981, 1982), at Julia Major in central Hungary (1982, 1983), and at Hanu Conachi in eastern Rumania (1982). During the same periods, pheromone trials were carried out at these localities (Tóth *et al.* 1985).

The abundance and distribution of *A. zoegana* larvae on *C. maculosa* were studied at Dürnstein (dry grassland on a steep, south-facing slope on silicate rock), at Sopron,
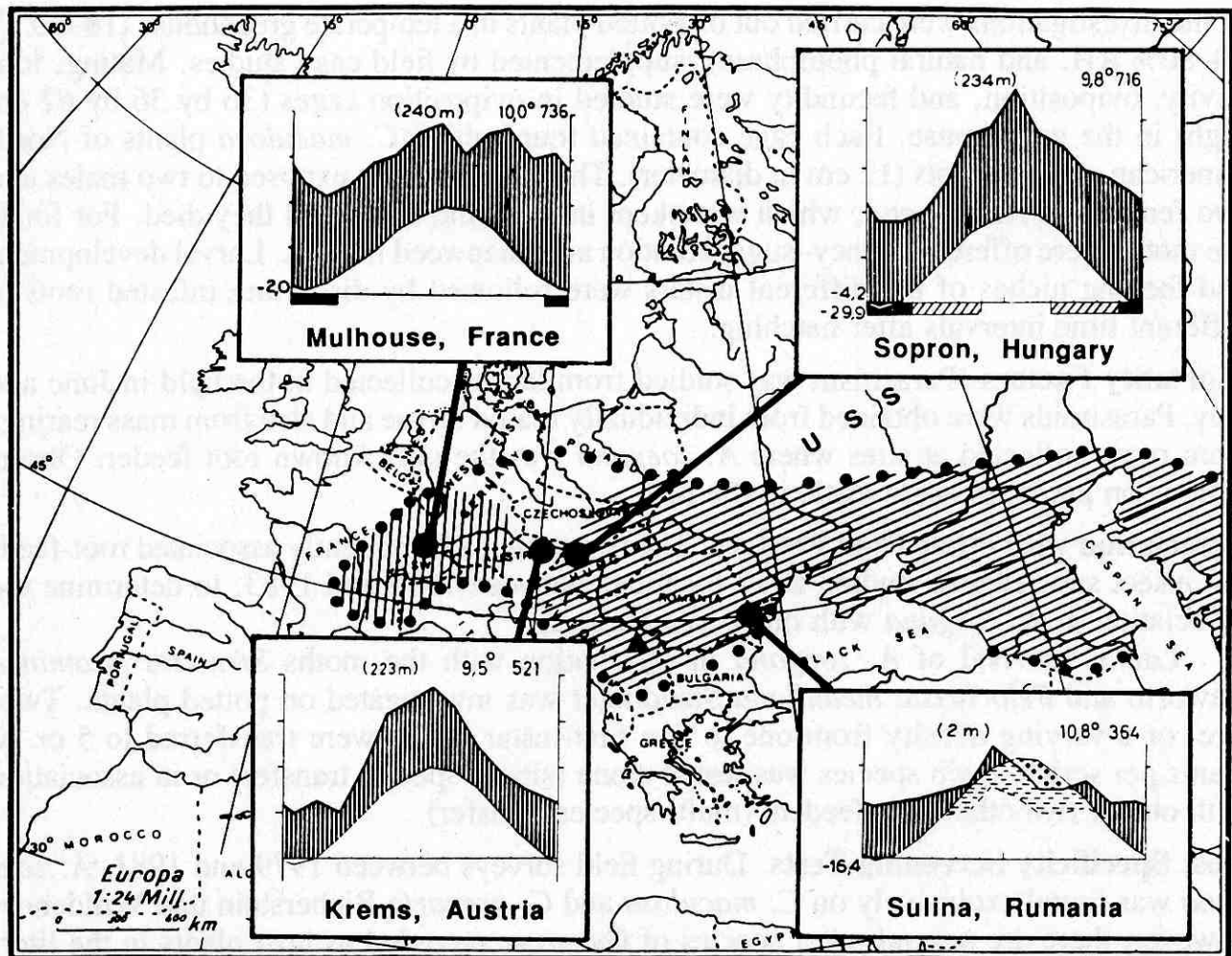
III   C. maculosa Lam. ssp. maculosa (= C.stoebe ssp. maculosa (Lam.) Hayek)

Z   C. biebersteinii DC ssp. biebersteinii (= C. micranthos S. G. Gmelin ex Hayek)
(= C. maculosa Lam, 2n = 36; ≈ target weed in North America)

O   C. rhenana Boreau (incl. all ssp.)
(= C. maculosa Lam, 2n = 18; studied host plant in Europe)

●   Main collection and study area for A. zoegana, with corresponding climatic
diagrams (legend see Fig. 2D)

FIG. 1. Main collection and study areas of *Agapeta zoegana*, corresponding climatic diagrams (Walter and Lieth 1967), and geographic distribution of three taxa of the *Centaurea maculosa* group of species.

western Hungary (dry wasteland on limestone), and at Sollenau, eastern Austria (a chalk–gravel pit). A transect method (2 by 50 m long) was applied (Whaba 1970) to determine knapweed density. At each locality, 200 randomly selected plants were collected and dissected to assess incidence and level of infestation and dispersion of *A. zoegana* larvae on host plants. Large samples of up to 1000 infested roots were collected at the end of May or in early June at Dürnstein, Sollenau, Sopron, and Hanu Conachi. All material used for laboratory studies at Delémont originated from these areas.

Laboratory Rearings and Life History Studies. Roots containing final-instar larvae and pupae of *A. zoegana* were collected from the various sites and brought to Delémont. The material was kept in emergence cages between layers of moistened cellulose sheets in a 16L:8D cycle, at 23–25°C and 80–90% RH. Adults emerging from the cages were used to study mating and oviposition, and to obtain larvae for host specificity screening. Most

of the investigations were carried out on potted plants in a temperate greenhouse (18–30°C, 30–80% RH, and natural photophase), supplemented by field cage studies. Mating, longevity, oviposition, and fecundity were studied in oviposition cages (36 by 36 by 62 cm high) in the greenhouse. Each cage contained four bolting *C. maculosa* plants of North American origin in pots (12 cm in diameter). These plants were exposed to two males and two females of *A. zoegana*, which were kept in the same cage until they died. For food, the moths were offered a honey–sugar solution and knapweed flowers. Larval development and feeding niches of the different instars were followed by dissecting infested roots at different time intervals after hatching.

Mortality Factors. Parasitism was studied from larvae collected in the field in June and July. Parasitoids were obtained from individually reared larvae and also from mass rearings from roots collected at sites where *A. zoegana* was the only known root feeder. Observations on predators were made in the field.

Association with other Root Feeders. The occurrence of frequently associated root-feeding insect species was studied at 12 localities between 1979 and 1983, to determine the association of *A. zoegana* with other root feeders.

Larval survival of *A. zoegana* in association with the moths *Stenodes straminea* Haworth and *Pelochrista medullana* Staudinger was investigated on potted plants. Two, five, or a varying density from one to five first-instar larvae were transferred to 5 or 10 plants per series. Each species was tested alone (single-species transfer) or in association with one or two other root feeders (multi-species transfer).

Host Specificity Screening Tests. During field surveys between 1979 and 1981, *A. zoegana* was found exclusively on *C. maculosa* and *C. arenaria* Bieberstein und Willdenov; however, there are several other species of Cynareae recorded as host plants in the literature. To collect information on the potential host range of the moth, oviposition and larval feeding tests were carried out. Test plants were selected in cooperation with Dr. P. Harris and the Working Group on the Biological Control of Weeds, Beltsville, MD. Systematically closely related crop plants of economic importance are safflower, *Carthamus tinctorius* L., and globe artichoke, *Cynara scolymus* L. Oviposition tests were conducted at Delémont during July and August in a greenhouse at natural photoperiod and a temperature range of 15–30°C. Four potted plants in cages (36 by 36 by 62 cm high) were exposed to two or three couples of *A. zoegana* for the entire life of the moths (ca. 10 days). Oviposition tests were conducted first in the presence and second in the absence of spotted or diffuse knapweed. Only cages containing fertilized eggs were included in the analysis. Between two and eight replicates were made. The plants were arranged in random combinations and the position of the cages was changed periodically. Further oviposition tests were carried out in field cages (100 by 200 by 100 cm high) with the test species transplanted in the field.

Eggs obtained from oviposition tests were incubated in glass tubes and newly emerged larvae were used for larval transfer tests. Two or three vigorous and actively moving larvae per plant were transferred with a fine brush. Infested plants were kept in the garden at Delémont until November, at which time the plants were dissected to check plant acceptance and larval development.

Effect on the Host Plant. The ability of larvae to move from the first attacked plant to a neighboring plant was also assessed. Three *C. maculosa* rosettes, grown from Chase, B.C., seeds, were planted 10 cm apart in each of 15 large pots (20 cm diameter). In 10 pots, 15 first-instar larvae were put on one of the three plants and each rosette was isolated by a plastic cylinder to exclude above ground migration of the larvae. Five pots were used as controls for plant mortality other than root mining. In addition, experiments in glass-faced root containers (5 by 50 by 100 cm long) (Müller 1984, 1987) and with potted

rosettes were conducted to study the effect of root mining on spotted knapweed rosettes of different origin (genome), different age, and grown in different soil types. Plants were infested by transferring three first-instar larvae to the bases of the rosette leaves.

Results

Taxonomy and Host Plant Records of *Agapeta*. The genus *Agapeta* Hübner belongs to the family Cochylidae and consists of four Palearctic species and one subspecies, *A. zoegana* ssp. *brunneocycla* Razowski. Synonyms for *A. zoegana* (L.) are *Tortrix ferrugana* Haworth, *Aethes zoegana* Billberg, and *Euxanthis* ab. *ferrugana* Kennel (Razowski 1970). The biology of *A. zoegana* ssp. *brunneocycla* Razowski is unknown and its distribution is limited to southeastern Yugoslavia.

Agapeta zoegana is known to occur throughout Europe with the exception of Greece. The northern distribution limit follows latitude 60°N, the eastern border apparently reaches the Urals, the southern and western borders are not defined (Razowski 1970). The morphological description for the moth and the final-instar larva of *A. zoegana* are given by Razowski (1970) and Swatchek (1958), respectively. Host plants are only known for two *Agapeta* species, *A. hamana* L. and *A. zoegana*. According to literature records, *A. hamana* feeds on the leaves of *Ononis repens* L., and possibly also on *Trifolium pratense* L. and *Cirsium arvense* (L.) Scopoli. *Agapeta zoegana* has been recorded to feed on the roots of *Scabiosa columbaria* L., *Centaurea jacea* L., *C. maculosa*, *C. nigra* L., *C. paniculata* L., *Jurinea linearifolia* de Candolle, and probably *C. scabiosa* L. (Hannemann 1964; Razowski 1970; Schütze 1931; Bradley *et al.* 1973).

Knapweed Taxonomy. Three species of the *C. maculosa* groups were found within the area surveyed during this study (eastern France, southern Germany, Switzerland, northern Italy, Austria, Czechoslovakia, Hungary, and Rumania). According to Flora Europea (Dostál 1976), these were *C. maculosa* Monnet de la Marck ssp. *maculosa* (= *C. stoebe* ssp. *maculosa* (Monnet de la Marck) Hayek), *C. rhenana* Boreau (incl. all ssp.), and *C. biebersteinii* de Candolle ssp. *biebersteinii* (= *C. micranthos* Gmelin ex Hayek) (Fig. 1).

Investigations of *A. zoegana* carried out in Austria, France, and Hungary were made on the diploid host plant classified as *C. rhenana*. However, the problem species in North America keys out to *C. biebersteinii* ssp. *biebersteinii* (2n = 36). This species occurs mainly in southeastern Europe and was not included in the European CIBC surveys (see also Schroeder 1985). The morphology, biology, and distribution of *C. biebersteinii* ssp. *biebersteinii* in Canada is described by Watson and Renney (1974). In this report, the name *C. maculosa* (sensu Lat.) is used for both the European and the American spotted knapweeds. *Centaurea diffusa* is taxonomically well defined, and North American and European plants seem to belong to the same species (Watson and Renney 1974; Moore and Frankton 1974).

Geographic Distribution of *Agapeta zoegana* in Europe and Potential Range in North America. In our surveys between 1979 and 1981, *A. zoegana* was found on *C. maculosa* in eastern Austria (Lower Austria and Burgenland) and western and central Hungary (Sopron and Budapest area). The moth also occurred on *C. arenaria* in eastern Europe (Hanu Conachi and Danube Delta) and small populations were found on *C. maculosa* in the upper Rhine Valley (Alsace and Istein). Possibly, ''local species'' (sensu Fox and Morrow 1981) of *A. zoegana* have evolved within the general European distribution area.

Field observations suggested that the presence of *A. zoegana* in knapweed stands was determined primarily by site conditions, and to a lesser extent by host plant species. Within the survey area *A. zoegana* occurred predominantly in semi-natural, undisturbed sites (e.g. dry grassland, steppic biotopes, and south-facing slopes) and ruderal habitats (e.g. gravel quarries), but was rare or absent on sites with strongly fluctuating populations of spotted knapweed. Grazing by sheep has apparently no adverse effect on its occurrence.
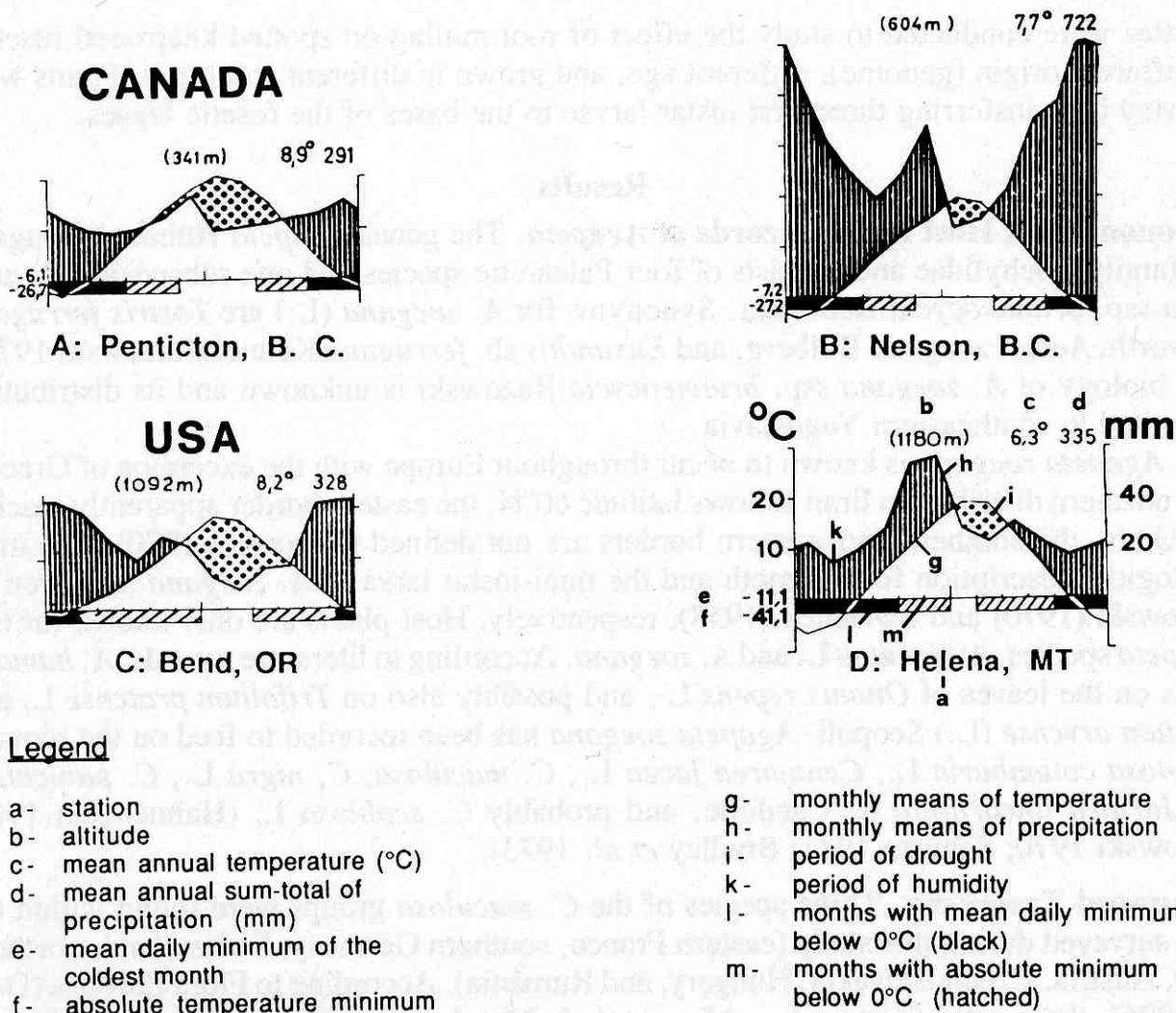
FIG. 2. Climatic diagrams of North American *Centaurea maculosa* and *C. diffusa* infestation areas (Walter and Lieth 1964).

In Europe *A. zoegana* occurred in areas with a moderately humid temperate climate and in areas with an arid sub-continental climate (Fig. 1). This corresponds with summer conditions of spotted and diffuse knapweed-infested areas in Canada, although these regions have colder winters and a shorter summer season than infested sites in Europe (Fig. 2).

Agapeta zoegana may, therefore, need some period of time to acclimatize to the colder climate in southern Canada and the northern USA before it is able to colonize the entire area presently infested by spotted knapweed. Collections from the more arid sub-continental Rumanian areas may be better suited for release in the southern part of the spotted knapweed distribution in the USA and diffuse knapweed sites in Canada, whereas the Austrian and Hungarian populations from a moderately continental climate should be released in spotted knapweed sites in the interior of British Columbia and Montana.

Analyses of root samples and data from pheromone traps indicate that *A. zoegana* had two generations per year in eastern Austria and western and central Hungary (June to early August and end of August to September). Up to three annual generations may occur in southeastern Rumania (moths are found from May to September; F. König, pers. communication), two generations were found in 1982 at Hanu Conachi (June to mid-July and July to late August), but only one generation occurs in western Europe (moths from July to August; Alsace, Delémont). In North America, *A. zoegana* will probably have one annual generation in most areas, but possibly two generations in areas with climatic conditions shown in Figure 2A.

Table 1. Infestation and dispersion of *Agapeta zoegana* larvae on *Centaurea maculosa* ($n = 200$ randomly collected plants)

	Dürnstein, Austria		Sollenau, Austria		Sopron, Hungary	
	1981	1982	1981	1982	1981	1982
Host plants/m²	0.5	0.2	3.0	2.1	0.5	0.1
Infestation (%)	16	18	20	15	36	15
Dispersion index						
$s^2/\bar{x}$	1.0	1.6	2.1	1.3	2.4	2.2
No. of larvae/						
attacked root	1.21	1.41	1.43	1.25	2.03	1.70
$\bar{x}(\pm SD)$	(0.41)	(0.75)	(1.20)	(0.58)	(1.53)	(1.13)

The mean larval densities and the distribution of multiple attack on *C. maculosa* at Dürnstein, Sollenau, and Sopron are given in Table 1. Spotted knapweed reached densities of only up to 0.5 plants/m² in the more natural, undisturbed habitats with relatively high plant cover (Dürnstein, Sopron), but knapweed densities up to 3 plants/m² were found in ruderal areas at Sopron. The variance:mean ratio, an index for dispersion that is unity for a Poisson (random) distribution (Southwood 1978), was calculated for the six samples and indicates random and slightly clumped distributions for *A. zoegana* larvae on individual roots; clumping depends on the availability of larger roots which can support several larvae (Table 1). Altogether 25% of the attacked *C. maculosa* had two or more larvae in their roots.

Emergence, Mating, and Longevity. In the laboratory, emergence from overwintered, field-collected material took place over an 8-week period, from mid-June to mid-August. Collections from warmer sites produced adults earlier than those from cooler sites (Table 2). Emergence after hibernation of *A. zoegana* may be largely determined by temperature, as demonstrated by transferring potted plants infested by hibernating final-instar larvae from the Institute's garden into the insectary in February 1980. The larvae kept at 20°C and natural photophase emerged in March and April compared with July for those under field conditions.

Comparisons of emergence between males and females were made for populations from Sopron and Hanu Conachi in 1980. The difference between mean emergence dates of the two sexes, based on 3-day intervals, was not statistically different ($p = 0.05$) for both populations ($n = 138$, $t = 0.375$ and $n = 27$, $t = 0.767$, respectively).

The females mated within 24 h of emergence. Successful mating occurred in a temperature range between 18 and 30°C (outdoors, insectary) and did not require the presence of the host plant.

Under the test conditions described, males ($n = 75$, $\bar{x} \pm SD = 11.8 \pm 1.96$ days) lived significantly longer ($t = 6.08$, $p < 0.01$) than females ($n = 66$, $\bar{x} \pm SD = 9.9 \pm 1.77$ days).

Table 2. Emergence of *Agapeta zoegana* in 1981

	Centaurea maculosa		*Centaurea arenaria*
	Dürnstein, Austria	Sopron, Hungary	Hanu Conachi, Rum.
Mean annual temp. (°C)*	9.5	9.8	10.8
No. of moths	20	51	91
Emergence period	1 July – 14 Aug.	26 June – 9 Aug.	16 June – 30 July
Mean emergence date†	16 July a	14 July a	6 July b

*Walter and Lieth (1967).

†Analysis based on 3-day intervals; ANOVA: $F = 19.3$, $p < 0.001$. Means with the same letter are not significantly different ($p = 0.05$; Scheffé F-test)

Table 3. Longevity, fecundity, and fertility of eggs of *Agapeta zoegana* emerged at different periods

Emergence period	Mean longevity (days)				Temp.* (°C)	Mean no. of eggs/fem.	Incidence of fertility‡
	n	Male	*n*	Female			
1980							
26 June – 3 July	10	14.4	8	9.3	17.0a†	20.5a†	59.8%b†
14 July – 18 July	12	11.2	8	10.3	26.3b	55.0c	44.6%b
24 July – 13 Aug.	10	10.9	9	9.1	22.0b	35.0b	25.6%a
1981							
29 June – 5 July	12	10.1	9	12.6	24.4ab†	62.4a†	32.7%a†
8 July – 11 July	12	11.1	9	12.6	23.5a	66.4a	45.8%ab
14 July – 1 Aug.	14	13.2	10	8.1	25.4b	94.4b	51.1%b

*Average of mean daily temperature during life of moths (emergence period plus mean longevity of the females).
†Values followed by the same letter are not significantly different at $p = 0.05$ (ANOVA, Scheffé *F*-test).
‡Data were angularly transformed (arc sin $\sqrt{p}$) prior to statistical analysis.

Oviposition and Fecundity. Oviposition began 1 day after mating. The eggs were laid singly, or in groups of up to three eggs, on the surface of stems and leaves, predominantly in crevices. Approximately 30% of the eggs were laid on the frame of the oviposition cages. However, in a field cage containing different phenological stages of *C. maculosa*, the majority of the eggs were laid on the lower leaves, mostly on rosettes.

The eggs were oval in shape and somewhat flattened, length = 0.73 ± 0.04 mm, width = 0.44 ± 0.04 mm ($\bar{x} \pm$ SD). The eggs were whitish when freshly laid and turned reddish with 3–4 days. The chorion was reticularly scupltured and quite robust.

Experiments on fecundity and fertility of eggs were conducted in the insectary during the same time period in 1980 and 1981 (Table 3). Females that emerged in the middle (1980) or the end (1981) of the emergence periods and that lived at higher temperatures laid more eggs than females from the beginning (1980) or the middle (1981) of the emergence period and that lived under cooler temperatures. However, in 1980 successful mating was more frequent in the beginning (lower temperature) than at the end of the emergence period, but was reversed in 1981, i.e. more frequent at the end and under higher temperatures. Hence, although temperature may influence total fecundity of *A. zoegana*, other factors were responsible for the fertility of the eggs.

Hatching and Larval Development. In the laboratory, the larvae emerged 7–10 days after oviposition when kept in a 16L:8D cycle, at 90% RH and 23–24°C. The larvae emerged through a lid-like portion of the chorion and moved immediately to the root crown area where they started mining. There are six larval instars. Roots dissected 10 days after the transfer of newly emerged larvae contained 6% first-instar and 94% second-instar larvae. Only fourth-instar larvae, which had already mined up to 10 cm into the cortical tissue of the taproot, were observed 40–45 days after transfer, and only sixth-instar larvae were found beyond the 70th day. Young larvae mined the tissue just below the exodermis, but older larvae mined progressively downwards in open, irregular, sometimes spiral mines which were covered with a whitish web spun by the larvae. Heap capsule widths of the instars were as follows: first, 0.19–0.20 mm; second, 0.26–0.27 mm; third, 0.36–0.44 mm; fourth, 0.56–0.68 mm; fifth, 0.71–0.86 mm; sixth, 0.95–1.50 mm ($n = 2$–32). The increase in head capsule widths from one larval instar to the next agreed with predicted values from Dyar's Law, indicating a geometrical growth.

Mortality Factors. In laboratory rearings, natural mortality of embryos was low. Mortality in the first instar was important, especially on small plants with multiple attack, as larval transfer tests on potted plants demonstrated. Predaceous staphylinids (*Ontholestes haraldi* (Eppelsheim) and *Xantholinus linearis* Heer) and elaterid larvae were found in empty mines of *A. zoegana* in *C. maculosa* roots from Austria and Hungary.

Only parasitoids emerging from final-instar larvae or pupae were assessed. Parasitism of *A. zoegana* was relatively high, ranging from 11 to 60% (Müller 1984). It varied from locality to locality and from year to year. Sixteen species of hymenopterous parasites (see Müller 1984) emerged from roots of *C. maculosa* and *C. arenaria* infested by *A. zoegana*. Nine parasite species were reared from *A. zoegana*, including six braconid species, each of which occurred at less than six sites. The ectoparasites *Bracon larvicida* Wesmael, *B. praetermissus* Marshall, and *B. indubius* Szépligeti accounted for less than 5% parasitism, but the solitary endoparasites *Chelonus annulipes* Wesmael and *Chelonus sculpturatus* (Szépligeti) parasitized up to 30% of the larvae. *Chelonus intermedius* Szépligeti was only found at Sopron, Hungary, where it parasitized 43% of *A. zoegana* larvae in 1980. The ichneumonids *Glypta sculpturata* Gravenhorst parasitized 10% of the larvae at two sites, and four specimens of *G. bivolveolata* Gravenhorst were reared from east Rumanian material. A polyembryonic *Copidosoma* species (Encyrtidae) parasitized up to 35% of the larvae at three localities.

The only available host record from North America concerns *Chelonus annulipes*, a common parasite of *Ostrinia nubilalis* Hübner, introduced and established in the USA (Muesebeck *et al.* 1951; Herting and Simmonds 1975).

The abundance of *A. zoegana* in most of the root-feeding guilds on *C. maculosa* in central Europe despite relatively high rates of parasitism indicates, therefore, its importance as a natural enemy of spotted knapweed populations.

Association with other Root Feeders. *Agapeta zoegana* was the second most common species in eastern Austria/northwestern Hungary on *C. maculosa* following the pooled *Apion* spp. (Müller 1984; unpublished data). An average of 23.6 larvae per 100 knapweed roots was found in eastern Austria/northwestern Hungary, but less than 8 larvae per 100 roots were found in central Hungary and the Alsace, France (Müller 1984).

Eight species were frequently associated with *A. zoegana*. These were three Lepidoptera (*S. straminea* (Cochylidae), *P. medullana* (Tortricidae), and *Pterolonche inspersa* Staudinger (Pterolonchidae)), two weevils (*Cleonus piger* Scopoli and *Cyphocleonus achates* Faber), two Diptera (*Cheilosia* sp. (Syrphidae) and *Pegohylemyia centaureae* Hennig (Anthomyiidae)), and the buprestid beetle *S. jugoslavica*. In addition, four *Apion* species (Coleoptera: Curculionidae) occurred in the collections, but they are recorded as a single taxon in this study.

The interspecific association (Southwood 1978), i.e. the joint occurrence of species on the same root, was random, except for *C. achates*, which was positively associated with *A. zoegana*. Both species hibernate as larvae within the taproot. Preliminary observations that *C. achates* selected larger rosettes for oviposition (C.S.A. Stinson, pers. communication), and the fact that smaller rosettes infested by *A. zoegana* often die during winter, is a possible explanation for this positive association found in late spring before the emergence of these two species.

The survival of *A. zoegana* in different densities, as well as in association with *S. straminae* and *P. medullana*, was also tested on potted rosettes in the greenhouse. When feeding alone, about half of the *A. zoegana* and *S. straminea* larvae survived (Table 4*a*). Cannibalistic behavior accounted for the reduced survival of *P. medullana* (Gassmann *et al.* 1982). The higher herbivore load in the case of multi-species transfer was responsible for the increased mortality of the larvae, but no asymmetrical competition occurred (Table 4*b*).

The reduced survival of *A. zoegana* in association with *P. medullana* compared with the association with *S. straminea* can be explained by the different feeding site of *S. straminea* (at the bases of the rosette leaves and the root collar) (Müller 1983); *A. zoegana* and *P. medullana* share the same feeding site in the root cortex. Thus, field and laboratory experiments indicate that *A. zoegana* will be compatible with *P. medullana*, an additional

Table 4. Survival of *Agapeta zoegana* (A), *Stenodes straminea* (S), and *Pelochrista medullana* (P) in various intra- and inter-specific associations in 1983/1984

(a) Single-species transfer

	Agapeta	Stenodes	Pelochrista
Infestation (July/Aug.)			
No. of pots	5	5	5
No. of larvae/pot	1,2,3,4,5	1,2,3,4,5	1,2,3,4,5
No. of larvae alive			
in April (total survival)	7 = 46.7%	8 = 53.7%	2 = 13.3%

(b) Multi-species transfer

	Association of larvae transferred					
	A + S		A + P		A + S + P	
No. of pots	5	5	5	5	10	10
No. of larvae/ species/pot	1 to 5	2	1 to 5	2	2	5
No. of larvae alive in April in association of						
A	2	0	1	1	0	0
S	3	2	—	—	4	3
P	—	—	1	0	0	0
A + S	3 + 2	7 + 7	—	—	3 + 3	4 + 3
A + P	—	—	3 + 2	1 + 1	0	0
A + S + P	—	—	—	—	1 + 1 + 1	1 + 1 + 1
Survival (n) of						
A (Total (%)	5	7	4	3	4	5 = 23.3%
S of species	5	9	—	—	8	7 = 30.9%
P survival)	—	—	3	1	1	1 = 6.3%
Total larval survival (%)	33.3	80.0	23.3	20.0	21.6	8.7

root feeder recently imported for the biological control of *C. diffusa*, as well as with *S. jugoslavica*, a root feeder already established in British Columbia on diffuse knapweed (Harris and Myers 1984).

Host Specificity Screening Tests. The results of the oviposition tests are summarized in Tables 5 and 6. Altogether 51 plant species, comprising 45 Compositae and six representatives of four other families, were screened. Although the orientation of ovipositing females in the cages may be disturbed, 17 of the tested plant species were consistently avoided, including *S. columbaria*, which is recorded as a host plant in the literature. However, eggs were laid on many plant species unsuitable for larval development and 30% of the eggs were deposited on the wooden frames of the test cages. A few eggs were deposited on *C. tinctorius* and *C. scolymus* in the presence of *C. maculosa* (Table 5), but these crop plants received no eggs in the absence of *C. maculosa* (Table 6).

To demonstrate that *C. tinctorius* and *C. scolymus* are not acceptable for oviposition in the field, even in close proximity to *C. maculosa*, five males and three females of *A. zoegana* were released into a field cage containing five naturally growing plants, in different phenological stages, of each of the following species: *C. maculosa, C. montana* L., *C. nigrescens* Willdenow, *C. tinctorius*, and *C. scolymus*. A total of 176 eggs was recovered, of which 84% were found on *C. maculosa*, 15% on *C. nigrescens*, and 1% on *C. montana*. No eggs were found on *C. tinctorius* or *C. scolymus*, and no larvae had moved to the roots of these species from the adjacent *C. maculosa* plants, on which up to 25 larvae were found on a single root. Only one living larva was found on *C. montana*

and two larvae on *C. nigrescens*. Two additional tests in field cages were conducted. One rosette and one flowering plant of each *C. tinctorius, C. scolymus* (two rosettes), and four knapweed species including *C. maculosa* were exposed to three and five pairs of *A. zoegana*. No eggs or larvae were found on the two critical crop plants and *C. maculosa* was strongly preferred. These tests also showed that rosettes of *C. maculosa* were preferred over flowering plants for oviposition; 81% of the eggs laid on *C. maculosa* were found on rosettes.

A total of 970 first-instar larvae were transferred onto 56 plant species, including different phenological stages of the host and target species. Successful establishment and normal larval development were restricted to a few closely related species of *Centaurea*, i.e. *C. maculosa, C. arenaria*, and to a lesser extent *C. diffusa, C. vallesiaca*, and *C. nigrescens*. A single larvae survived until November on *Arctium lappa* L. and *C. orientalis* L., and two larvae were found on *Plectocephalus americana* (Nuttall) in very small mines. These larvae were all retarded in their development. Not a single larva became established on *C. jacea* L., and only a small percentage of the transferred larvae survived on *C. nigrescens* which was readily accepted for oviposition in the field tests. Three larvae of *A. zoegana* nibbled on the roots of *C. tinctorius* and developed to second and third instar before they died. Two additional plants per species were tested by transferring a total of 15 newly hatched larve, three at a time in a 5-day interval on each plant. All these larvae died in the first instar without nibbling.

Experimental investigations of the potential host range of *A. zoegana* therefore indicate that the species is restricted to a few closely related species of *Centaurea*. The tests clearly demonstrated a strong preference for the European host plants (including *C. vallesiaca*, formerly treated as a subspecies of *C. maculosa* (Hess *et al.* 1977)) and the two North American target species, and that the two closely related crop plants safflower and globe artichoke are not at risk. Moreover, *C. tinctorius* is harvested in late summer, 1 month after the expected oviposition of *A. zoegana*.

Effect on the Host Plant. The larvae of *A. zoegana* damaged their host plant by mining the roots. The damage caused by first and second instars, which mine the root collar area just below the exodermis, is negligible. The feeding of late instars, however, caused considerable damage, especially on small roots or when several larvae were present on large roots. The larvae produced irregular mines in the cortex and the endodermis of roots over 7 mm in diameter, whereas in smaller roots, or near the tip of the taproot, mining occurred predominantly in the central part of the root, i.e. in the vascular system. Smaller roots, however, were completely destroyed, with just a small part of the root collar left.

To determine the effect of larval feeding, 15 potted young rosettes each of spotted and diffuse knapweed were infested with three first-instar larvae of *A. zoegana*. On examination 70–80 days later, one plant had died for unknown reasons, the roots of 26 wilting plants (11 spotted and 15 diffuse knapweed) had been completely destroyed, and no trace of larval feeding was found on three healthy plants. All larvae found had reached the final instar.

Small plants were destroyed by the feeding of a single larva. As most of the eggs were laid on young rosettes of the predominantly biennial European *C. maculosa*, attacked plants often were killed before producing flowers. At a high plant density, in which the majority of the rosettes remain small, a single larva may destroy several rosettes before completing its development.

The experiment to test below ground migration of *A. zoegana* from one plant to another showed that larvae were able to find a new host plant within 10 cm, if the root of their primary host plant had been consumed. All the infested and half of the neighboring plants died, compared with only 2 of the 15 plants in the control pots. Although 81% of the larvae transferred died, 27 of the 28 survivors were found on the originally uninfested

Table 5. Synopsis of oviposition tests in the presence of Centaurea maculosa or Centaurea diffusa and larval transfer tests with Agapeta zoegana during 1980–1981

Test plant	Plant type*	Oviposition test		Larval development test			
		No. of repl.	Mean no. of eggs laid/fem./test on the plant	No. of larvae transf.	% survival to		% alive as 6th inst. in Nov.
					1st instar	4th instar	
FAM. PAPILIONACEAE							
Lathyrus odoratus L.	A	4	0	15	0	0	0
Medicago sativa L.	P	3	0	15	0	0	0
Trifolium pratense L.	B-P	—	—	15	0	0	0
FAM. CARYOPHYLLACEAE							
Silene cucubalus Wib.	P	4	0	15	0	0	0
FAM. DIPSACACEAE							
Dipsacus sp.	B	7	3.0	15	0	0	0
Scabiosa columbaria L.	P	3	0	15	0	0	0
FAM. CYSTACEAE							
Helianthemum vulgare Gaertn.	A	2	12.5	—			
FAM. COMPOSITAE							
Tribe: Astereae							
Aster novi-belgii L.	P	6	1.8	15	0	0	0
Aster amellus L.	P	—	—	4	0	0	0
Erigeron annuus (L.) Pers.	A	7	1.8	15	0	0	0
Solidago canadensis L.	P	4	8.0	15	0	0	0
Grindelia nana (Nutt.)	B-P	—	—	15	0	0	0
Tribe: Heliantheae							
Helianthus tuberosus L.	P	3	8.7	30	0	0	0
Helianthus decapetatus L.	P	7	5.4	10	0	0	0
Helianthus annuus L.	A	—	—	6	0	0	0
Rudbeckia hirta L.	P	6	1.7	18	0	0	0
Tribe: Helenieae							
Tagetes erectus L.	A	8	5.3	16	0	0	0
Tribe: Anthemideae							
Achillea millefolium L.	P	3	3.0	20	0	0	0
Achillea filipendulina Lam.	P	7	3.0	12	0	0	0
Artemisia vulgaris L.	P	3	0.3	15	0	0	0
Artemisia tridentata Nutt.	P	4	0.8	15	0	0	0
Artemisia cana Pursh.	P	4	0	15	0	0	0
Chrysanthemum leucanthemum L.	P	3	0	15	0	0	0
Santolina chamaecyparissus L.	P	6	11.8	15	0	0	0
Anthemis tinctoris L.	P	8	0	15	0	0	0
Matricaria matricaroides (Less.) Porter	A	3	0	15	0	0	0
Tribe: Senecioneae							
Senecio jacobaea L.	B-P	3	1.0	15	0	0	0
Tribe: Calenduleae							
Calendula officinalis L.	A	6	2.7	15	0	0	0

Plant	Life cycle*						
Tribe: Cichorieae							
Cichorium intybus L.	P	5	7.6	15	0	0	
Lactuca sativa L.	A	4	0	24	0	0	
Sonchus arvensis L.	P	6	0	15	0	0	
Taraxacum officinale Web.	P	3	0	15	0	0	
Tribe: Cynareae							
Arctium lappa L.	P	3		15	7	7	
Cnicus benedictus L.	A	4	1.6	16	0	0	
Cynara scolymus L.	P	8	0	30	0	0	
Cirsium arvense (L.) Scop.	P	2	0.3	15	0	0	
Cirsium undulatum (Nutt.) Spreng.	B	6	0.3	15	0	0	
Echinops sphaerocephalus L.	B	3	0	15	0	0	
Onopordum acanthium L.	P	2	1.7	15	0	0	
Silybum marianum (L.) Gaertn.	A–B	3	1.3	17	7	0	0
Carthamus tinctorius L.	A	3	0.1	46	0	0	
Carthamus lanatus L.	A	7	6.3	14	0	0	
Rhaponticum scariosum Lam.	B–P	6	17.7	15	20	13	13
Plectocephalus americanus (Nutt.)		3		15			
Genus: Centaurea							
Subgenus: Lopholema							
Centaurea orientalis L.	P	6	2.0	20	5	5	
Subgenus: Acrolophus							
Centaurea cineraria (gymnocarpa) L.	P	4	0	15	0	0	
Centaurea maculosa Lam. (Europe)	B–P						
Rosettes		36	9.1	35	60	60	27
Flowering plants		18	42.2	15	27	27	
Centaurea maculosa (North Am.)	P						
Rosettes		25	23.2	15	80	67	
Centaurea vallesiaca (DC) Jordan	B						
Rosettes		8	19	35	66	66	
Centaurea diffusa Lam. (North. Am.)	B–P						
Rosettes		26	7.0	35	77	54	54
Flowering plants		11	10.7	25	96	56	
Centaurea arenaria L.	P	—	—			11†	
Subgenus: Jacea							
Centaurea jacea L.	P	3	3.3	15	0	0	
Centaurea nigrescens Willd.	P	3	17.3	35	17	0	
Subgenus: Psephellus							
Centaurea dealbata Willd.	P	3	5.3	15	0	0	
Subgenus: Cyanus							
Centaurea montana L.	P	6	4.0	15	0	0	
Centaurea cyanus L.	A	6	4.8	15	0	0	
Subgenus: Chartolepsis							
Centaurea macrocephala		4	9.5	17	0	0	

*A: annual; B: biennial; P: perennial.

†One specimen died in the pupal stage.

Table 6. Oviposition and larval development test in the absence of *Centaurea maculosa* and *Centaurea diffusa*

Test plant (3 repl./plant species)	Mean no. of hatched eggs/ female/test on the plant	No. of larvae alive after 50 days
Carthamus tinctorius L.	0	0
Cynara scolymus L.	0	0
Helianthus tuberosus L.	18	0
Centaurea montana L.	3	1(L₁)
Centaurea orientalis L.	5	0
Centaurea jacea L.	6	2(L₄)
Centaurea nigrescens Willd.	43	1(L₄)

neighboring plants. This further demonstrated the potential effectiveness of *A. zoegana* as a knapweed control agent.

Experiments in root containers revealed distinct differences in the biology between the European diploid host plant *C. maculosa* and the North American tetraploid target species (Müller 1984, 1987). It is expected that the smaller biomass of the tetraploid species (root length, dry weight, and number of flower heads and seeds per year) and its polycarpic, perennial life cycle compared with the monocarpic, biennial diploid plants (Müller 1984, 1987) may influence the effect of *A. zoegana*.

Table 7 summarizes experiments with potted plants to compare the impact of *A. zoegana* on the mortality of spotted knapweed rosettes of different origin, different age, and grown in different soil types. No statistical differences in plant mortality could be found due to the limited number of replicates. However, the results suggest that the impact of larval feeding did not differ among plants of different age (A versus C, Table 7), that the North American target plants were more susceptible to attack than the European host plants (A versus B), and that plants grown in poor soil were more susceptible than plants grown in nutrient-rich soil (C versus D).

The potential control value of *A. zoegana* was earlier assessed by Müller *et al.* (1982) on the system developed by Harris (1973) and revised by Goeden (1983). This indicated a good prospect as a biological control agent compared with other insects imported for weed control (Goeden 1983). However, this system only scores attributes of species, which in general increase the probability of a relevant damage to the plant (Wapshere 1985) without considering its potential for a regulative impact on the target weed population. A recently developed population model for diffuse knapweed in Canada (J. Myers, pers. communication) suggests that population dynamics is buffered from effects of reduced seed numbers, but that rosette survival is essential in determining knapweed equilibrium density. *Agapeta zoegana* can severely damage North American spotted knapweed rosettes. Feeding on roots directly reduces the storage capacity of the root as well as the uptake of

Table 7. Impact of *Agapeta zoegana* on mortality of potted *Centaurea maculosa* rosettes of different origin (genome) and age, and grown in different soil types (three first-instar larvae per pot were transferred in July)

	Treatment			
	A	B	C	D
Origin of plant (genome)	Europe $2n = 18$	Canada $2n = 36$	Europe $2n = 18$	Europe $2n = 18$
Plants infested (*n*)	20	20	10	10
Age of rosettes (months)	8	8	4	4
Soil type (cf. text)	Humus	Humus	Humus	Sand
Dead plants after 5 months (*n*)	8	13	4	8

water and nutrients (Crawley 1983). Mining of roots also enhances the susceptibility to infection by pathogens. Our study showed that several larvae developed on the same plant, and that the larvae searched for additional plants if they depleted their food supply before termination of larval development. This suggests that *A. zoegana* should be a highly effective biological control agent.

Several moths of *A. zoegana* caught in pheromone traps in Summerland, B.C., in August 1985, from field releases in 1983 (unpublished data), confirmed a first successful establishment. Large populations of moths reared in field cages at Kamloops, B.C., were released in 1986 in areas infested by spotted knapweed near Kamloops. They were caught in pheromone traps in 1987, proving their successful overwintering in the field. However, the insect's progress in North America needs to be carefully monitored to test our prediction that the additional stress imposed by *A. zoegana* will decrease knapweed density by increasing rosette mortality, and hence will complement the effects of the seed-feeding species already established.

Acknowledgment

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