Bioclimatic model of Melanoplus sanguinipes (Fabricius) (Orthoptera: Acrididae) populations in Canada and the potential impacts of climate change

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Abstract

The northern Great Plains of North America has experienced a number of severe grasshopper infestations over the last 100 y. Grasshopper densities have been observed to be in synchrony over vast geographical areas. Weather is probably the most significant factor that affects fluctuations in population abundance of *Melanoplus sanguinipes*, the migratory grasshopper. Inferential modeling was used to develop a bioclimatic model of *M. sanguinipes* that closely agreed with current distribution and abundance patterns of this species in North America over a 30-y period. Incremental climate change scenarios were then applied to the bioclimatic model to predict changes to potential distribution and relative abundance of *M. sanguinipes*, resulting from climate change. Compared to predicted range and distribution under current climate conditions, model results indicated that *M. sanguinipes* would have increased range and relative abundance for temperature increases between 1 and 7°C. The model predicted that the range of this crop pest would be extended to regions that are not currently used for agricultural production in North America.

Key words

Melanoplus sanguinipes, migratory grasshopper, crop pest, bioclimate model, climate change, CLIMEX®

Introduction

The northern Great Plains of North America has experienced a number of severe grasshopper infestations over the last 100 y (Shotwell 1941, Riegert 1968, Smith & Holmes 1977, Olfert & Chapco 2001). Grasshopper densities have been observed to be in synchrony over vast geographical areas across this region (Edwards 1960, Pickford 1972, Gage & Mukerji 1977, Mukerji *et al*. 1977). Climate is the dominant force determining the distribution and abundance of most insect pest species, although numerous physical and biotic factors, such as habitat, food and the abundance of other species (natural enemies, competitors), modify the population density (Sutherst 2000). Weather is probably the most significant factor that affects fluctuations in grasshopper populations (Pickford 1972, Smith & Holmes 1977). In North America, meteorological conditions exhibit wide variations from year to year and grasshopper densities may range from outbreak levels to very low numbers, depending on whether conditions are hot and dry or cool and wet (Hewitt 1985).

Melanoplus sanguinipes (Fabricius), the migratory grasshopper, is the predominant grasshopper species that occurs across the northern Great Plains. The distribution of *M. sanguinipes* has been described by Brooks (1958), Vickery (1967), Vickery & Kevan (1983) and Pfadt (1994). In Canada, the species is found from Newfoundland and Labrador to British Columbia, and its distribution extends north to include the Yukon and Northwest Territories. Vickery & Kevan (1983) reported that *M. sanguinipes* has the ability to colonize a wide range of habitats, due to its wide range of food types and propensity to migrate over large distances. It prefers warm, dry weather conditions and infestations are generally associated with a prolonged period of consecutive seasons with increasing temperatures (Gage & Mukerji 1977). Intermittent warm seasons are not conducive to development of large grasshopper populations, but rather, fluctuating population densities (Mukerji *et al*. 1977). Cool, moist conditions, followed by early frost in the autumn, can reduce populations in the following year (Pickford 1966a). Extreme winter temperatures, particularly when snow cover is removed, can be an important factor in reducing populations (Pickford 1966b).

Several climate-based predictive models have been developed and successfully utilized to assess movement and potential distributions of invasive species (CLIMEX®—Olfert *et al*. 2004; BIOCLIM®—Beaumont *et al*. 2005; Gaussian—Gavin & Hu 2005). In relation to grasshoppers, a number of descriptive, rule-based, statistical and process models have been developed to study various aspects of *M. sanguinipes* ecology (Pickford 1966a, 1966b; Gage *et al*. 1976; Mukerji *et al*. 1976; Gage & Mukerji 1977; Hardman & Mukerji, 1982; Mukerji & Hayhoe 1988; Sanchez & Onsager 1988; Berry *et al*. 1995). In some cases, models were developed over a narrow range of conditions. Sutherst (1998) questioned the ability of process and statistical models to predict a species' geographical distribution. An alternative approach involves development of inverse (or inferential) models, which infer a species' response to climate, based on its geographic range, phenology and relative abundance (Sutherst & Maywald 2005). Bioclimatic inferential models have been successfully used to predict potential distribution and abundance of a diverse group of insect species (Hughes & Maywald 1990, Worner 1994, Dosdall *et al*. 2002, Mason *et al*. 2003, McKenney *et al*. 2003, Olfert *et al*. 2004). CLIMEX® software enables the development of models that describe the potential distribution and relative abundance of a species based on climate (Sutherst *et al*. 1999, Sutherst & Maywald 2005).

The issue of climatic changes caused by human activities and the effects on agriculture has raised concern. The overall global temperature has increased 0.7°C over the last 100 y, with the 1990's being the warmest decade on record (Rosenzweig *et al*. 2000). Scenarios, using low greenhouse gas emission, suggest that temperatures will increase by 1 to 3°C over the next 100 y and temperatures have been predicted to increase by 3.5 to 7.5°C for scenarios with high gas emission (Cohen & Miller 2001). However,

Walther *et al.* (2002) suggest that species respond to regional changes that are highly heterogeneous and not to approximated global averages. Many species have already responded to regional conditions that have occurred during the 20th century. In a study of 694 animal and plant species, Root *et al.* (2003) reported that changes in timing of spring events (breeding, blooming) occurred 5.1 d earlier per decade. Warming conditions may impact insect populations by extending their growing season, altering timing of emergence from overwintering sites, increasing growth and development rates, shortening generation times, reducing overwintering mortality and changing geographic distribution (Porter *et al.* 1991, Gitay *et al.* 2002).

General circulation models (GCM) have evolved, since their first application in the 1970's to study the effect of increased greenhouse gases. Current GCM's produce relatively detailed modelling of important ecological processes and increased spatial resolution (Mearns 2000); however, results from different GCM's can vary substantially. Ecological sensitivity studies, using incremental scenarios, involve incrementally changing variables by arbitrary amounts (+1, +2, +3°C) in order to study the sensitivity of a specific system's response to a wide range of potential climatic changes. Incremental scenarios permit comparison of responses in a consistent, replicable manner, for different species across many regions. As a result, they are useful in studying the behavior or responsiveness of a species to a range of conditions and may give insight into the range within which the effects of climate change are likely to occur (Sutherst *et al.* 1996, Sutherst 2000).

The literature related to the effect of climate change on insect population dynamics is relatively sparse (Gutierrez 2000, Kerr 2001, Olfert & Weiss 2006). Our capacity to analyse climate change-related vulnerabilities, will assist the development of adaptive strategies in an attempt to mitigate the effects of climate change. In this study, incremental scenarios were developed to reflect the possible range of temperature and precipitation values that could be expected to occur in North America by the mid to late 21st century (Brlacich *et al.* 1997, Cohen & Miller 2001) and derived climates were used as inputs into the CLIMEX® model for *M. sanguinipes*.

The objectives of the study were to develop a bioclimatic model that described current distribution and abundance of *M. sanguinipes* and to use the model to assess sensitivity to impacts associated with climate change, specifically, increasing temperatures and variable precipitation amounts, on potential range and abundance of *M. sanguinipes* in Canada.

Methods

CLIMEX® modelling software consists of a set of population parameters that define the favored ranges of temperature and moisture conditions that allow the population growth of an organism and a set of biological stress parameters that define a species' ability to survive unfavorable conditions (Sutherst & Maywald 2005). Model parameters include temperature, light, moisture, heat stress, cold stress, and moisture stress. Growth and stress indices are calculated and combined to derive an Ecoclimatic Index (EI), which describes the suitability of specific georeferenced locations for species survival and reproduction. The CLIMEX® modeling process involving insect species has been previously described by Mason *et al.* (2003) and Olfert & Weiss (2006).

In this study, simulation runs were conducted using CLIMEX® 2.0. The model was developed through an iterative process and parameter values were individually adjusted, where necessary, so

that model output was similar to population distributions reported in Brooks (1958) and Pfadt (1994). Initial parameter values were obtained from published papers (Shotwell 1941; Riegert 1961; Putnam 1963; Pickford 1966a, 1966b; Pickford 1972; Mukerji & Randell 1975; Gage *et al.* 1976; Mukerji *et al.* 1977; Hardman & Mukerji 1982; Hayhoe & Mukerji 1987; Mukerji & Braun 1988; Lactin & Johnson 1998). Model parameters were adjusted to ensure that EI ≥ 30 in geographical regions historically affected by *M. sanguinipes*, indicating that climatic conditions were favorable for development of densities associated with crop loss. Two types of data were used as inputs into the model: data from New *et al.* (1999) as input for *Compare Locations* analysis, daily data sets, including daily values for temperature and precipitation, as input for the *Compare Years* analysis. Daily meteorological data for the period of 1970 to 2004 were obtained from Environment Canada (2005). Relative humidity data were obtained from New *et al.* (1999).

Historical grasshopper population data were used for model validation. Annual surveys of abundance of adult grasshoppers have been conducted in Saskatchewan since 1931 (Riegert 1968). The surveys have been conducted for the purpose of determining potential threat in the following year and describe annual changes in *M. sanguinipes* distribution and abundance. Population estimates were based on the number of sightings in a 100-m transect along the roadside, as well as an arc into the adjacent crop (Gage & Mukerji 1977). Samples were taken at intervals of 10 km, resulting in one sample per 4500 ha of crop (Mukerji *et al.* 1977).

Araujo *et al.* (2005) stress the importance of validation in development of climate-related models. Three methods were used to validate models in the current study. Validation of distribution was based on Vickery (1967), Riegert (1968), Vickery & Kevan (1983) and Olfert & Chapco (2001). Relative abundance was validated by comparison with adult grasshopper survey data from Saskatchewan over the period of 1970 to 2004, as well as data from Riegert (1968) and Smith & Holmes (1977). The model was tested by comparing the occurrence of observed life history events against those predicted by the model.

Ecological sensitivity analyses entailed using incremental scenarios for all possible combinations (n = 72) for temperature (0, +1, +2, +3, +4, +5, +6, +7°C of climate normal temperature for each grid) and precipitation (-60%, -40%, -20%, -10%, 0%, 10%, 20%, 40%, 60% of climate normal precipitation for each grid). Incremental changes were applied in a similar fashion to all monthly values. Models were run with the North American dataset (n = 12452 grids) and analysis was limited to Canada, south of 65°N latitude (n = 4472 grids). Specific locations were selected to examine the impact of the incremental scenarios on index values over a wide geographic range of Canada. Locations included Kentville, Nova Scotia (lat 45°04'N, long 64°30'W), Harrow, Ontario (lat 42°02'N, long 82°54'W), Churchill, Manitoba (lat 58°47'N, long 94°13'W), La Ronge, Saskatchewan (lat 55°05'N, long 105°18'W), Saskatoon, Saskatchewan (lat 52°08'N, long 106°38'W), Swift Current, Saskatchewan (lat 50°17'N, long 107°48'W), Peace River, Alberta (lat 56°15'N, long 117°17'W) and Yellowknife, Northwest Territories (lat 62°27'N, long 114°20'W).

Ecoclimatic Index values generated by the model were used to develop a surface map of potential distribution and relative abundance of *M. sanguinipes* in North America with SPANS® v.5.31 for OS/2 (PCI Geomatics 2003). Ecoclimatic Index values were displayed in four categories: 'Unfavorable' (EI = 0 to 5); 'Suitable' (EI = 5 to 20); 'Favorable' (EI = 20 to 30); and 'Very Favorable' (EI = >30). The EI categories were set to correspond to broad categories of grasshop-

Table 1. CLIMEX® parameter values used to predict potential distribution and relative abundance of *M. sanguinipes* in North America.

CLIMEX® Growth Parameters		
Temperature		
DV0	Limiting low average weekly temperature	10.01C
DV1	Lower optimal average weekly minimum temperature	16.01C
DV2	Upper optimal average weekly maximum temperature	28.01C
DV3	Limiting high average weekly maximum temperature	32.01C
Moisture		
SM0	Limiting low soil moisture	0.02
SM1	Lower optimal soil moisture	0.05
SM2	Upper optimal soil moisture	0.30
SM3	Limiting high soil moisture	0.70
Diapause		
DPD0	Diapause induction day length	11h
DPT0	Diapause induction temperature (average weekly minimum)	11.01C
DPD1	Diapause termination temperature (average weekly minimum)	3.01C
DPD	Diapause development days	120
DPSW	Summer or winter diapause	0
CLIMEX® Stress Parameters:		
Cold Stress		
TTCS	Cold stress threshold (average weekly minimum temperature)	-18.01C
THCS	Rate of cold stress accumulation	-0.0004
Heat Stress		
TTHS	Heat stress threshold (mean weekly maximum temperature)	35.01C
THHS	Rate of heat stress accumulation	0.008
Dry Stress		
SMDS	Dry stress threshold (mean weekly minimum soil moisture)	0.020
HDS	Rate of dry stress accumulation	-0.003
Wet Stress		
SMWS	Wet stress threshold (mean weekly maximum soil moisture)	0.7
HWS	Rate of wet stress accumulation	0.001

per infestations. 'Unfavorable' defined areas where grasshoppers would be very rare or might not occur at all. 'Suitable' defined areas where grasshoppers would likely occur. 'Favorable' defined areas where grasshopper infestations could result in crop damage. 'Very Favorable' defined areas where grasshoppers commonly appear at densities that cause crop damage.

Results

1. Bioclimatic model

Model parameters.—Model parameters are detailed in Table 1. The limiting average weekly temperature parameter (DV0) was set at +10°C (Gage *et al.* 1976) and the lower optimal weekly minimum temperature (DV1) was set at +16°C (Pickford 1966a). The upper optimal temperature threshold (DV2) and limiting high temperature (DV3) required some refining. Optimal temperatures enhance oviposition and subsequent egg development (Pickford 1972, Sanchez *et al.* 1988). Excessive heat can result in nymphal mortality, particularly in early instars. A 50% nymphal mortality occurred with two consecutive days of +35°C (Pickford 1966a). Parker (1930) reported that the upper limit for nymphal survival was +37°C, while adults could survive for several weeks at +38°C. From these results, the upper optimal temperature threshold (DV2), based on average weekly maximum temperature, was set to +28°C and the limiting high temperature (DV3), based on average weekly maximum temperature, was set to +32°C. The DV3 initially appeared low; however, the model uses weekly average maximum air temperatures as opposed to soil temperatures. Air temperatures are generally lower than soil temperatures and DV3 = +32°C closely predicted observed grasshopper densities. Higher values (DV3 = +35°C) did not agree with observations in Saskatchewan and Alberta. The temperature at which heat stress occurs (TTHS) was set to +35°C. This value applies to conditions when the average weekly maximum temperature is +35°C. Although this condition may occur, it is not common on the Canadian prairies. Furthermore, grasshoppers can behaviorly alter their exposure to excessive temperature (orientation to the sun, movement within the plant canopy, flight).

The moisture index (MI) was based on computed weekly soil moisture values. Moisture values were set to reflect the fact that population growth is greatest during dry seasons (Gage & Mukerji 1977, Pickford 1966a). Excessively dry conditions may reduce fecundity due to lower quality in food sources and also to eggs desiccating in dry soil (Pickford 1963, 1966b, 1972). The limiting low moisture (SM0) and lower optimal moisture (SM1) were set to values that favored dry climates. The upper optimal soil moisture threshold (SM2) and limiting high soil moisture (SM3) were set to limit EI values, without entirely negating distribution in eastern
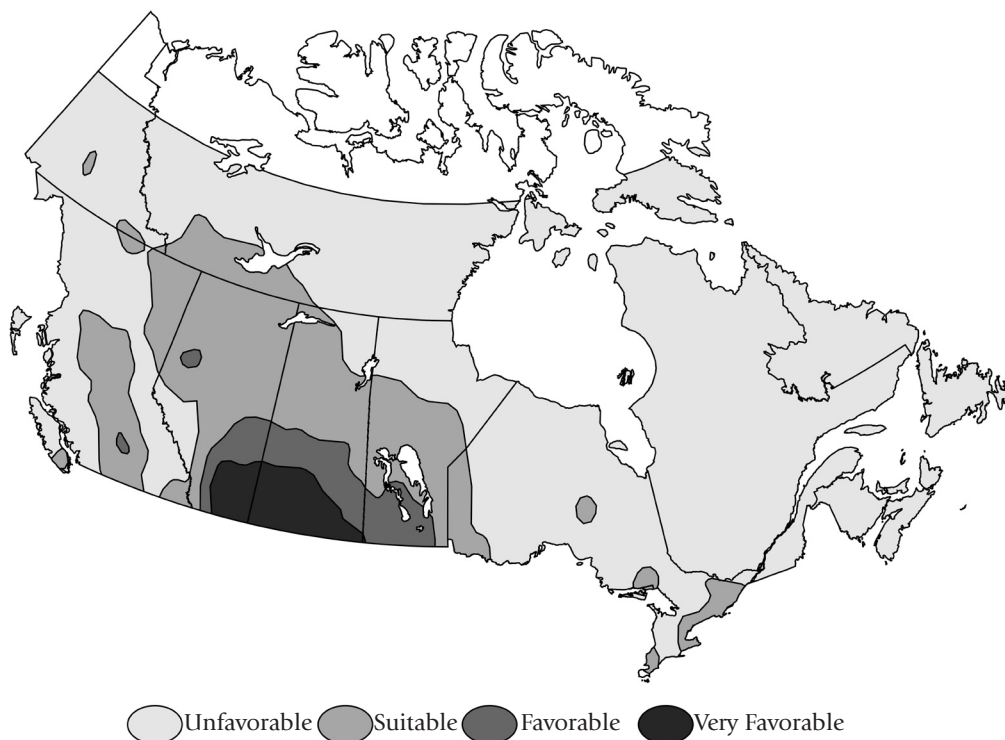
Unfavorable　Suitable　Favorable　Very Favorable

Fig. 1. Potential distribution and relative abundance of *M. sanguinipes* for Canada as predicted by the CLIMEX® model (surface map developed using SPANS® v.5.31).

North America.

Mukerji & Braun (1988) reported that in relation to cold stress, substantial egg mortality occurred at -15°C. They did acknowledge that, due to sufficient snow cover, eggs were generally not exposed to these temperatures. Pickford (1966b) reported that eggs with lower developmental rates had higher mortality than eggs with higher rates of embryonic development. Winter soil temperatures, 2 to 5 cm below soil surface are related to snow depth. Hayhoe & Mukerji (1987) found that a snow-free site had a soil temperature of -15.9°C, while the soil temperature below 20 cm of snow was -5.2°C. The initial parameter for cold stress (TTCS) was set to -15°C. This value, which is based on air temperature, resulted in high cold-stress values in the Saskatoon area. The value, in order to account for differences between air and soil temperature, was decreased to -18°C. The rate of cold stress accumulation (THCS) was iteratively defined to address Pickford's (1966b) findings that the length of exposure to cold temperature also had an effect on mortality. These parameters (TTCS and THCS) resulted in minimal cold stress (CS = 6) in Saskatoon and a higher cold stress value (CS = 25) at La Ronge, which is approximately 350 km north of Saskatoon.

Model validation.—Model output (Fig. 1) agreed with the distribution of *M. sanguinipes* as described by Vickery (1967), Riegert (1968), Vickery & Kevan (1983) and Olfert & Chapco (2001). Model output also agreed with observations that *M. sanguinipes* abundance is greatest on the Great Plains of North America. Output for relative population abundance was also similar to historical survey data (Riegert 1968, Smith & Homes 1977). The model accurately predicted that the core distribution would be associated with the Great Plains (Fig. 2F) and also agreed with observations in northern regions of the continent. For example, Fielding (2004) reported that

M. sanguinipes occurs in Alaska as a sporadic, potentially damaging, pest of small grain crops. The Ecoclimatic Index for the area where their field studies were conducted, Delta Junction, Alaska (lat 64°N, long 145.43°W) was EI = 9, which indicated that *M. sanguinipes* could occur in this region of Alaska. The modeled distribution throughout northern Canada agreed with record data for peripheral locations as presented by Vickery & Kevan (1983): they reported localities near Great Slave Lake, Northwest Territories, where *M. sanguinipes* had been collected; here the model produced EI = 6-9. Modeled data agreed with collections of *M. sanguinipes* made in the Yukon basin of the Yukon Territory and Alaska. *M. sanguinipes* has also been collected in New Brunswick, Nova Scotia and Newfoundland and Labrador. The model predicted that moisture conditions would limit distribution in maritime Canada (Figs 2D, 2E). Wet stress values in this region were greater than 100, indicating that moisture stress would be severely limiting.

The model demonstrated *M. sanguinipes* distributions were limited by cold stress (cold stress index, CS), length of growing season (diapause index, DI), suboptimal growing season temperatures (temperature index, TI), and excessive precipitation (moisture index, MI and wet stress, WS) (Table 2, Figs 2A-E). Cold stress limited northern distribution, as CS values increased in a northerly direction. A species cannot persist in locations where CS >100. At Yellowknife, CS = 85, as compared to Saskatoon, located in the core area of *M. sanguinipes* distribution, where CS = 6. The diapause index (DI) indicates the number of weeks in which conditions are suitable for population growth. At Swift Current, DI = 44 as compared to DI = 31 at Churchill, confirming that the growing season is longer in Swift Current. Suboptimal growing season temperatures were also limiting in northern Canada. Low TI values indicated that the growing season would not be sufficient for optimal population growth
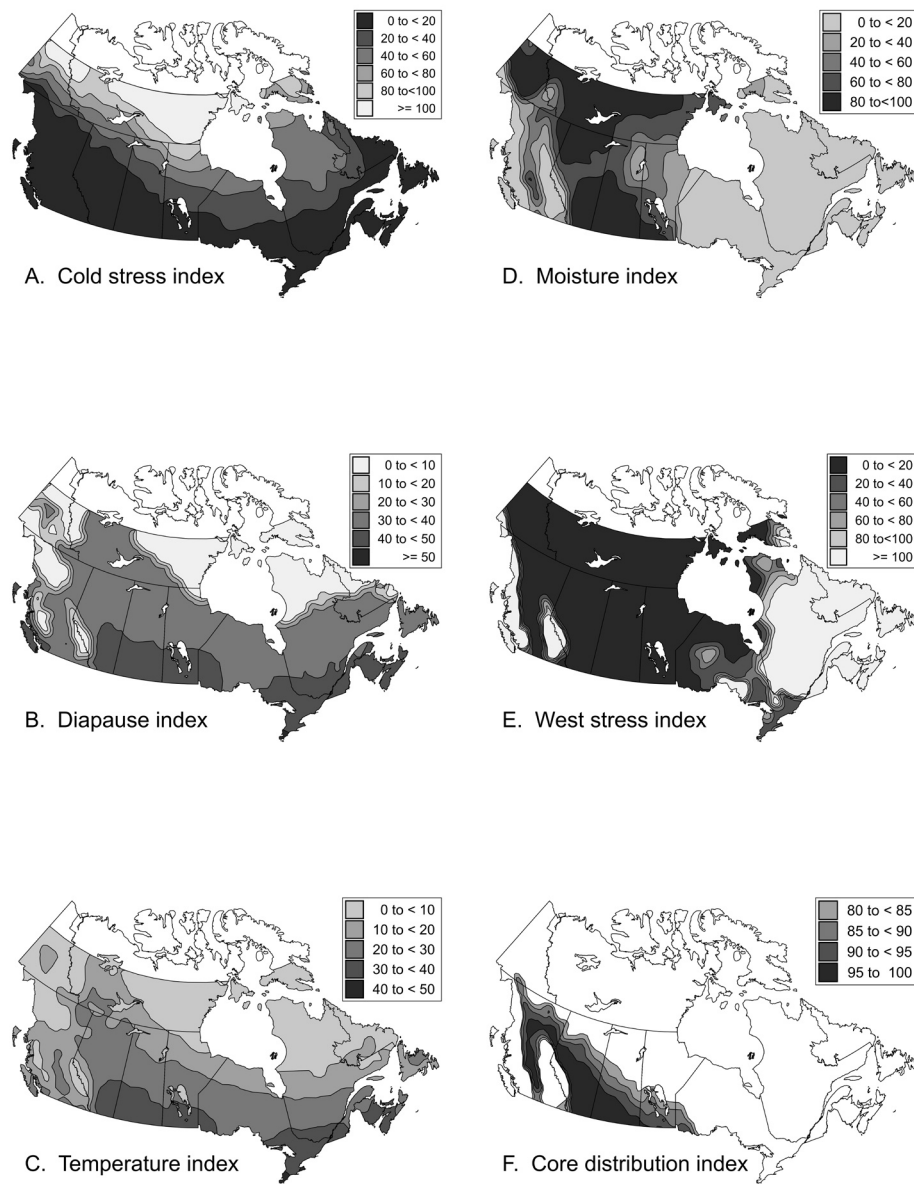
Fig. 2. CLIMEX® cold stress (A), diapause (B), temperature (C), moisture (D), wet stress (E) and core distribution (F) indices for *M. sanguinipes* for current climate.

and could be expected to reduce developmental rates; for example, TI = 8 at Churchill, as compared to Swift Current where TI = 34. The model predicted that short, cool growing seasons in northern Canada would limit the potential for this species to increase to large numbers. Low MI or large WS values indicate that precipitation is excessive (limiting) and the species would not be expected to occur, or if so, the species would be very rare in this region of Canada. For example, MI = 0 and WS = 235 at Kentville.

In Canada grasshoppers are largely associated with the Prairie ecozone. The range of the 'Favorable' and 'Very Favorable' categories fits well with the Prairie ecozone and the 'Suitable' category corresponds to the Boreal Plains and Boreal Shield. Based on the Agroecological Resource Areas (ARA) for the Canadian prairies (Kirkwood *et al.* 1993), the 'Very Favorable' region is associated with the Mixed Grassland and Moist Mixed Grassland ecoregions and the 'Favorable' region is comparable to the Aspen Parkland and Boreal Transition ecoregions.

Adult grasshopper densities, obtained from Saskatchewan survey data, were averaged for the period of 1972 to 2004 (Fig. 3). Not surprisingly, the greatest densities occur in the Mixed Grassland and Moist Mixed Grassland ecoregions. These ecoregions correspond to the 'Favorable' and 'Very Favorable' categories using model output (Fig. 1). Infestations have occurred in the Aspen Parkland and Boreal Transition ecoregions of Saskatchewan; however, outbreaks in these areas are rare.

The suggested economic threshold for cereals is 8 to 12 grasshoppers/m^2 (Anonymous 1999). Infestations exceeded 8 grasshoppers/m^2 24%, 20%, 5% and 2% of the time, for the Mixed

Table 2. Site-specific annual values for Ecoclimatic Index (EI), Temperature Index (TI), Moisture Index (MI), Diapause Index (DI), Cold Stress (CS) and Wet Stress (WS) at selected locations in Canada.

Location	Latitude, Longitude	EI	TI	MI	DI	CS	WS
Churchill MB	N 58° 45′, W 094° 07′	1	8	26	31	67	1
Harrow ON	N 42° 02′, W 082° 55′	7	43	10	52	0	24
Kentville NS	N 45° 05′, W 064° 30′	0	32	0	44	0	235
La Ronge SK	N 55° 06′, W 105° 17′	12	24	58	38	25	0
Peace River AB	N 56° 14′, W 117° 17′	24	27	95	40	8	0
Saskatoon SK	N 52° 10′, W 106° 41′	30	32	100	44	6	0
Swift Current SK	N 50° 16′, W 107° 44′	33	34	100	44	0	0
Yellowknife NWT	N 62° 27′, W 114° 11′	2	16	89	35	85	0

Grassland, Moist Mixed Grassland, Aspen Parkland and Boreal Transition ecoregions, respectively (Olfert & Chapco 2001). These authors calculated risk estimates, based on the percentage of time (number of years, 1972 to 1998) that areas of Saskatchewan had a severe grasshopper infestation (10 or more grasshoppers per square metre). The risk estimates agreed with model output.

2. Climate Change

Current Climate.—Current climate conditions provided a base line for comparison against each of the incremental climate change scenarios (Fig. 1). The model indicated that 7.2% of Canada would have climate suitable ('Favorable' and 'Very Favorable') for potential pest populations of *M. sanguinipes* (Table 3). Under current conditions, the mean EI was 14 for selected locations, and ranged between EI = 0 (Kentville) and EI = 33 (Swift Current) (Table 2). La Ronge (cold), Churchill (cold), Yellowknife, (cold), Harrow, (wet) and Kentville (wet), had below average EI values. Cold stress (CS) occurred at five of the eight study sites. Of the eight identified locations, Swift Current was predicted to be most suitable for de-velopment of grasshopper infestations, having the highest index (EI = 33). The model predicted EI < 10 for Churchill, Yellowknife, Harrow and Kentville, indicating that, on average, *M. sanguinipes* would likely be rare at these sites (Table 2).

+2°C and precipitation analyses.—An increase of two degrees in temperature, with no change in precipitation, resulted in an increase of EI values across most of Canada (Fig. 4A). Warmer conditions resulted in 17.3% of Canada being exposed to potential outbreaks of grasshoppers (Table 3). Compared to current climate, higher EI values were associated with higher temperature index (TI) values and lower cold stress (CS) values (Figs 5B and 5F). Mean EI for the selected locations increased from 14 under current climate conditions to 19, and ranged from EI = 0 (Kentville) to 38 (Swift Current) (Table 4). Peace River, at EI = 32, was similar to Saskatoon under current climate conditions. Stress values greater than CS = 100 suggest that the species may not be able to persist over a number of years at the given location. The model predicted that the species could likely persist for more than one season at Harrow, where EI = 12. However, cold temperatures negatively impacted the suitability of Churchill and Yellowknife to support grasshopper populations.
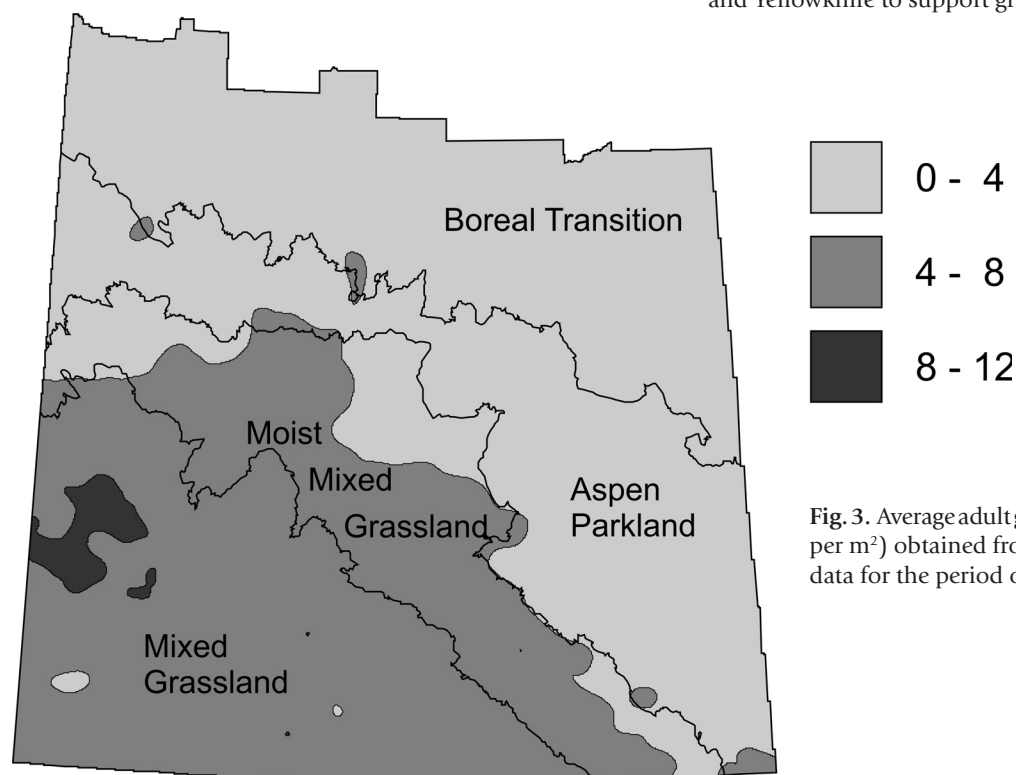

Fig. 3. Average adult grasshopper density values (number per m²) obtained from Saskatchewan provincial survey data for the period of 1972-2004.
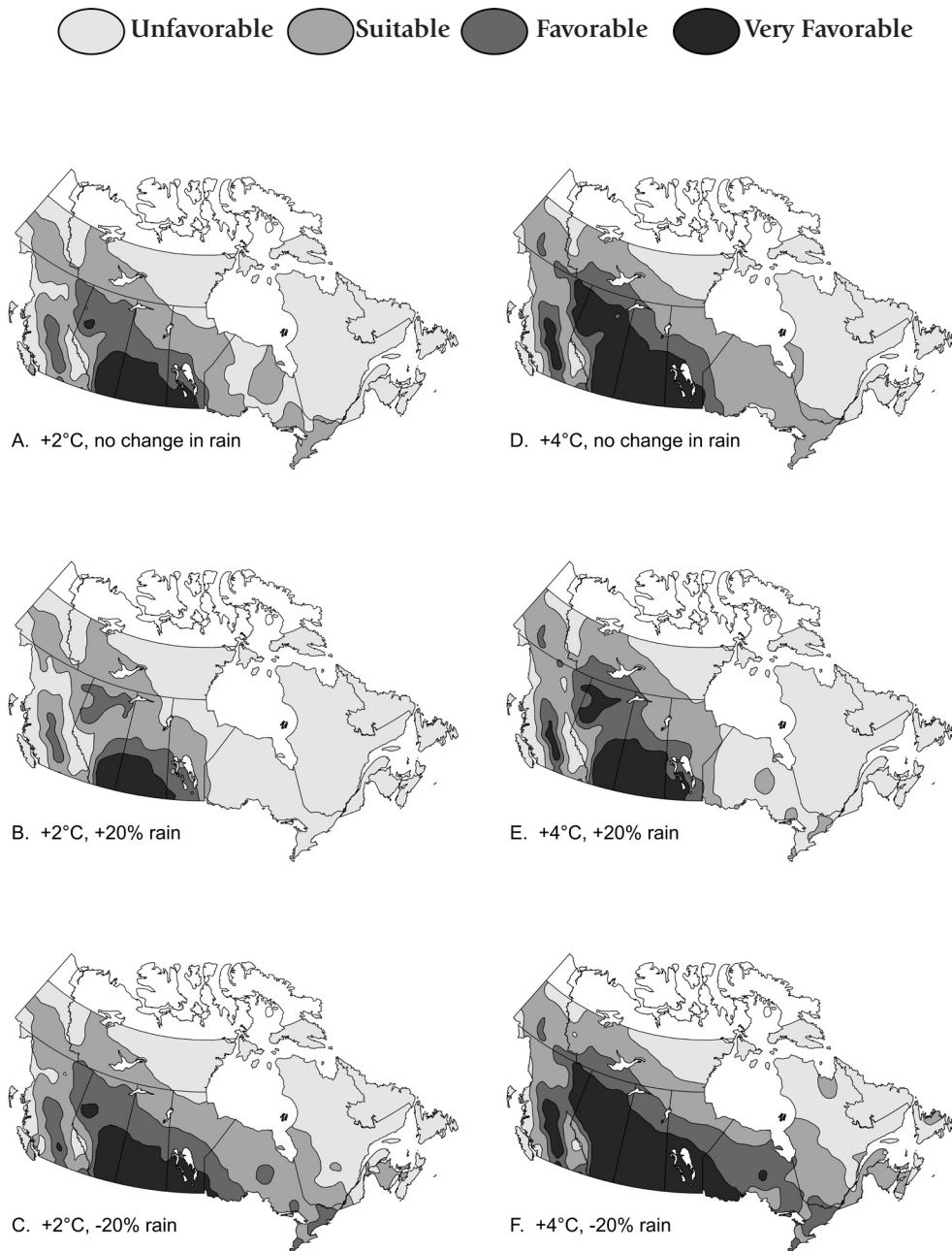
Fig. 4. Ecoclimatic Index values for six climate scenarios for *M. sanguinipes*: A) +2 °C, no precipitation change; B) +2 °C, +20% precipitation; C) +2 °C, -20% precipitation; D) +4 °C, no precipitation change; E) +4 °C, +20% precipitation; F) +4 °C, -20% precipitation.

Model output demonstrated that potential range and relative abundance of *M. sanguinipes* was affected by both temperature and moisture. Compared to +2 °C with no precipitation change, a 10% or 20% decrease in precipitation resulted in a further increase in climate suitability for *M. sanguinipes*. The areas for 'Favorable' and 'Very Favorable' categories for the -20% precipitation were two times greater than for the +20% scenario (Figs 4B, 4C; Table 3). Dryer conditions resulted in higher MI and lower WS, which in turn, translated into a higher mean EI. The model was not as sensitive to -20% precipitation as it was for -10% across each of the eight locations. Wetter locations (Harrow and Kentville) had the greatest increase in EI values for scenarios with reduced annual precipitation. A decrease in precipitation of 20% resulted in an increase in

EI for Harrow and indicated that conditions could be suitable for grasshopper populations developing to pest status. Results indicated that -40% or -60% precipitation at Harrow would result in higher EI values than any other location/scenario combination. The model predicted that *M. sanguinipes*' range and abundance would decrease for wetter scenarios (Fig. 4B, Table 3). Higher levels of precipitation resulted in decreased MI and increased WS, which in turn, translated into a lower mean EI value. Model output predicted that, in spite of +20% precipitation, a temperature increase of 2 °C would result in a greater area susceptible to pest levels of *M. sanguinipes*, up from 7.2% under current climate conditions to 11.3% (Table 3).

Table 3. Percentage of total areas mapped for each Ecoclimatic Index category at current climate and selected incremental scenarios.

Scenario	EI Category	% of Total	EI > 20
Current climate	Unfavorable	70.7	
	Suitable	22.1	
	Favorable	4.4	
	Very Favorable	2.8	7.2 % of Total
+2 °C; no change in rain	Unfavorable	52.4	
	Suitable	30.3	
	Favorable	10.5	
	Very Favorable	6.8	17.3 % of Total
+4 °C; no change in rain	Unfavorable	39.2	
	Suitable	32.6	
	Favorable	12.5	
	Very Favorable	15.7	28.2 % of Total
+6 °C; no change in rain	Unfavorable	29.0	
	Suitable	28.9	
	Favorable	18.5	
	Very Favorable	23.7	42.2 % of Total
+2 °C; +20% rain	Unfavorable	65.7	
	Suitable	23.0	
	Favorable	7.0	
	Very Favorable	4.3	11.3 % of Total
+2 °C; -20% rain	Unfavorable	41.3	
	Suitable	34.4	
	Favorable	14.6	
	Very Favorable	9.7	24.3 % of Total
+4 °C; +20% rain	Unfavorable	52.2	
	Suitable	25.6	
	Favorable	12.3	
	Very Favorable	9.9	22.2 % of Total
+4 °C; -20% rain	Unfavorable	29.6	
	Suitable	31.3	
	Favorable	18.6	
	Very Favorable	20.5	39.1 % of Total

+4°C and precipitation analyses.—At +4°C, model output predicted that the range and abundance of *M. sanguinipes* would increase substantially, compared to the current climate. The area susceptible to pest outbreaks would increase to 28.2% (Table 3). Increased temperature, with no increase in precipitation, would likely result in larger areas of Canada being suitable for *M. sanguinipes*, range extending in both northerly and in easterly directions (Fig. 4D). Under this scenario, cold stress (CS) decreased while the temperature index (TI) increased, suggesting that most regions south of 60° N would not be affected by cold (Fig. 5C, 5G). Mean EI values were predicted to increase for all eight locations (Table 4). Compared to current climate, EI values were predicted to be greater at Saskatoon and Peace River than at Swift Current; La Ronge would be similar to Saskatoon under current climate conditions. Cold stress at La Ronge, 300 km north of Saskatoon, was predicted to be similar to Saskatoon under current climate conditions.

An increase of 20% precipitation resulted in lower MI and higher WS and the model predicted that distribution in eastern Canada would change marginally from current climate (Fig. 4E). However, a decrease of 20% precipitation resulted in increased potential range and relative abundance in both northward and eastward directions

(Fig. 4F). For example, EI values for Harrow suggested that grasshopper populations could increase to pest status.

+6°C and precipitation analyses.—The model predicted that *M. sanguinipes* would occur over large areas of Canada and that potential for crop loss could be significant for scenarios with a 6°C-increase in temperature (Tables 3 and 4). Near Yellowknife NT, warmer temperatures were predicted to reduce cold stress from CS = 85 (current climate) to CS = 28 (+6°C) and TI would be similar to Saskatoon for current climate conditions (Figs 5D, 5H). As a result, the species could be expected to become more abundant north of 60°N. At this level of temperature increase, EI values could be expected to decrease in areas that currently have experienced high populations of grasshoppers, including Swift Current and Saskatoon. Excessive heat resulted in reduced TI values. In eastern Canada, the +6°C scenario, combined with dryer than normal conditions, could result in higher densities of *M. sanguinipes*.

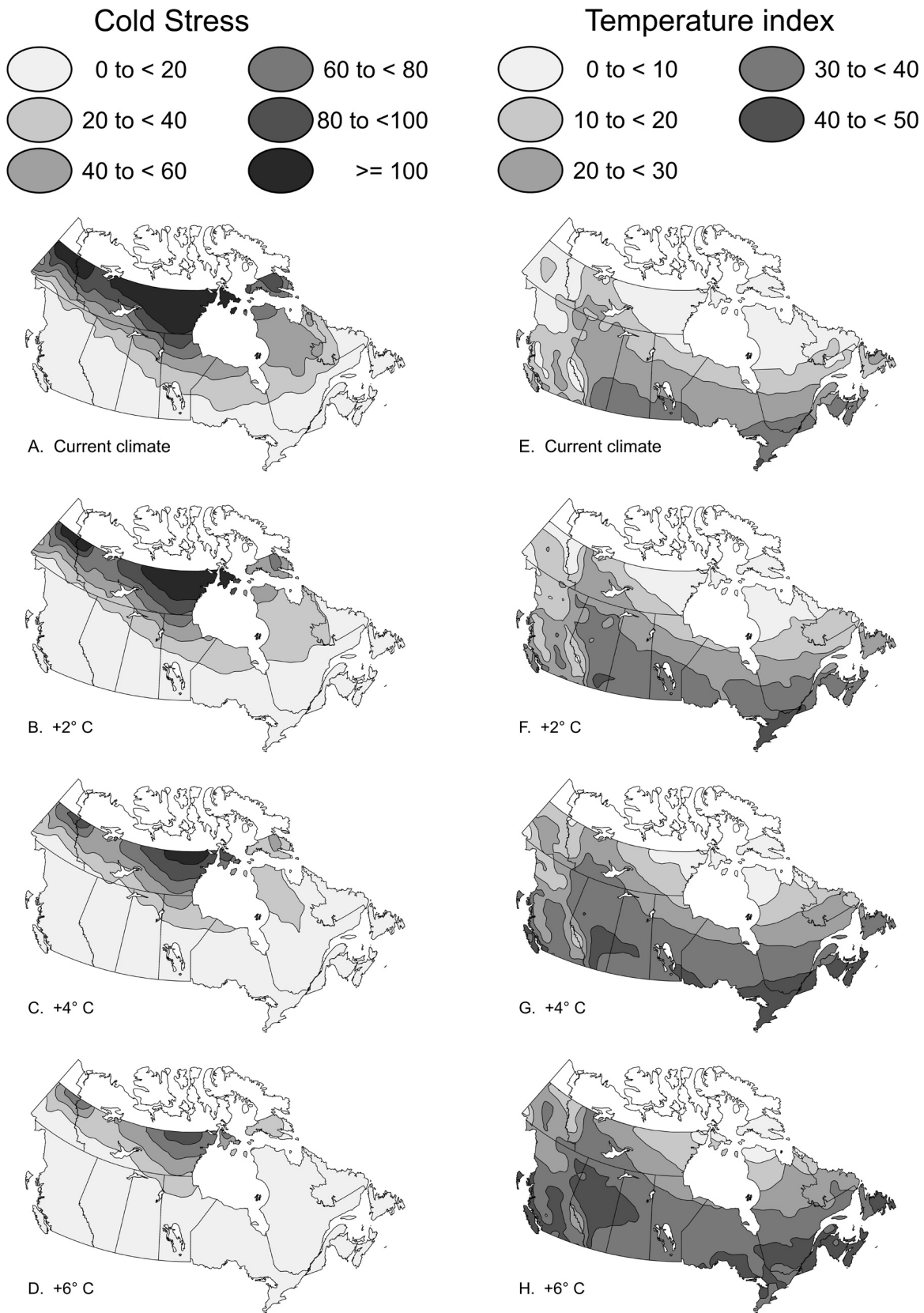**Fig. 5.** CLIMEX® parameter values for *M. sanguinipes:* cold stress and temperature index values for Cold Stress: A) Current climate; B) +2°C; C) +4°C; D) + 6°C; and for Temperature Index: E) Current climate; F) +2°C; G) +4°C; H) +6°C.

Table 4. Ecoclimatic Index values for eight selected locations in Canada under current and incremental climate changes from long-term normals.

Location	°C	-60	-40	-20	-10	0	10	20	40	60
					Precipitation (%)					
Churchill MB	0					1				
	2	7	7	6	5	4	3	1	0	0
	4	14	14	13	12	10	8	6	1	0
	6	20	20	20	19	17	14	11	4	0
Harrow ON	0					7				
	2	45	41	24	18	12	7	2	0	0
	4	41	37	22	17	13	9	5	0	0
	6	34	30	18	13	10	7	4	1	0
Kentville NS	0					0				
	2	35	19	7	2	0	0	0	0	0
	4	39	24	12	6	2	0	0	0	0
	6	39	24	13	8	5	2	0	0	0
La Ronge SK	0					12				
	2	25	25	25	23	20	17	14	5	0
	4	32	32	32	32	30	23	23	14	2
	6	38	38	38	38	38	35	32	23	11
Peace River AB	0					24				
	2	32	32	32	32	32	32	30	25	18
	4	39	39	39	39	39	39	38	34	28
	6	42	42	42	42	42	42	42	41	36
Saskatoon SK	0					30				
	2	36	36	36	36	36	36	35	32	26
	4	40	40	40	40	40	40	40	38	34
	6	36	36	36	36	36	36	36	36	33
Swift Current SK	0					33				
	2	38	38	38	38	38	38	38	35	32
	4	37	37	37	37	37	37	37	36	33
	6	30	31	31	31	31	31	31	31	28
Yellowknife NT	0					2				
	2	8	8	8	8	8	8	8	8	8
	4	14	15	15	15	15	15	15	15	15
	6	19	22	22	22	22	22	22	22	22

Discussion

Overall, model output agreed with published population distributions of *M. sanguinipes* in Canada. The model reflected that populations are generally endemic in the northern Great Plains and the highest densities occur in southern and central regions of Saskatchewan and Alberta. Mukerji & Hayhoe (1988) reported that grasshopper outbreaks often began in southwestern Saskatchewan and spread north and east. In Alberta, grasshopper populations generally spread from regions south of the Bow and South Saskatchewan Rivers (Smith & Holmes 1977). Model output showed that EI values are highest in southern Saskatchewan and Alberta and the model describes this area as 'Very Favorable'. Species are more vulnerable to variations in temperature and precipitation when located near the outer limits of their geographic range, than when located in the core area of the range. Sutherst *et al.* (2004) define a core area as a region with high EI values and little or no stress. Populations near the outer limits of the core area spend a greater amount of time in climates that are marginally suitable (exposed to climatic stress), while populations near the core, experience a greater amount of time in favorable conditions (minimal exposure to climatic stress). Our model predicted that southern regions of Alberta, Saskatchewan and Manitoba were in the core area. The Aspen Parkland and Boreal Transition ecoregions represent the edge of their distribution. As a result, populations in these two ecoregions are likely to develop to pest densities if climate becomes more suitable.

The model did not agree well with observed distribution in maritime Canada, in that it predicted excessive moisture during the summer and winter, would limit *M. sanguinipes*' distribution. However, two points must be considered.

First, the *Compare Locations* function is based on climate data which is based on 30-y averages of meteorological data. Year to year variation allows for some seasons to be warmer and dryer than normal. Records based on the map by Vickery & Kevan (1983) indicate neither the years when specimens were collected nor population abundance at collection. It is possible that collections were made in years where conditions were conducive for growth of grasshopper populations, to a level where specimens could be collected easily. To test this theory, a scenario was developed to assess the effect of dryer than average summer conditions. Model output for a conservative scenario, with temperature 1°C warmer than average, and precipitation 20% below normal, revealed that New Brunswick and Nova Scotia would increase from EI = 0 to EI = 7-10. Vickery & Kevan (1983) stated that the potential for increase of this pest species was so great that outbreaks could occur almost anywhere when conditions were favorable.

Second, the model was developed to accumulate stress during periods of the year when the species is not actively growing, that is, stress accumulates during the period of year when *M. sanguinipes* is in diapause. Moisture stress accumulation during the nongrowing season is difficult to assess for this species since the insects overwinter in the egg stage. To our knowledge, no studies have been conducted to assess the effect of high soil-moisture levels on survival of the eggs. Furthermore, the algorithm that calculates soil moisture is general in nature, and computed soil moisture values often appeared unusually high. In many maritime locations the model predicted that soil moisture would exceed the saturation point for all 52 w of the year. Attempts were made to define parameters that would reduce accumulation of stress due to wet conditions, however resulting values were unrealistic.

Melanopline eggs are capable of developing to 80% of total development between the time eggs are laid and the onset of winter. Egg development recommences in the spring, after diapause termination (Pickford & Randell 1969). The model predicted diapause termination to occur during the week of April 30 to May 7 in both 1964 and 2003. In general, egg hatch does not occur when maximum air temperatures are < +15°C, when soil temperatures at the 1-cm depth fail to reach +24°C, or when daily solar radiation levels are below 500 L (Pickford 1976). In both 1964 and 2003, the mean weekly maximum temperature first exceeded +15°C during the week of April 23-30.

Bioclimatic models are useful for analyzing the effect of weather on populations, however, the impact of biotic factors, including disease and parasites, must also be considered. The end of grasshopper outbreaks during the 1930's, late 1940's and early 1960's were associated with cool, wet weather and epizootics of *Entomophthora grylli* Fres. (Riegert 1968, Pickford & Riegert 1964). Even though weather conditions may be conducive to grasshopper populations, disease will result in population decline. In these cases, CLIMEX® cannot account for changes in population, and may calculate EI

values that overestimate populations. The outbreak of 1963 was followed by rapid declines in grasshopper density in 1964 and 1965. Decline of grasshopper populations in 1964 was associated with an *E. grylli* epizootic (Pickford & Riegert 1964). Extreme heat and drought tends to reduce crop growth while increasing grasshopper feeding activity. Increased competition for food can result in population decline due to high mortality because of starvation (Mukerkji *et al.* 1977).

CLIMEX®indices corresponded to historical grasshopper population trends. To the best of our knowledge, this is the first paper to validate a bioclimatic model using observed population densities that extended over such a lengthy period of time. Also, previous models have not related EI values to population density or infestation categories. Applying grasshopper survey abundance data and estimates of risk (Olfert & Chapco 2001) to the Ecoclimatic Index, the 'Very Favorable' category (EI >= 30) was associated with areas that have greater than a 20% probability of grasshopper infestations that exceed eight grasshoppers/m^2. The 'Favorable' category (EI = 20-30) corresponded to areas that have less than a 5% probability of infestations that exceed eight grasshoppers/m^2. The 'Suitable' category (EI = 5- 20) was associated with areas that have less than a 2% probability of grasshopper densities exceeding the economic threshold. Given that model output closely agreed with current distribution and abundance patterns of *M. sanguinipes* in Canada over a 30-y period, it was determined that the model could be used to assess the potential impact of climate change on this species.

Incremental climate change analyses were conducted for increasingly warm temperatures from +1 to +7°C and for precipitation changes from -60 to +60% of current climate (1960-1991) values (IPPC 2001). Scenarios with warm, dry conditions tended to have higher EI values than scenarios with cooler or wetter conditions. Results showed that grasshopper range and distribution are positively and negatively affected, depending on the combination of temperature and precipitation. The model predicted that increased temperatures would result in the northward and eastward extension of *M. sanguinipes*' distribution. Moisture changes resulted in an extension of range to the east under dry scenarios and the range retreated to western Canada in wet scenarios. In many cases, a 10% change in precipitation (+ or -), resulted in noticeable changes in EI values and the subsequent range of the insect.

At Saskatoon, larger EI values were a result of increased DI and TI as well as reduced CS. The increase in DI (approximately 5%) predicted longer summers. As a result, grasshoppers could become active earlier in the year, which in turn, would result in a longer oviposition period and allow time for the eggs to maximize development (*i.e.*, develop to 80%) prior to declining temperatures in the fall. Early oviposition and sustained high temperatures ensure maximum embryological development in the late summer and fall, contributing to an early hatch in the spring and an increase in the insects' damage potential (Pickford 1972). Crop loss is most severe when the hatch occurs early in the season (Mukerji *et al.* 1977). In central Saskatchewan, for example, *M. sanguinipes* hatch generally begins in late May or early June. The model predicted that grasshopper hatch could occur in early May for the '+2°C' scenario and in late April for the '+4°C' scenario. The growing season for the '+4°C' scenario was predicted to be 14 to 21 d longer than under current climate conditions.

Not surprisingly, increased temperatures also resulted in a large decrease in cold stress. In La Ronge, grasshopper populations were predicted to increase in density across all scenarios. Northern regions of provinces like Alberta and Saskatchewan appear to be sensitive to both temperature and precipitation and these areas would be vulnerable to grasshopper infestations. Increases in temperature could be somewhat offset by increases in precipitation, however, decreased precipitation could exacerbate the situation.

Climate change analyses identified the sensitivity and vulnerability of Canada's agricultural regions. Model output indicated that locations can be defined by one of three categories. First, low sensitivity and high vulnerability included areas that are near the current geographic center of the modeled range of *M. sanguinipes* and where EI >20. These areas are currently vulnerable to *M. sanguinipes* outbreaks and it would be expected that the species would remain persistent, as indicated by minimal change in EI values for the scenarios investigated in this study. Second, high sensitivity and high vulnerability included regions that are east and north of the current geographic center of the modeled range of *M. sanguinipes*, and where EI = 10-20. In this category, increased temperatures will result in an increase in EI, so that these regions would likely experience grasshopper outbreaks. Third, high sensitivity and low vulnerability included regions that are north or south of the current geographic center of the modeled range of *M. sanguinipes* and where EI = 0 to 10. In areas to the north of the current modeled range, increased temperatures may result in an increase of EI values, however, results indicated that populations would rarely reach outbreak levels. In southern areas, increased temperatures will likely exceed the upper limit for optimum grasshopper growth, and EI values will decline.

Bioclimatic models have been utilized to predict the potential distributions and relative abundances of invasive alien species in Canada (Olfert & Weiss 2006); the present study analyzed the interactions between a native insect pest and climate change. Our results indicate that the percent of total area susceptible to pest populations of *M. sanguinipes* would increase from 7.2%, under current climate conditions, to 17.3%, 28.2% and 42.2% of the study area with temperature increases of +2, +4, and +6°C, respectively. The Canadian prairies could experience crop losses greater than those experienced in 1961, 1985-89, 2001 or 2003 under such conditions. Similarly, Olfert & Weiss (2006) found that, compared with predicted range and distribution under current climate conditions, *Ceutorhynchus obstrictus* (Marsham), *Meligethes viridescens* (Fabricius) and *Oulema melanopus* L. would have increased ranges and relative abundances for temperature increases between 1 and 7°C. It was further predicted that risks associated with these three species would likely become more intense, both in terms of severity in regions where they presently occur and in terms of their ability to become established in areas where they do not occur. As with the invasive species (Olfert & Weiss 2006), our study of a native insect pest also predicted that range extensions for *M. sanguinipes* could extend into regions of Canada that are not currently used for agriculture. Mills (1994) predicted that areas north of 55°N and west of 110° W have soils that are suitable for agricultural production and that warmer temperatures, associated with climate change, could result in arable land capable of small grain production. So it is likely that *M. sanguinipes* populations would become established in these new agricultural areas in the event that they become accessible in the future.

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