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Biological control in a cold climate: Temperature responses and climatic adaptation of weed biocontrol agents

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Abstract

The Canadian prairies include the most northerly regions of the world in which classical biological control of weeds has been practiced. Climatic conditions are characterized by short growing seasons and extremely cold winters. Under these conditions, the adaptation of biological control agents to the physical environment can become a major limiting factor to the success of biological control, and failure of biological control agents to establish has sometimes been attributed to lack of adaptation to the climate. The development, survival, and reproduction of several biocontrol agents were studied experimentally under controlled temperature conditions to assess their adaptation to the climatic conditions of Alberta. The results to date suggest that the noctuid moth *Calophasia lunula*, an agent for toadflax (*Linaria* spp.) is unlikely to become established in Alberta. The chrysomelid beetle *Lema cyanella*, agent for Canada thistle (*Cirsium arvense*), should be able to complete development, but its rate of population increase may be limited by low fecundity in cool conditions. The geometrid moth *Minoa murinata*, an agent for leafy spurge (*Euphorbia esula*) in contrast, should be able to complete two generations in large areas of Alberta. These results have been used to guide the selection of agents for release and the selection of release sites.

Introduction

The province of Alberta, Canada, lies between latitudes 49°N and 60°N, with the main agricultural areas extending up to approximately 56.5°N. Alberta has a continental climate, with long cold winters and warm but short summers. The warmest area is the shortgrass prairie in the south-east. The climate becomes cooler to the north and towards the Rocky

Mountains, which run along the province's south-western border. The short duration of the growing season is a limiting factor for agriculture, the main crops being wheat, barley, canola (rapeseed), flax, and alfalfa, with increasing areas of field peas. Warmer-season crops such as corn and sunflowers are grown only in limited parts of the province. There are extensive areas of grazing land including native and 'improved' pastures. Some climatic data for selected locations in Alberta are shown in Table 1.

Classical biological control of weeds is carried out in Alberta by staff at the Lethbridge Research Station of Agriculture and Agri-Food Canada, the Alberta Environmental Centre, and Alberta Agriculture, Food and Rural Development. To our knowledge, Alberta is the most northerly region of the world in which there is an active classical biological control of weeds programme. (Programmes also exist in the other Canadian prairie provinces, Manitoba and Saskatchewan, but the agricultural areas of Alberta extend further north than in those provinces.) Most of the biological control agents which have been released and established in Alberta have been introduced from regions such as western or central Europe, with warmer, longer growing-seasons and shorter, less-severe winters. The physical environment may be a limiting factor for the establishment of biological control agents in Alberta and the failure of some agents to establish has been attributed to a lack of adaptation to the climatic conditions of Alberta or the other prairie provinces (Harris 1984; Peschken 1984a, b).

Although winter air-temperatures in Alberta can reach remarkably low levels, temperatures in the soil, where many insects overwinter, are much less extreme and are further moderated in sites with good snowcover. A depth of 20-50 cm of snow will stabilize the surface temperature of the underlying ground between 0°C and –10°C (Danks 1991). The supercooling points of a number of biological control agents released in Alberta. ranged from –17°C to –27°C (A.S. McClay and R.A. Butts unpublished data). Direct cold-induced mortality of overwintering insects is thus not necessarily the most important climatic limitation for establishment of introduced biological control agents. This study, therefore, examines the possibility that the establishment of some agents may be limited by the

Table 1. Climatic data for selected locations in Alberta (Anonymous 1982; Dzikowski and Heywood 1990).

		Medicine Hat (50°N)	Vegreville (53.5°N)	Peace River (56.25°N)
July	Mean daily maximum temperature (°C)	27.3	23.2	22.3
	Mean daily minimum temperature (°C)	12.4	9.4	9.0
January	Mean daily maximum temperature (°C)	-7.0	-12.4	-14.9
	Mean daily minimum temperature (°C)	-18.3	-23.8	-25.6
Absolute maximum (°C)		42.2	35.6	36.7
Absolute minimum (°C)		-46.1	-51.1	-49.4
Average number of frost-free days		c. 115	c. 100	c. 100
Annual precipitation (mm)		348	404	375
Percentage of annual precipitation received as snow		36	25	39

shortage of days during the growing season, that are warm enough for complete development of the immature stages and, or, for oviposition.

The effects of temperature on insect development rates have been extensively studied and modelled (Wagner *et al.* 1984: Lactin *et al.* 1995). In general, the relationship between development rate and temperature is curvilinear, showing a lower threshold temperature below which no development occurs, an increasing phase which may be sigmoidal, and an upper threshold after which development rate decreases as the upper lethal temperature is approached (Liu *et al.* 1995). However, for the three insects studied here, development rate over a realistic range of temperatures for Alberta was fairly well approximated by a linear function of temperature. This allows us to use degree-days (temperature above the developmental threshold integrated over time) as a measure of physiological time, and to calculate the number of degree-days required for an insect to complete development of its immature stages. If the time required for adult females to initiate and complete oviposition shows a similar relationship with temperature, we can also calculate oviposition degree-days. Available degree-days above any given threshold can be calculated from historical weather records for specific locations, and then used to estimate whether that location will provide sufficient physiological time for a particular insect species to complete its development and to lay a full complement of eggs. Contour maps of these estimated degree-day totals can be used to predict areas in which the insect should be able to establish (McClay and Hughes 1995).

McClay and Hughes (1995) showed that a degree-day model was quite effective in explaining the success or failure of establishment of *Calophasia lunula* Hufnagel (Lepidoptera: Noctuidae) in various release areas in North America, and was also consistent with its known distribution in Europe. The aim of these studies was to determine whether degree-day models cut be used to predict success of establishment of other biocontrol agents in Alberta.

Methods

Degree-day models were developed for three biological control agents in Alberta: (i) *Calophasia lunula,* an agent for common and Dalmatian toadflax, *Linaria vulgaris* Miller and *Linaria genistifolia* ssp. *dalmatica* (L.) Maire and Petitmengin; (ii) *Minoa murinata* (Scop.) (Lepidoptera: Geometridae), an agent for leafy spurge, *Euphorbia esula* L.; and (iii) *Lema cyanella* (L.) (Coleoptera: Chrysomelidae), an agent for Canada thistle, *Cirsium arvense* (L.) Scop. All these species lay their eggs on leaves of the host plant, feed on foliage as larvae, and pupate in the soil or litter. *Minoa murinata* and *C. lunula* overwinter as pupae, while *L. cyanella* overwinters as an adult. Field-releases of all three species have been made in Alberta. Releases of *C. lunula* were made from 1985 to 1991, releases of *M. murinata* started in 1991 and are still continuing, and releases of *L. cyanella* started in 1993.

Methods used to develop the degree-day model for *C. lunula* were described by McClay and Hughes (1995); procedures were similar for *M. murinata* and *L. cyanella.* Each species was reared individually from egg to adult in incubators at four constant temperatures (seven for *C. lunula),* in petri dishes and was provided with fresh foliage of the host plant. All temperature treatments were given a 16-hour photoperiod. The dates of oviposition, hatching, larval moults, cocoon formation, pupation and adult emergence were recorded for each individual. For *M. murinata* and *C. lunula,* pupae were sexed and pupal weights recorded. Male and female adults of these species were paired on emergence and maintained in oviposition cases at the same temperature at which larval development had taken place. They were provided with a branch of the host plant in a vial of water, and eggs were removed daily and counted until egg production ceased. Newly-emerged adults of *L. cyanella* are normally in reproductive diapause (Peschken and Johnson 1979). They were allowed to feed on *C. arvense* foliage for 2-4 weeks and then placed in ventilated plastic storage containers with foliage at 4°C for 16 weeks. They were then placed on caged *C. arvense* plants in the greenhouse to feed and mating pairs were removed. Pairs were placed in petri dishes at four constant temperatures with *C. arvense* foliage, and eggs were counted and removed daily.

Development rates (reciprocal of development duration) were plotted against temperature for each species and degree-day models were developed by fitting a straight line to these data. Estimated mean annual degree-day accumulations above the developmental threshold for each species were then calculated for 41 locations in Alberta using the published climatic norms for 1951-1980, and contours for the estimated number of potential generations were plotted as described by McClay and Hughes (1995).

A colony of *M. murinata* was maintained in an outdoor rearing-cage on potted leafy spurge plants at the Alberta Environmental Centre. Adults emerged in this cage each spring from pupae which had overwintered in the soil, under the pots, or under the wooden boards on which the pots stood. In 1995, the degree-day model for *M. murinata* was tested by recording air temperature hourly in the cage from April 25 to October 27, at the height of the plant canopy, using a 101B thermistor probe and CR-21 datalogger (Campbell Scientific). Degree-days above the developmental threshold for *M. murinata* were calculated for each day and accumulated over the growing season. The cage was monitored regularly over the growing season and records kept of the dates of occurrence and approximate abundance of adults, eggs, larvae and pupae.

Results and discussion

Calophasia lunula

Developmental parameters for *C. lunula* were reported by McClay and Hughes (1995). Figure 1 shows the areas of Alberta where it is predicted that *C. lunula* should be able to complete a full generation (i.e. with all eggs completing development to pupae) or a marginal generation (only the earliest laid eggs having time to complete development). A full generation should be possible in the southeastern corner of Alberta around the Medicine Hat area, although toadflax is not common in this area. Most releases of *C. lunula* were made in the central and north-western regions of Alberta where common toadflax is abundant. As can be seen in Fig. 1, these sites are mainly near or outside the contour line for even a marginal generation. Consistent with these predictions, *C. lunula* has never been found breeding at any of the release sites. Further monitoring should be conducted at the two release sites on Dalmatian toadflax in southeastern Alberta to determine whether establishment may have gone undetected at these sites.

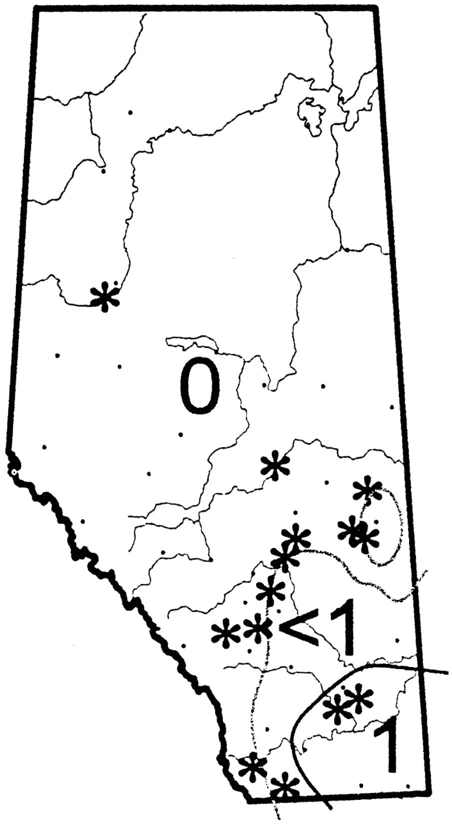

Fig. 1. Release sites of *Calophasia lunula* (asterisks) in Alberta and predicted areas allowing a complete generation (542 degree-days above 13.5°C: 1) and a marginal generation (418 degree-days above 13.5°C: <1). Small dots: climate stations used in calculating degree-days.

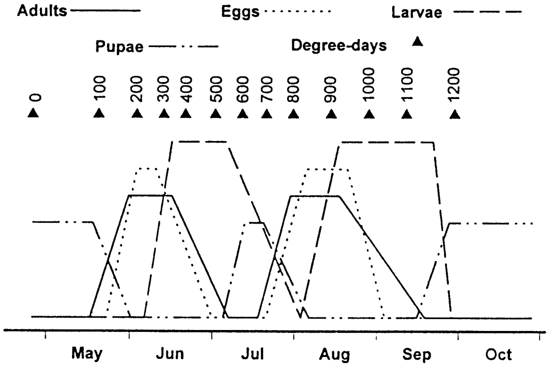

Fig. 2. Phenology of *Minoa murinata* in rearing cages at Vegreville, Alberta, 1995, and degree-days accumulations above 7.2°C.

Releases of *C. lunula* have now been discontinued, and efforts are underway to establish other biological control agents such as *Mecinus janthinus* and *Eteobalea serratella* against common toadflax in Alberta. The use of this degree-day model has provided a simple explanation for the failure of *C. lunula* to establish and has allowed us to avoid the waste of resources that would be involved in continuing efforts to establish this species in Alberta.

Minoa murinata

From the laboratory-rearing data, the estimated parameters of the model for complete development of *M. murinata* are 584 degree-days and a threshold of 7.2°C. No eggs were obtained at 15°C or at 30°C, so it was not possible to calculate oviposition degree-days. Phenological predictions were therefore based only on the egg-to-adult development times. Figure 2 shows the observed phenotogy of *M. murinata* in the outdoor rearing-cage at Vegreville, and the accumulated degree-days above 7.2°C. The total degree-day accumulation over the season was 1264, just over twice the number needed for a generation, according to the model. Consistent with this prediction, two full generations occurred in the cage, with adults of the first generation emerging in late May and the second in late July. The first generation was completed with the appearance of pupae on July 4, when 544 degree-days had accumulated; pupae of the second generation were first observed on September 14 at 1146 degree-days. The degree-day model thus accords with the observed phenology of *M. murinata* in the rearing-cages.

Figure 3 shows the predicted number of generations for *M. murinata* in the field in Alberta. Two generations should be possible over a large area of southeastern Alberta, which includes many of the areas with leafy

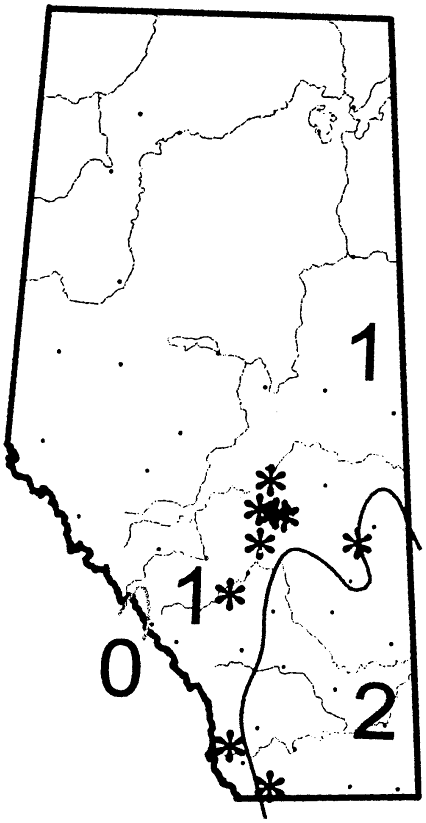

Fig. 3. Release sites of *Minoa murinata* (asterisks) in Alberta and predicted areas allowing 1 or 2 generations (584 or 1168 degree-days above 7.2°C.

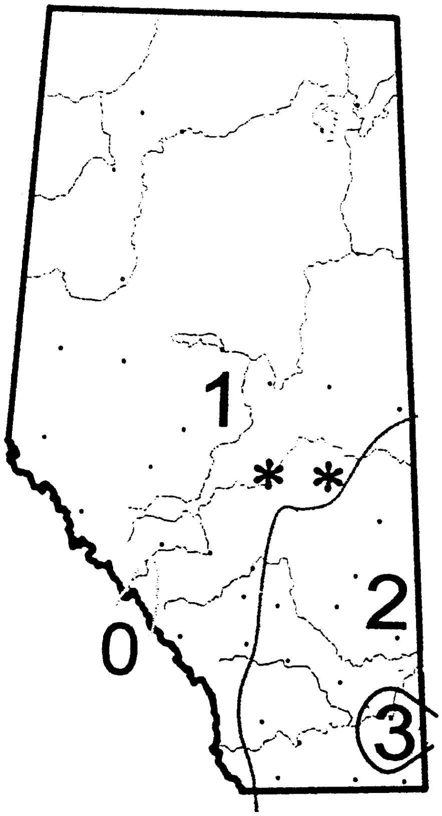

Fig. 4. Release sites of *Lema cyanella* (asterisks) in Alberta and predicted areas allowing 1, 2 or 3 generations (293, 586 and 879 degree-days above 11.3°C).

spurge infestations. A single generation should be possible through the entire remaining area of the province, with the exception of high altitude areas in the Rocky Mountains, along the south-western border of the province.

Most releases of *M. murinata* have been made within the area where a single generation is predicted. The species has not yet been recovered from open field-releases, but has persisted for over four years in a field cage on a leafy spurge infestation at Millet, south of Edmonton. In 1994 and 1995 the population in the cage increased to a level sufficient to cause defoliation by the end of the summer. This site is within the predicted single-generation area, but fairly close to the two-generation contour. The annual degree-day totals at this site were estimated from hourly data from the nearest available climatic station at Edmonton International Airport, approximately 18 km northeast of the site. Over the period for which this population has persisted, annual degree-day totals ranged from 1030 to 1212. The predicted requirement for two generations is 1168 degree-days. Monitoring of the site suggests that two generations have in fact occurred in most years; possibly microclimatic effects within the cage have increased the degree-day total to allow this to occur.

Release sites for *M. murinata* were selected on the assumption that this species requires relatively cool conditions (Harris 1985). This was supported by data from the laboratory constant-temperature studies, which showed high mortality of eggs and young larvae at 30°C (McClay unpublished data). Releases were therefore not made in the warmer southeastern areas of Alberta, where temperatures in this range occur more frequently. However, the results shown in Fig. 2 suggest that it would be worthwhile to attempt releases in this area. As shown in the field-cage-rearing *M. murinata* will attempt to initiate a second generation under field conditions in Alberta, and its chances of establishment may therefore be improved by making releases in areas where the second generation can be completed. Leafy spurge is abundant along river valleys in southern Alberta (McClay *et al.* 1995) inside the two-generation contour line for *M. murinata.* Exposure of early stages to excessive heat could perhaps be minimized by selecting shaded sites within this area.

Lema cyanella

The parameters for the model for development of *L. cyanella* from egg to adult were 293 degree-days over a threshold of 11.3°C. The model predicts that *L. cyanella* should be able to complete at least one generation in virtually all parts of Alberta except at high elevations in the Rocky Mountains (Fig. 4). An extensive area of south-eastern Alberta, including approximately half the agricultural area of the province, has sufficient degree-days for two generations, and the area around Medicine Hat may allow three generations. Whether *L. cyanella* will in fact be bivoltine or multivoltine in any area of the province will depend on its diapause behaviour. Zwölfer and Pattullo (1970) found no evidence for a second generation in the field in Europe. In laboratory rearing, however, Peschken and Johnson (1979) found that a small proportion of adults mated and laid fertile eggs soon after emergence, although most fed for about three weeks and then entered diapause. We obtained similar results in our greenhouse rearing.

The fecundity of *L. cyanella* under laboratory conditions varies widely. In 1994 we found an apparently strong relationship between temperature and oviposition, with a total production of about 360 eggs over a 50-60 day period at 25°C and 30°C, while egg production was greatly reduced at 20°C and virtually suppressed at 15°C. In 1995, fecundity was much lower in all temperature treatments and differences among the treatments were less marked. Further study is required to clarify the effects of temperature on the egg production of *L. cyanella* but the rates of population increase may be limited by low temperatures in the field during the oviposition period.

The results from field releases of *L. cyanella* in Alberta are preliminary. Two releases were made in 1994, and survival and breeding was found at both release sites in summer 1995. Overwintered adults and eggs were seen in late May and early June, and larval feeding appeared to be complete by mid- to late-July. This is consistent with the prediction that *L. cyanella* should be able to complete a single generation in this area. Further monitoring at these sites will be necessary to compare the phenology of *L. cyanella* with the predictions of the model. These results, however, are encouraging enough to suggest that further releases of *L. cyanella* in Alberta would be worthwhile.

Conclusions

Temperature-development models have been estimated for a number of predatory and parasitic arthropods used as biological control agents (e.g. Lysyk and Nealis 1988; Ryoo *et al.* 1991; Miller 1992; Miller and Gerth 1994). There have been fewer efforts to develop such models for weed biological control agents (Smith and Kok 1985; Godfrey and Anderson 1994; Fornasari 1995), and still fewer attempts to predict the potential areas of establishment of agents from such models. The CLIMEX program (Sutherst and Maywald 1985) was used by Julien *et al.* (1995) to estimate the potential areas where *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae) may be successful in controlling alligator weed, *Alternanthera phylloxeroides* (Mart.) Griseb. (Amaranthaceae). Scott (1992) also used CLIMEX to assess the potential of *Perapion antiquum* (Gyllenhal) (Coleoptera: Apionidae) against *Emex* spp. (Polygonaceae). CLIMEX is a multiparameter model which includes parameters describing humidity and precipitation tolerances as well as temperature. As such it requires more extensive data on a species' environmental requirements, which must often be estimated iteratively by fitting parameters from the species' known distribution.

The use of degree-day models to predict possible areas of establishment has had several benefits in our programme. It has avoided the waste of effort involved in continuing to attempt to establish an agent which is not adapted to local climatic conditions; it has suggested a change in release strategy for an agent which did not establish from initial releases; and it has provided encouragement to continue with releases of an agent whose potential was previously unknown. A further benefit of the models may lie in facilitating field-monitoring. If late-instar larvae of an agent, for example, are the easiest stage to detect in the field, a degree-day model may be able to predict the most suitable dates for monitoring field releases.

The development of a degree-day model for a biological control agent is labour-intensive, even with foliage-feeding species such as those studied here. The development of a model for species feeding internally in plants or in the soil would be technically more difficult; the life stages of such species are less accessible for observation, and it is more difficult to hold insects individually through their whole life-cycle in a controlled-temperature cabinet when whole living plants must be provided for feeding. The work required could be reduced somewhat by recording only the dates of oviposition and adult emergence for each species; this would be sufficient information to construct a model for overall egg-to-adult development such as those presented above. Data on the duration of individual stages in the life-cycle may, however, be useful in making more detailed comparisons of field observations with model predictions.

Because of the labour involved, it would probably not be cost-effective to develop degree-day models as a routine component of pre-release studies for all new candidate biological control agents. The most appropriate time to develop such models may be when difficulties are encountered in establishing an agent from initial releases, particularly when introducing agents originating from climates significantly different from those of the release area.

Acknowledgements

I thank John O'Donovan and Richard A. Butts for their comments on an earlier draft of the manuscript, Robert B. Hughes, Irving Switzer, Philippe Lacasse, and Leslie Dietz for technical assistance, Peter Harris for providing *C. lunula* and *M. murinata***,** Robert Nowierski for providing additional material of *C. lunula***,** Toni Jessep for providing *L. cyanella***,** and Marion Herbut and Brenda Dew for assistance with mapping and graphics.

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