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Modelling and Mapping Geographic Ranges to Evaluate Weed Biocontrol Agents: A Case Study Using *Altica carduorum* (Coleoptera: Chrysomelidae) and *Cirsium arvense* (Asteraceae)

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Leaf-feeding beetles, *Altica carduorum*, from a population in NW China have been identified as candidate agents for biocontrol of Canada thistle, *Cirsium arvense*. This paper assesses the potential of beetles from this population to establish on the Canadian prairies. A phenological model is applied to determine where sufficient heat accumulates to allow completion of at least one generation per year. The model was applied both with and without a submodel of adult thermoregulation. The model was driven using meteorological data from a grid covering the agricultural region of the Canadian prairies, i.e. ca. 670 000 km², at a resolution of $\leq (50 \times 50)$ km. In each grid square, the percentage of the years 1960–89 for which the model indicated that at least one generation could have been completed was calculated; these proportions were categorized (0–80%; 80–99% and 100%) and mapped. Maps of *C. arvense* density over the simulation region were also produced, and compared to the maps of predicted beetle distribution. The model suggests that *A. carduorum* could establish over much of the prairies. Without thermoregulation, the predicted range (i.e. the area in which one generation was completed in every year) is restricted to the warmer parts of the prairies, where *C. arvense* is generally sparse. Inclusion of thermoregulation almost doubled the predicted range to cover most of the range of *C. arvense* on the Canadian prairies, missing only the cooler peripheral areas. These results suggest that this strain of *A. carduorum* has potential to overlap the range of *C. arvense* on the Canadian prairies, and so has potential to control this weed.

Keywords: *Altica carduorum*, *Cirsium arvense*, phenology model, behavioral thermoregulation, biocontrol, geographic range

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INTRODUCTION

Canada thistle, *Cirsium arvense* (L.) Scop., is an introduced weed that causes significant economic losses in crops and pastures in North America (Hodgson, 1968). This weed thrives only in open sites where summer temperatures are moderate and soil moisture is adequate. Moisture requirements are fulfilled by annual rainfall of 450–900 mm (Donald, 1990) or by irrigation. In North America, the weed is distributed in a transcontinental band which is limited to the south by high summer temperatures and to the north by forest (Donald, 1990). In Canada, it extends to latitudes of 58–59 N (Moore, 1975) and is a particularly serious problem in the black soil zone of the prairies (Alex, 1966; Thomas, 1980), which extends to the northern limits of sustainable agriculture. In wheat alone, the thistle causes annual losses of ca. \$Can 3.6 million despite extensive herbicide use (Peschken *et al.*, 1980). Given the geographic magnitude of the problem, biological control (biocontrol) is an attractive alternative to chemical and cultural control methods.

The foliage-feeding flea beetle *Altica carduorum* Guer. (Coleoptera: Chrysomelidae) was identified in the 1960s as a promising agent for biocontrol of *C. arvense* in North America. Initial releases used insects collected from Western Europe; these failed to establish, in part because the relative humidity on the prairies is too low for optimum egg development (Peschken *et al.*, 1970; Schaber *et al.*, 1975). However, an isolated population of this beetle suppresses *C. arvense* within an area of ca. 1105 km² in the arid region near Wusu, Xinjiang, China at latitude 44.5 N (Wan *et al.*, 1996). The tolerance of this population for low humidity makes it promising for the Canadian prairies if the cooler summers do not preclude completion of development. Three hundred adult beetles were collected from this population and propagated in the laboratory; this stock is the subject of the following investigations.

Adult *A. carduorum* is a metallic blue-black beetle ca. 4 mm long. Overwintering adults emerge from the soil in the spring to feed on young thistle leaves. After an obligate pre-oviposition period, females oviposit on the underside of thistle leaves for up to 2 months. The eggs hatch in about a week and the larvae feed from the bottom of the leaf to the upper cuticle, which is left intact, forming a transparent 'window'. Mature larvae drop to the soil, bury themselves to a depth of ca. 1 cm and pupate. At Wusu, adults emerge and initiate a summer generation. The progeny of this second generation emerge as adults, starting in about mid-July; these do not oviposit, but enter the soil in September–October to overwinter (Wan *et al.*, 1996).

In preliminary calculations using air temperature, Wan *et al.* (1996) concluded that beetles from this stock could potentially establish only in a few relatively small warm areas of the southern Canadian prairies; however, these calculations did not include the effects of solar radiation and thermoregulation, which raise the body temperatures of many diurnal ectotherms significantly above air temperature (Heinrich, 1993). In Xinjiang, *A. carduorum* adults spend most of their time on the upper side of tender *C. arvense* leaves, but move between sunlit and shaded sites over the day (Wan *et al.*, 1996); this behavior may be thermoregulatory.

In this paper, a phenology model was applied to estimate the area of the Canadian prairies in which beetles from this stock could establish permanent populations. The model was driven using input from a historical meteorological database, and determined the proportion of the years 1960–89 in which *A. carduorum* could have completed at least one generation per year in each square of a grid covering the agricultural region of the Canadian prairies. It was assumed that these data represent a forecast of future meteorological conditions in this region, and that the proportion represents the probability of future establishment.

This study had two purposes. The first was to determine the area of the Canadian prairies in which heat accumulation would be sufficient to allow completion of at least one

beetle generation per year, which is the minimum requirement for establishment. Several aspects of establishment were not considered in this study because data are not available; these include mortality and host finding. It was also assumed that reproductive diapause in adults will preclude initiation of generations which are unlikely to be completed. This is consistent with the failure of second-generation females to oviposit in Xinjiang.

Furthermore, the study was aimed primarily at making general statements about the likelihood of generations being completed in specified areas. The simulation utilized meteorological data from a grid which gives mean conditions in 50×50 km squares. It was judged that the precision of the simulation utilized meteorological data from a grid which gives mean conditions in 50×50 km squares. It was judged that the precision of the simulation was limited by the precision of this grid; therefore, variance in developmental rates was neglected, because the additional precision which might result from considering this factor would be illusory.

The second purpose of this study was to assess the beetle's potential to affect the distribution and abundance of the weed, by comparing this area with the distribution of *C. arvensis* to evaluate whether the two species are likely to overlap geographically.

MATERIALS AND METHODS

The phenology model used temperature-dependent developmental rate parameters from Wan *et al.* (1996), iterated hourly from 1 January to 31 December to accumulate increments of development. At the end of each year, the model reported the number of generations completed. A generation was defined as the time required for the average female to lay 50% of her eggs, plus the average time for the progeny to become adults. Generations were considered to start and end at adult eclosion. The model was applied both with and without a submodel for adult thermoregulation.

Thermal Biology of *A. carduorum*

Developmental rate descriptions. All temperature-dependent rate phenomena were described using linear equations. These include developmental rates of eggs, larvae and pupae; and the rates of adult maturation and oviposition (Wan *et al.*, 1996). Larval development rate declines at temperatures above 25 C, so these temperatures were disregarded when fitting the linear developmental equations.

The model treated the populations in the simplest manner: all individuals were assumed to be identical (i.e. to develop at the average rate at any temperature and to be exposed to identical meteorological conditions). Overwintering adults were assumed to emerge from the soil when they had completed half of their preovipositional requirements. Thus, development was driven by soil temperatures at 1 cm before emergence, and by air temperature thereafter. All females were assumed to require the average pre-oviposition period, and to lay all of their eggs in the middle of the oviposition period. Development of eggs and larvae were driven by air temperature, and those of the prepupae and pupae by soil temperature at 1 cm. Second-generation adults were assumed to emerge from the soil immediately after eclosion and to fulfill their pre-ovipositional requirements above ground. In the model, these second-generation adults are allowed to oviposit, although this does not occur in Xinjiang. This allowance was made to determine where heat accumulation could in theory allow a complete second generation. The model is outlined in more detail in Appendix A.

A. carduorum phenology was also simulated using a second model which acknowledged the non-linear relationship between developmental rates and temperature. The range predicted by this model differed by < 1% from that of the model described here, because: (1) the temperature-dependent developmental rate was notably non-linear only in the larval stage and (2) larval body temperatures above the thermal optimum were rare over the

geoclimatic range of the simulations. The similarity between the two models may break down in warmer climates. For clarity of presentation, the second model is not presented here.

Effect of solar radiation on beetle body temperature. Adult *A. carduorum* were restrained under measured conditions of air temperature and solar radiation (in W m^{-2}). Each beetle was glued by the abdomen to the head of an insect pin which was attached to a cork stopper which was in turn mounted on a horizontally oriented board (Lactin & Johnson, 1996) set 20 cm above a concrete pad in a wind-sheltered site. Air temperatures were ≈ 15 C during the test period.

Beetle body temperatures were measured using 0.127-mm diameter copper-constantan thermocouples (Omega Corp., Stamford, CT, USA), inserted into the abdomen to a depth of ≈ 1 mm. Temperatures of each beetle were recorded in full sunlight and under one, two and four layers of 42 mesh cm^{-2} black nylon window screen. Twenty-one beetles were tested in groups of three; for each group, a similarly treated reference beetle, mounted in a sunshade, was used to measure air temperatures. Solar radiation was measured using a pyranometer (LI-200SZ, LI-COR Instruments, Lincoln, NE, USA).

Temperatures and solar radiation were measured every 0.5 s; readings were averaged in 12-s increments and the means output to a datalogger (Model 21X, Campbell Scientific, Edmonton, Alberta, Canada). For each group of insects, measurements were taken until the temperature of the restrained beetles had stabilized (2–3 min). The solar-heating effect was calculated from measured solar radiation, the stabilized body temperatures of the restrained beetles and the concurrent temperature of the reference beetle.

Thermoregulation submodel. The model was applied with and without the following adult thermoregulation submodel. The effect of solar radiation on body temperature was estimated by incrementing air temperature by an amount related to solar radiation, as determined in the previous section (see Results). This submodel also incorporated the effects of above-ground temperature gradients. During the day, soil temperature is generally heated by the sun to several degrees above air temperature (Campbell, 1977), and a vertical gradient of air temperature results. The gradient was incorporated into the submodel by calculating the maximum and minimum possible temperature within the vertical gradient (i.e. on the ground in full sun and at 1.2 m above the ground in full shade respectively). The beetles were assumed to maintain their body temperature as close as possible to the optimum temperature for larval development (25.5 C). These assumptions fit the observed movements of the beetle in China. Larval optimum temperature was used because there is no information on the adult optimum; this assumption requires testing.

Meteorological Data

Basic data. Input data were: total daily insolation (MJ m^{-2}); daily maximum and minimum Stevenson screen air temperature at 1.2 m (C); and rainfall (mm). These data were extracted from the Gridded Prairie Climate Database (GRIPCD), which is available on compact disk from Environment Canada, Downsview, Ontario. This database represents the Canadian Prairies as a grid of points separated by 0.41 latitude and 0.75 longitude; at 49 N this corresponds to rectangles of approximately 50×50 km. These data were processed from historical weather data collected from an irregular array of weather stations (McGinn *et al.*, 1995). Where data did not cover the 30 years without interruption, squares were not included in the simulation; the geographical coverage of the remaining 406 squares corresponds approximately to the region of sustainable crop production.

Soil temperature estimation. Soil temperatures enter the phenology model by affecting development of prepupae and pupae. The GRIPCD data does not include soil temperatures, so these were estimated using data from a second meteorological database maintained at Agriculture and Agri-Food Canada Research Centre at Lethbridge, Alberta, which is more comprehensive but restricted to one side. In addition to the basic data listed in the previous section, this data includes morning and afternoon soil temperatures at 5 cm. Regression equations were used to relate these temperatures to other meteorological variables, and these equations were used to estimate soil temperatures over the grid.

Equations were fitted to the data by stepwise multiple regression (SAS, 1989) using the MAXR algorithm, which finds the best models with $1-n$ variables, where n is the number of candidate variables. Candidate variables were: the daily values of all variables included in the grid database, the squares of all these variables, and the previous day's values of all variables and their squares.

Regressions were calculated separately for morning and afternoon soil temperatures. Because inspection of plots revealed that distinct linear relationships applied for minimum air temperatures above and below 0 C, regressions were fitted separately at those conditions. The regressions each had from five to nine parameters, and all had $F > 65$; $P(> F) \leq 0.0001$ and $r^2 > 0.72$. Parameter estimates for equations are given in Appendix B. Daily afternoon and morning soil temperatures at 5 cm were estimated for all grid points using these equations; these were used to estimate temperatures at 1 cm, following Campbell (1977).

Interpolation of hourly values. Hourly values were interpolated for all variables. Hourly solar radiation was estimated from the daily total observed solar radiation and the theoretical maximum daily and hourly insolation for the latitude and date (Robertson & Russelo, 1968). The ratio of observed to theoretical maximum was assumed to remain constant over the day, and this ratio was used to estimate hourly values from theoretical maximum hourly values.

Hourly air and soil temperatures were each estimated by cosine interpolation from the daily maxima and minima. Based on examination of the meteorological database, the times of daily maximum temperature were fixed at 15.25 for air and 15.55 for soil. For soil temperatures, this implies that the morning and afternoon soil temperatures are the daily minima and maxima respectively. Half-cycle length was fixed at 12 h.

Prediction of *A. carduorum* Geographic Range

The phenology model was applied with and without the thermoregulation submodel over 30 years in all grid points with complete meteorological data. The results were categorized and mapped according to the percentage of years in which at least one generation was completed. For mapping purposes, these percentages were assigned into three classes: 0–80, 80–99 and 100, corresponding to establishment probabilities of unlikely, marginal and possible respectively.

Mapping Distribution and Abundance of *C. arvensis* and *A. carduorum*

Data on the distribution and abundance of Canada thistle on the Canadian Prairies were obtained from the AAFC weed survey (Thomas, 1980). The thistle database contained 214 sites in Saskatchewan surveyed in 1986, 234 sites in Manitoba surveyed in 1986 and 392 sites surveyed in Alberta from 1987 to 1989. At each site, 20 quadrats (each 1 m²) were placed randomly and observations consisted of the mean number of thistle plants observed per m² and the percentage of quadrats in which Canada thistles occurred.

For mapping purposes, data were expressed as percentage of quadrats with thistles and assigned into classes: 0–10, 10–20, 20–30 and > 30% of quadrats with thistles. Thistle abundances were smoothed by construction of a grid of weighted average values, with points every 0.5° of latitude and longitude in the region from 49 to 58 N, between 95 and

120 W. This grid is distinct from the weather grid. Canada thistle density at each point on the thistle grid was interpolated as the average of survey observations within a radius of 60 km of the point, weighted by the inverse of the distance from the point to the site. This resulted in the most distant points having weights of 1.7%, compared to 100% for observations within 1 km of the point. Some grid points in the dry, mixed-grass ecoregion, in which Canada thistle is sparse, were not within 60 km of any survey point, and these points were assigned a value of 0.1% of quadrats with thistles, on the basis of summaries of surveys in the region (Thomas, 1980).

The estimated thistle densities were imported into SPANS GIS 5.4 (OS/2 Warp operating system), and values between grid points were estimated by linear contouring using a triangular irregular network. Linear contouring was chosen to preserve the integrity of the values at the grid points. Contouring and interpolation were restricted to the region of the original set of survey points. The entire Canada thistle study area mapped was ca. 670 000 km².

Output from the *A. carduorum* phenology model was mapped in the same way, via weighted average grid calculation. Maps were verified to ensure that values on grid points were the same as the original data values.

Two-map overlays were constructed using SPANS, in which polygon comparisons are summarized to assess the overlap of the three classes of beetle establishment with the four classes of thistle density.

RESULTS

Thermal Biology of *A. carduorum*

Developmental rate functions. The linear functions (Table 1) indicate that the lower threshold temperature for the development of each beetle stage was between 7.6 and 9.9 °C. Development proceeds according to accumulation of degree-days (DD) above the threshold; the model used the threshold temperature specific to each age class (Table 1). To complete their development, the immature stages require a total of nearly 383 DD above their respective lower threshold temperatures. The females require nearly 372 DD from eclosion until 50% of their eggs are laid. This suggests a generation time of ≈ 754 DD.

Effect of solar radiation on beetle body temperature. The body temperature of *A. carduorum* adults increased linearly with solar radiation. The intercept of this regression was not significantly different from zero ($P > 0.9$), and so was omitted from the model. The slope of the no-intercept regression was $0.00965 \text{ C (W m}^{-2}\text{)}^{-1}$, with a standard error of $0.00050 \text{ C (W m}^{-2}\text{)}^{-1}$ ($F_{1,19} = 367$, $P \leq 0.0001$, $r^2 = 0.9508$). Solar radiation can exceed 1000 W m^{-2} ; thus, in a sunny location, beetle body temperature may exceed air temperature by $> 10 \text{ C}$.

TABLE 1. Regression parameters, lower developmental temperatures (LDT) and degree-day (DD) requirements using a linear developmental model to describe development of life stages of *A. carduorum* reared at constant temperature

Life stage	Intercept		Slope		F^a	r^2	LDT ^b	DD ^c
	Est.	SE	Est.	SE				
Egg (< 25 °C)	-0.0881	0.0031	0.01019	0.0016	40.8	0.95	8.6	98.1
Larva (< 25 °C)	-0.0724	0.0117	0.00728	0.0073	143.0	0.98	9.9	137.4
Pupa + prepupa	-0.0540	0.0038	0.00680	0.0003	1105.4	0.99	7.9	147.1
Pre-oviposit ^d	-0.0204	0.0052	0.00269	0.0003	110.7	0.99	7.6	371.7

^a All $P(> F) < 0.05$, except pre-oviposit, where $P(> F) = 0.06$.

^b Lower developmental threshold temperature (= -intercept/slope).

^c Thermal units $>$ LDT required to complete stage (= $1/\text{slope}$).

^d Pre-oviposition period + days to lay 50% of eggs.

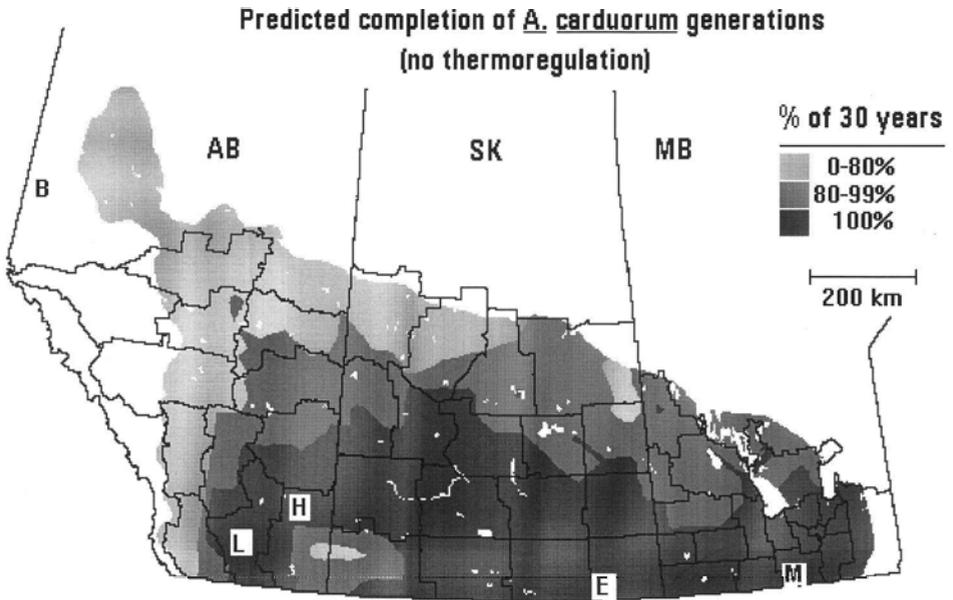


FIGURE 1. Percentage of the years 1960–89 in which an average *A. carduorum* completed one generation, in response to the average climatic conditions in each grid square. Thermoregulation not included in the estimate of body temperature. Capital letters within the map locate towns mentioned in the text: B, Beaverlodge AB; L, Lethbridge AB; H, Medicine Hat AB; E, Estevan SK; M, Morden MB.

Simulation of *A. carduorum* Geographic Range

Model versions. Results of the simulations which did not consider thermoregulation are given in Figure 1. Output is presented as generation-completion classes, defined as the percentage of years in which local *A. carduorum* populations completed at least one generation. The predicted range of the beetle on the Canadian prairies is ca. 290 000 km². Results of the simulations which do consider thermoregulation are given in Figure 2. The predicted range of the beetle on the Canadian prairies is ca. 530 000 km². Table 2 gives more detailed output from three locations which represent the approximate geographic limits of the simulation area.

Inclusion of the thermoregulation submodel resulted in two important changes in the simulation output. First, the predicted range increased remarkably, nearly doubling in area and extending up to 450 km further north. The second change was that with the thermoregulation submodel, the phenology model predicted that two generations per year were occasionally completed in some areas, e.g. near Morden, Manitoba (49 11' N, 98 06' W); Estevan, Saskatchewan (49 08' N, 102 59' W) and Medicine Hat, Alberta (50 03' N, 110 40' W).

Geographic range and density of Canada thistle are mapped in Figure 3. A contour is included which delimits the predicted range of *A. carduorum* where behavioral thermoregulation is considered; this overlaps extensively with the range of the thistle. However, the range overlap of the two species is imperfect. Near the periphery of the thistle range, the model suggests that some dense infestations may escape beetle herbivory.

Figure 4 compares thistle occurrence and beetle establishment classes. The area in which thistles occur, but the model suggests that the beetle will fail to establish (< 100% of years with at least one generation), is about 19.7% of the simulation area. Cases where this escape from attack is most serious economically (> 30% of quadrats with thistles, and beetles establish in < 100% of years) cover 1% of the area.

From the inverse perspective, the model also indicates that heat accumulation is often sufficient to allow beetle establishment in areas where thistles are scarce (< 10% of quadrats); this combination occurs in approximately 35% of the simulation area, typically in the dry, mixed-grass ecoregion. However, although the thistle is generally sparse in this region, pockets of dense thistles occur, particularly in irrigated sheep pastures (e.g. near Hays, Alberta (50 06' N, 111 48' W)); in these areas, site-targeted introductions may be valuable.

DISCUSSION

This phenology model suggests that *A. carduorum* can establish permanent populations over a large part of the region infested by *C. arvensis* on the Canadian prairies, and that two generations may be completed occasionally in some locations. Comparison of distributions predicted with and without the thermoregulation submodel illustrates the profound influence that thermoregulation may have on species distributions.

The effect of thermoregulation may explain observations by McClay and Hughes (1995) that populations of *Calophasia lunula* (Lepidoptera: Noctuidae) persist outside of the range predicted by a simple phenology model based entirely on Stevenson screen air temperature. McClay (1996) also used phenology modelling to conclude *post-hoc* that four different species of biocontrol agents had failed to establish at several release sites because of insufficient heat accumulation. Neglect of the effects of thermoregulation may undermine this conclusion. Because of the ubiquity of thermoregulation in diurnal insects (e.g. Heinrich, 1993), it is recommended that models of phenology and biogeography should explicitly consider this behavior. Combined with the results presented here, those of McClay (1996) and McClay and Hughes (1995) suggest strongly that this recommendation pertains especially to species which are to be released near to their climatic limits for establishment.

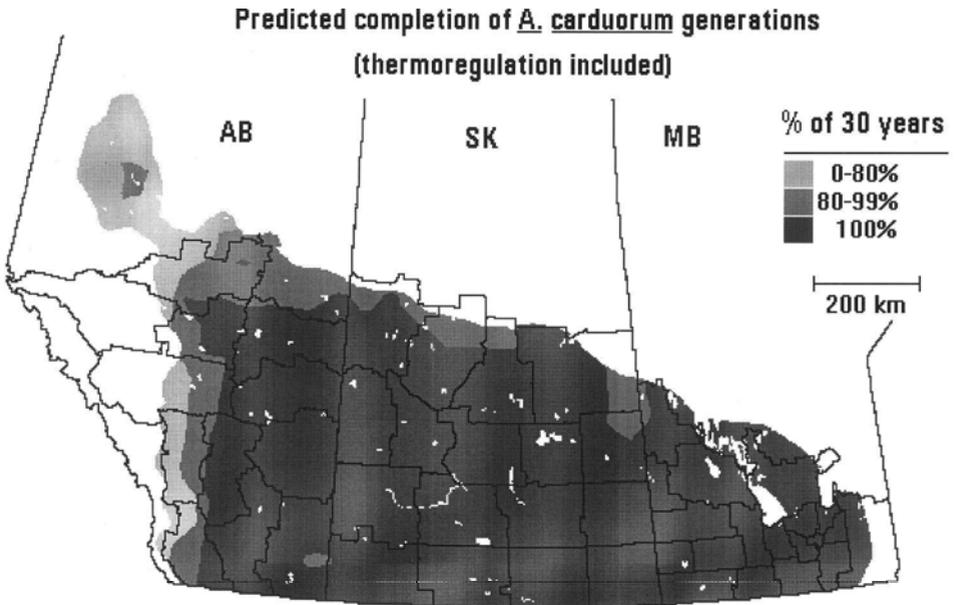


FIGURE 2. Percentage of the years 1960–89 in which an average *A. carduorum* completed one generation, in response to the average climatic conditions in each grid square. Thermoregulation included in the estimate of body temperature.

TABLE 2. Generations completed by *A. carduorum* over each of 30 years, at three locations near the limits of the Canadian prairies. Models include the effects of solar heating and behavioral thermoregulation

Year	Beaverlodge, AB		Lethbridge, AB		Morden, MB	
	55 13' N, DD ^a	119 26' W GEN ^b	49 42' N, DD	112 26' W GEN	49 11' N, DD	98 06' W GEN
1960	877	1	1223	1	1462	1
1961	1105	1	1311	1	1536	2
1962	724	0	1149	1	1333	1
1963	916	1	1263	1	1652	2
1964	649	0	1033	1	1328	1
1965	852	1	1063	1	1211	1
1966	620	0	1144	1	1384	1
1967	922	1	1238	1	1377	1
1968	619	0	935	1	1202	1
1969	666	0	1117	1	1306	1
1970	714	0	1201	1	1419	1
1971	950	1	1178	1	1317	1
1972	743	0	1038	1	1351	1
1973	650	0	1122	1	1353	1
1974	625	0	1052	1	1278	1
1975	662	0	1072	1	1358	1
1976	756	1	1141	1	1451	1
1977	715	0	1039	1	1384	1
1978	737	0	1088	1	1421	1
1979	876	1	1225	1	1249	1
1980	970	1	1143	1	1490	1
1981	1047	1	1111	1	1380	1
1982	748	0	1066	1	1259	1
1983	843	1	1124	1	1464	1
1984	718	0	1123	1	1464	1
1985	836	1	1087	1	1182	1
1986	884	1	1097	1	1345	1
1987	989	1	1244	1	1493	1
1988	1011	1	1299	1	1801	2
1989	1007	1	1067	1	1524	2
Mean	814.3667	0.5	1133.1	1.0	1391.4	1.1
SD	142.919	0.5	87	0.0	131.4806	0.3

^a DD = annual accumulated degree-days above stage-specific thresholds.

^b GEN = number of generations (adult to adult) completed.

This approach of integrating biological, behavioral and climatic information to model the possible geographic distribution of exotic biocontrol agents can be a valuable tool for evaluating whether introductions can be successful. Historically, the possibility that an exotic insect will establish has been evaluated by comparing climatic conditions in the area of origin and the introduction site. Where the insects introduced come from a small subsection of the ancestral geographic range, the most relevant comparison is between the climates at the sites of origin and introduction. However, such comparisons are qualitative and/or intuitive (Harris, 1979), and may be made more quantitative by assembling data into a model.

Construction of the model is relatively inexpensive and proper application may save considerable resources. If the model suggests that the insect is not likely to establish successfully in the target area, the subsequent pre-introduction evaluation process can be averted. This can save about two scientist years in host-specificity determination, and can preclude establishment studies which require several years (Harris, 1979). However, if the model suggests that establishment is possible, it may identify where releases are most likely

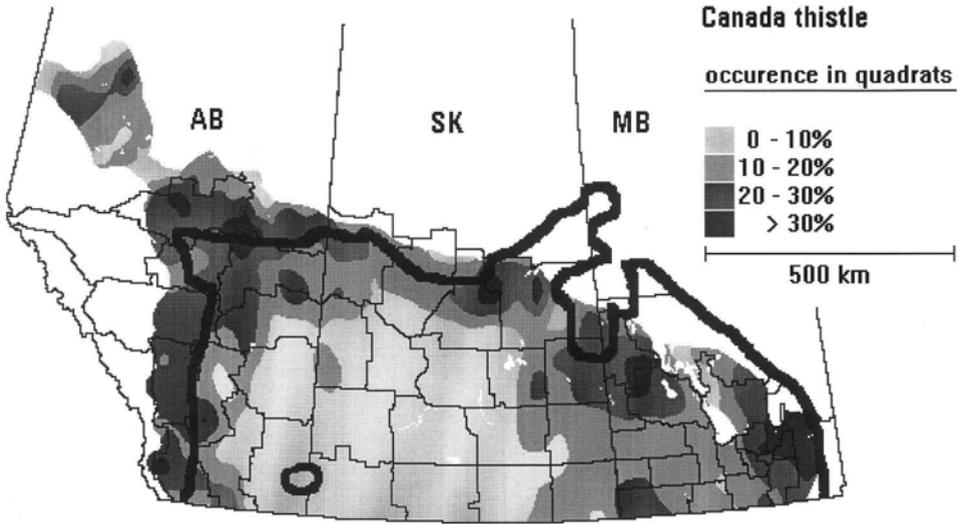


FIGURE 3. Occurrence frequency of Canada thistle on the Canadian prairies. Dark line defines the area in which modelled *A. carduorum* populations completed at least one generation in every year of the 30-year simulation, with the model including thermoregulation.

to be successful. Both outcomes are particularly important if the exotic species is to be released near its range limits.

The model has several limitations as a result of simplifications. Although these should not affect the general conclusion that beetles from this population can establish on the Canadian prairies, they may affect the geoclimatic limits to their range.

- (1) The model deals with average conditions within squares of approximately 50×50 km. However, each square consists of a spatially diverse mosaic of meteorological conditions, of which a portion is warmer than the average.
- (2) The model assumes that the eggs and larvae are at air temperature because they occur exclusively on the underside of the leaves. However, their temperature may be

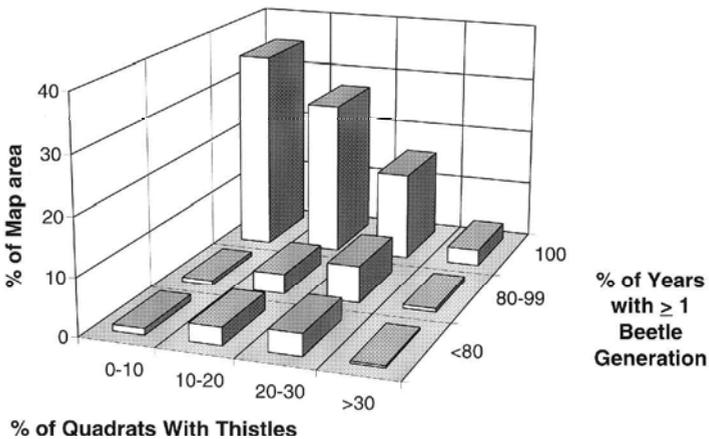


FIGURE 4. Overlap of beetle establishment categories and thistle occurrence frequency categories, as a percentage of total map area.

elevated by reflected or diffuse radiation; larvae may also be heated by direct radiation admitted by the window they create while feeding. Furthermore, the temperature of the leaf may exceed air temperature (May, 1982). If any of these effects is significant, eggs and larvae would develop more quickly than the model suggests.

- (3) The model treats all beetles as identical, i.e. that all experience the same conditions, develop at the mean rate and oviposit synchronously. More realistically, there is a range in these responses, with the result that some individuals complete a generation earlier than the average. Adults actually oviposit over about 2 months; therefore, a portion of the resulting larvae may complete development weeks earlier than those simulated in the model.
- (4) Selection for early developing individuals may result in the beetle eventually establishing populations in areas where the model suggests that this is currently not possible; such adaptation has occurred with other weed biocontrol agents (Harris, 1997).

If any of the preceding four factors apply, the range would be greater than predicted. The choice of a generation-completion category of 80–99% is a subjective estimate of the zone in which these factors may enable the beetle to establish permanent populations.

- (5) The thermoregulation submodel assumes that the beetles optimize their body temperature perfectly. Given the spatiotemporal climatic variability of the environment, and the relative cognitive limitations of the insects, this assumption is probably not valid. Imperfect thermoregulation would result in suboptimal body temperatures, reduce development rates and contract the predicted range.
- (6) The presence of adequate heat accumulation is not sufficient to guarantee establishment of a biocontrol agent, because other factors are involved. The beetles will encounter novel day-length cues because they will be at least 5° of latitude north of their site origin. Biotic factors, such as predation by native organisms (Peschken *et al.*, 1970), will also influence establishment.

The purpose of this model was to evaluate whether sufficient heat accumulates to allow establishment of beetles from the Wusu population of *A. carduorum* on the Canadian prairies. If the model had indicated that this did not occur, or that it occurred only in a small region which had limited overlap with *C. arvensis*, this beetle could have been rejected as a potential biocontrol agent for this weed. The model did not result in such rejection.

Conclusions

Successful establishment of the beetle is contingent upon simultaneous fulfillment of the weed's requirements, as well as on the accumulation of sufficient heat to allow completion of at least one beetle generation per year. The authors recommend that initial Canadian releases should be made in locations where heat accumulation is the greatest possible. The model indicates that two beetle generations may be completed occasionally near Morden, Estevan and Medicine Hat. However, of these, only Morden and Estevan are within the area in which thistles are relatively common; Medicine Hat is within the arid region in which thistles are uncommon except in irrigated pastures. (Since collection of the thistle data, the region of high thistle density on the eastern fringe of Figure 3 has expanded to include Morden (A. G. Thomas, personal observations).) Clearly, identification of the most promising sites must consider the distributions of both species. Other areas in Canada, which were not included in the modelled area, but in which it is suspected that this beetle strain will establish, include the southern Okanagan valley in British Columbia and the area around Harrow, Ontario in central Canada. It is also expected that *A. carduorum* populations would establish successfully throughout the range of Canada thistle on the US great plains.

The model also suggests that *A. carduorum* will not establish populations in the foothills of Alberta and, by extension, the mountains of British Columbia and the western US. This conclusion is relevant to the environmental concerns for the safety of some native *Cirsium* spp. in the event that *A. carduorum* is released. Subalpine native species such as *C. hookerianum* Nuttall, which extends to 2000 m elevation (Moore & Frankton, 1974), occur well outside the predicted range of this stock of *A. carduorum*; therefore, these species are not at risk.

A. carduorum populations exist which are adapted to cooler moister climates than is the stock tested here. Beetles from a population at Yining, Xinjiang, ca. 250 km west of Wusu, thrive at temperatures similar to those in areas where the simulation suggests that the Wusu stock does not consistently complete a generation per year, but where thistle densities can be high, e.g. at Olds Alberta (51° 47' N, 114° 06' W) (Walther & Leith, 1967; Environment Canada, 1993). Beetles from these populations may be useful in controlling Canada thistle in the area peripheral to the predicted Canadian range of the Wusu stock. The threat that these beetles pose to non-target native thistles should be determined.

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APPENDIX A: DETAILED OUTLINE OF MODEL PROCESS

- (1) Read input weather data (daily summaries).
- (2) Estimate a.m. and p.m. soil temperatures at 5-cm depth (Appendix B).
- (3) Interpolate hourly values of air temperature

$$\hat{T}_a [h] = M_a + A_a \cos(\theta) \tag{A1}$$

where M_a and A_a are the day's mean and amplitude of air temperature, and θ is time in radians from the time of maximum temperature.

- (4) Interpolate hourly values of soil temperature at 1-cm depth and surface

$$\hat{T}_s [h] = M_s + A_s \cos(\theta) \exp(d/r) \tag{A2}$$

where M_s and A_s are the day's mean and amplitude of soil temperature, θ is as above, r is 'damping depth' of the soil (18 cm) and d is the depth of the temperature measurement, in cm below reference depth, i.e. -4 for temperature at 1 cm depth and -5 for surface temperature (Campbell, 1977).

- (5) Estimate hourly insolation (Q_{est} , in $W m^{-2}$) where RAD is measured total daily insolation, $MJ m^{-2}$, RADMAX is theoretical maximum total daily insolation for site and julian date, and Q_{max} is theoretical maximum hourly insolation (Robertson & Russelo, 1968).

$$Q_{est} = Q_{max} \left[\frac{RAD}{RADMAX} \right] \tag{A3}$$

- (6) Calculate developmental rate increments for each hour (h). Start with subsoil adults (Stage I = 0); promote sequentially to above-ground adults (I = 1), eggs (I = 2), larvae (I = 3), pupae (I = 4) and offspring adults (I = 5). If offspring adults complete pre-oviposition development, then return to the loop at the egg stage; further generations are allowed. The linear developmental rate function is

$$R_{I,h} = a_i + b_i \hat{T} [h] \tag{A4}$$

where a_i and b_i are the intercept and slope of the stage-specific temperature-dependent developmental rate equations, listed in Table 1. For each stage, a developmental rate counter is initialized at 0 and increments are summed until they reach 1, indicating completion of the stage. At this point, the insect is promoted to the next stage, and the rate counter is reset to 0.

In equation [4], the developmental rates are dependent on temperature ($T[h]$); for subsoil stages (prepupae, pupae, and newly enclosed adults) this is soil temperature at 1 cm depth; for eggs and larvae this is air temperature. Where thermoregulation by adults is neglected, this is also air temperature; where thermoregulation is included, the body temperature (T_b) is estimated from air temperature (T_a), soil surface temperature ($T_s[0]$) and insolation (Q_{est}) by the following routine.

```

If  $Q_{est} = 0$  then  $T_b = \text{MAX}(T_g, T_s[0])$  /*If no solar heat, choose warmest site*/
Else  $T_b = T_a + 0.00965 \cdot Q_{est}$  /*Otherwise  $T_b = T_a +$  solar heating*/
/*But behave to modify  $T_b$  if necessary:*/
If  $(T_b \leq T_s[0])$  and  $(T_s[0] \leq 25.5)$  /*If  $T_b$  and  $T_s <$  optimal and  $T_s$  warmer*/
  then  $T_b = T_s[0]$  /*Then sit on soil surface*/
Else if  $T_b \geq 25.5$  then do /*Or if  $T_b >$  optimal*/
  If  $T_a \leq 25.5$  then  $T_b = 25.5$  /*Minimize  $T_b$  to optimal if possible*/
  Else  $T_b = T_a$  /*Or to  $T_a$  otherwise*/

```

APPENDIX B

Parameter estimates for regression equations estimating morning (i.e. minimum) and afternoon (i.e. maximum) soil temperatures at 5-cm depth, derived using meteorological data from Lethbridge, AB

Variable	If MIN > 0		If MIN ≤ 0	
	a.m.	p.m.	a.m.	p.m.
MAX	—	0.1882	—	0.1684
MIN	0.3459	0.2005	0.3511	0.2073
RAD	0.1262	0.2837	0.1749	—
PCP	0.3864	0.3487	—	—
MAX ²	0.002667	0.004260	—	0.006043
MIN ²	—	—	0.01143	0.007729
RAD ²	—	—	—	0.01152
PCP ²	-0.006846	-0.006305	—	—
LAG [MAX]	0.2474	0.1742	0.2456	0.2352
LAG [MIN]	0.2483	0.2574	0.1343	0.1288
LAG [PCP]	0.06093	0.07219	—	—

^a MAX, maximum air temperature (°C); MIN, minimum air temperature; RAD, total daily insolation, MJ m⁻²; PCP, precipitation (mm liquid); LAG [], previous day's value of bracketed variable.