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ORIGINAL PAPER

Climate suitability and management of the gypsy moth invasion into Canada

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Abstract The gypsy moth has become established throughout southern Canada east of Lake Superior where the climate is suitable for the completion of its univoltine life cycle. The spread of the gypsy moth to the north and west in Canada has so far been prevented by climatic barriers and host plant availability as well as by aggressive eradication of incipient populations. Climate change is expected to increase the area of climatic suitability and result in greater overlap with susceptible forest types throughout Canada, especially in the west. At the same time, the gypsy moth is spreading west in the USA into states bordering western Canadian provinces. These circumstances all lead to a greatly increased risk of further invasion into Canadian forests by the gypsy moth. Management actions need to be intensified in different ways in different parts of the country to reduce the impacts of spread in eastern Canada and to prevent the gypsy moth from invading western regions.

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Introduction

The gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), is a notorious insect defoliator of trees. It is native to the temperate forests of Europe and Asia where occasional outbreaks occur. A European strain of the gypsy moth was introduced accidentally to North America near Boston, USA, in 1869 and has subsequently invaded much of the susceptible forest of northeastern North America from the Atlantic Coast westward to the Great Lakes Basin, northward into the Canadian Maritime Provinces, Quebec and Ontario (Liebhold et al. 1992) and as far south in the USA as North Carolina (Hastings et al. 2002, Fig. 1). In the USA, expansion of the insect's range continues southward along the Appalachian mountains, threatening to reach the hardwood forests of the southeast down to northern Florida (Allen et al. 1993) and westward through the transition ecozones between the eastern forests and the Great Plains. This invasion has been countered by over a century of aggressive and often controversial pest control (Nealis and Erb 1993) which has, in some cases, slowed but not halted the rate of spread (Sharov et al. 2002). There have been repeated introductions of gypsy moth to western North

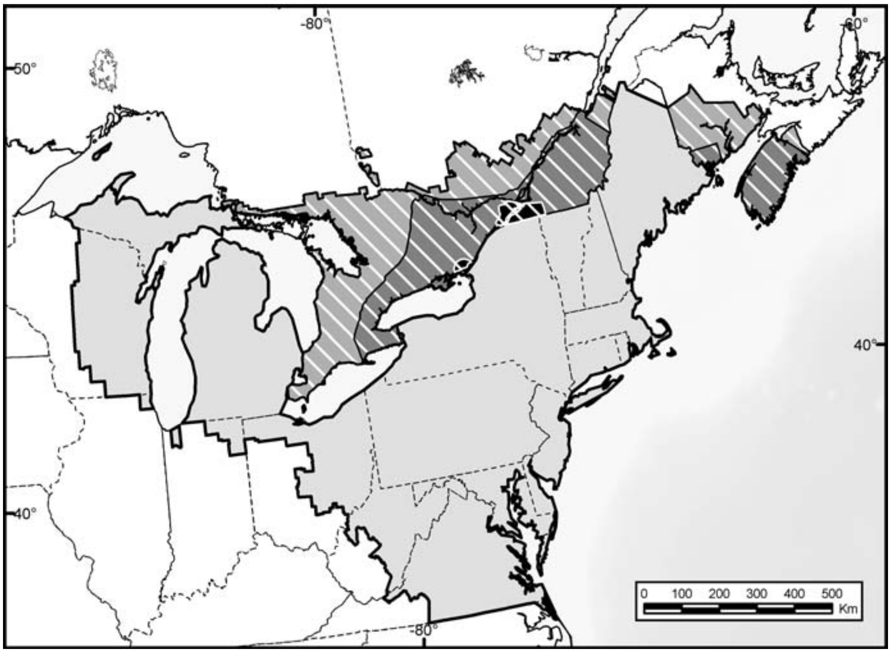


Fig. 1 Regulated area for the gypsy moth in the USA (2006, pale grey area), and Canada in 1974 (dark hatched area), 1989 (medium hatched area) and 2006 (pale hatched area)

America since the 1970s but to date (2007) these have been eradicated successfully or have otherwise failed to result in the establishment of viable populations (Nealis 2002; Weseloh 2003; Logan et al. 2007).

Adult females of the gypsy moth in North America are flightless so natural dispersal is limited to relatively short-distance ballooning of newly-hatched larvae on silk threads (Fosberg and Peterson 1986; Weseloh 1997). The rapid invasion into North America, and in particular the periodic infestations in western regions, has been aided by the insect's surreptitious association with humans. Many of the insect's numerous preferred host plants flourish in disturbed habitats and female moths tend to oviposit in protected shelters at ground level near the host trees (Lyons and Liebhold 1992). This often results in egg masses on outdoor articles such as lawn furniture, firewood and the underside of vehicles. When these articles are moved, the eggs are moved as well.

The gypsy moth was intercepted several times in Canada near the USA border during the first half of the 20th century as populations in the USA spread north and west. Eradication programs were carried out in southern Quebec in the 1920s and in southwestern New Brunswick in the 1930s. Significant increases in gypsy moth infestations in the USA in the mid-1950s (Doane and McManus 1981) coincided with repeated infestations in southern Quebec and Ontario leading to spray programs that were conducted every year beginning in 1960 (Brown 1975). By the late 1970s, defoliation was observed over a large area of southwestern Quebec and a few years later in southeastern Ontario (Jobin 1995), again following an increase in the intensity and area of a gypsy moth outbreak in the northeastern United States. By this time, authorities in Quebec and Ontario conceded that eradication was no longer feasible and pest management objectives shifted from eradication to suppression (Nealis and Erb 1993). In spite of these control efforts, the gypsy moth has continued to expand its range in eastern North America. Thus, the source area for new introductions of the gypsy moth has increased steadily for nearly 135 years. The increasing frequency of new introductions to western Canada since 1990 reflects both this increase in the source area and the high risk of successful transport *via* the pathway of westward movement of people and goods in North America (Nealis 2002).

The current policy of the Canadian federal government for management of the gypsy moth in Canada distinguishes two different situations: areas where the insect is considered established and therefore regulated by the federal Canadian Food Inspection Agency

(CFIA), and areas located outside this regulated zone. Within the regulated zone, the CFIA focuses on the management of pathways through inspection of specific commodities as defined by multilateral phytosanitary agreements. Once an area is regulated, response to outbreaks within the zone becomes the purview of provincial and municipal governments or private landowners and is determined essentially by their sensitivity to damage caused by outbreaks. The goal here is suppression and mitigation of damage. Outside of the regulated zone, the CFIA maintains a network of pheromone traps to update the boundaries of the regulated zone and to detect new isolated introductions far removed from the regulated area. The CFIA does not necessarily attempt to eradicate these isolated populations. The intent of the monitoring is to reveal where the gypsy moth has become established and, if necessary, regulate these areas. Jurisdictions wanting to avoid the potential economic penalty of regulation may carry out their own eradication programs to comply with the North American Plant Protection Organization's (NAPPO) definition of a pest-free state as "an officially identified area in which a target pest does not occur and is maintained as such". This has been, for example, the situation in British Columbia on Canada's West Coast since 1999 when the provincial government assumed responsibility for the eradication of the gypsy moth.

The maintenance of an annual network of traps to detect gypsy moth throughout the vast, unregulated area of Canada and to update continuously the boundaries along the several thousand km of the regulated zone is a formidable undertaking. Furthermore, regulation may be an effective instrument to facilitate the movement of goods and reduce pathways between countries but it seems to have had little practical influence on the invasion process within Canada. A re-evaluation of the strategies and policies for managing the invasion of Canada by the gypsy moth is needed.

In this paper, we apply our knowledge of Canada's climatic suitability for the gypsy moth to the design of a strategy for management of invasion. Our argument is guided by the following premises:

(1) The gypsy moth requires a suitable place to live, including an adequate supply of host plants and a climate suitable for the completion of its life cycle over several generations.
(2) Process modeling of temperature-dependent life history events can be used to map climatically suitable areas for gypsy moth (Régnière and Nealis 2002; Gray 2004) and to examine the influence of climate on historical patterns of invasion.
(3) Climate is changing and the distribution of areas climatically favourable to the gypsy moth can be expected to change accordingly (Logan et al. 2003; Pitt et al. 2007). Process-modeling is well suited to examining the consequences of this change on the likelihood of gypsy moth populations persisting in a particular area and the associated change in risk (Logan et al. 2007).
(4) Natural spread of gypsy moth along the broad contiguous frontier between regulated and unregulated areas cannot be stopped but can it be slowed, albeit at considerable effort and cost (Mayo et al. 2003). Benefits can be weighed against costs for the particular areas of concern (Sharov and Liebhold 1998a, b); Sharov et al. 1998).
(5) Eradication of isolated populations resulting from long-distance transport by humans is demonstrably feasible and cost-effective (Nealis 2002; Mayo et al. 2003).

We first evaluate the historical invasion and current range of the gypsy moth in Canada in the context of climate suitability. Then, we use a plausible, conservative 1% per year CO_2 increase climate-change scenario (Price et al. 2001) to drive a model of gypsy moth seasonality and to predict the potential future distribution of the gypsy moth. We discuss the relationship between these future potential distributions and the known ecology of the gypsy moth and propose management options that could be implemented in Canada.

Methods

Historical gypsy moth data

Regulated area

The Canadian Food Inspection Agency (CFIA) monitors exotic pests such as the gypsy moth in Canada, defines the zone where these organisms are established, and regulates the movement of potentially infested materials to un-infested regions both within and outside the country. To identify and demarcate areas requiring regulation, the CFIA deploys an extensive network of pheromone traps in unregulated areas. Thus the CFIA regulatory maps, updated annually, reflect accurately the insect's current range. We obtained maps of the CFIA-regulated area for the gypsy moth in Canada as of 1974, 1989, and the most recent update, 2006.

Until 1995, the Canadian Forest Service's Forest Insect and Disease Survey (FIDS) also deployed traps and reported annually on the status of populations. Data included evidence of tree damage, population density estimates and pheromone trap catch records and are included in a geo-referenced historical database called the FIDS INFOBASE (Power 1986). The database includes both positive and negative pheromone trap capture records and therefore provides a very good record of the actual distribution of finds. Verification of doubtful records and supplementary information was obtained by searching a digitized library of annual reports produced by the FIDS for the same period and assigning a geo-reference on the basis of maps and descriptive narrative.

Monitoring inside the regulated zone is less systematic and carried out by provincial and municipal governments. Quebec began gypsy moth surveys in 1986 and the Maritime Provinces in 1993. Monitoring of the gypsy moth populations in Ontario remained a joint venture of the Canadian Forest Service and the Ontario Ministry of Natural Resources until 2003. We obtained geo-referenced records of gypsy moth occurrence from New Brunswick, Nova Scotia and Quebec up to 2006 and from Ontario up to 2003 to complete the history started in the FIDS INFOBASE database described earlier. Information on the area of moderate to severe defoliation by the gypsy moth from 1975–1980 in Ontario and 1975–1990 in Quebec was obtained from Jobin (1995). For comparison, the total area under moderate to severe defoliation in the American states bordering eastern Canada was obtained for the period 1960–2006 from the Gypsy Moth Digest Web site (http://www.na.fs.fed.us/fhp/gm).

The gypsy moth is regularly detected in pheromone traps in western Canada (from Manitoba to British Columbia). Incipient populations have been successfully eradicated on several occasions over the past 20 years in British Columbia (Nealis 2002). Data from the CFIA, the CFS and the various provincial reports have been used to compile the history of the gypsy moth in western Canada.

Climate suitability maps

We used a detailed model of gypsy moth phenology (Gray et al. 1991, 1995, 2001; Logan et al. 1991; Sheehan 1992; Régnière and Sharov 1998; Régnière and Nealis 2002), hereafter the Gypsy Moth Life Stage (GMLS) model, to estimate the probability distribution of climatic suitability to support persistent gypsy moth populations throughout Canada under past, current and future climate conditions. Our method is similar to Logan et al. (2007) and Pitt et al. (2007). The approach consisted of determining whether the insect can successfully complete its life cycle under a specific climate. This was done in two steps. First, the GMLS model was run for 25,000 locations over the area of interest (Canada south of 60°N), using daily temperature time series generated from monthly normals as input (Régnière and St-Amant 2007). The process was replicated 50 times. Each run returned an establishment likelihood value $F = 0$ (non-viable seasonality) or $F = 1$ (viable). Because each time the model was run the weather data provided are slightly different (daily stochastic variation being restored to the monthly normals), the probability (p) of establishment in a given location was calculated as the proportion of replicates where the model returned $F = 1$ (successful completion of the life cycle). Second, an establishment probability map was generated by universal kriging with elevation as an external drift variable (Isaaks and Srivastava 1989), using a Digital Elevation Model of Canada at 30 arc-second resolution assembled from http://edc.usgs.gov/. This entire process was automated by the BioSIM system (Régnière 1996).

The climate change scenario was generated by the Canadian Global Circulation Model version 1 (CGCM-1), driven by a 1% CO_2 increase per year, over the time frame 2000–2070. The output of the CGCM-1 is a series of daily values from 1931 to 2070 over a low-resolution grid covering the planet. From these, deviations of monthly average minimum and maximum temperature from the standard

1961–1990 reference period were calculated for each year and grid point in Canada. The spatial resolution of these monthly deviations from the reference period, also called monthly anomalies, was increased through a spatial interpolation technique taking topography into account (Price et al. 2001). Daily observations of minimum and maximum temperature from all Environment Canada weather stations for years 1961 to 1990 were then modified by adding, by year and month, the monthly anomalies from the nearest high-resolution grid cell. For example, monthly anomalies for year 2041 and daily temperature observations from 1961 were used to produce climate-changed daily observations for year 2041. The same was done to 1962 daily observations using 2042 monthly anomalies, and so on. From these climate-changed daily values, normals were calculated in 10-year increments from 1981 (1981–2010 normals) to 2041 (2041–2070 normals). Actual normals were calculated from Environment Canada daily records for each decade from 1931 (1931–1960 normals) to 1971 (1971–2000 normals).

Annual climate fluctuation and establishment probability in Ontario

An analysis of the annual fluctuations in the geographical distribution of viable seasonality in Ontario, Canada was carried out using 250 simulation points located randomly across the province. The GMLS model was run for each point for each year between 1981 and 2006, using as input observed daily minimum and maximum air temperature records from Environment Canada weather stations. Temperature data were interpolated from the four recording stations nearest to each simulation point using the GIDS method (Nalder and Wein 1998). The relationship between the establishment flag F output by the GMLS model (described above) and latitude (L) was determined by binary logistic regression using the model:

$$g(p) = a + bL + \varepsilon \tag{1}$$

where $g(p)$ is the logit link function, p is the probability of establishment, ε is a binomially-distributed error term, and a, b are regression parameters. By rearranging Eq. 1, the latitude $L_{0.5}$ at which the probability of establishment $p = 0.5$, or $g(p) = 0$, can be calculated:

$$L_{0.5} = -\frac{a}{b} \tag{2}$$

The probability of establishment p (proportion of simulation outputs with an establishment flag value of $F = 1$) was calculated by year. The annual fluctuations and time trend of $L_{0.5}$ from 1981–2006 as determined by Eq. 2 were also examined.

Forest resources and area at risk

Consideration of area at risk in Canada depends on the location and abundance of susceptible host species. The gypsy moth is a polyphagous species with a large number of deciduous and coniferous host tree species (Liebhold et al. 1995). Spatial forest inventories from provincial governments and forest companies contain much of the required data but often do not adequately account for the many non-commercial host tree species of gypsy moth and would require a monumental effort to assemble due to differing protocols, varying formats and restricted access. Maps of the distribution of gypsy moth-susceptible forests in Canada, grouped by image analysis into three broad forest types were obtained from Beaubien et al. (2002): deciduous, closed (dense) and open (thin) mixed stands. The area of overlap between these forest types and the zone of high establishment probability ($p > 0.5$) of the gypsy moth, by decade under past and future climate conditions were calculated by GIS analysis.

Results

The historical record of recoveries of gypsy moth adults in pheromone traps and of other life stages in various samples from provincial surveys in Canada is illustrated in Fig. 2, and the area defoliated in Canada and the bordering USA is shown in Fig. 3. Until the late 1960s, the insect was confined to southwestern Quebec and the area around Kingston, Ontario (Fig. 2a), having crossed into Canada from adjacent New York State. In the early 1970s, the insect was also recovered from several locations in New Brunswick (Fig. 2b). Between 1975 and 1980, pheromone trap records indicated a significant increase in the gypsy moth's distribution in Quebec and New Brunswick, as well as new finds in Nova Scotia and Prince Edward Island (Fig. 2c). In the late 1970s,

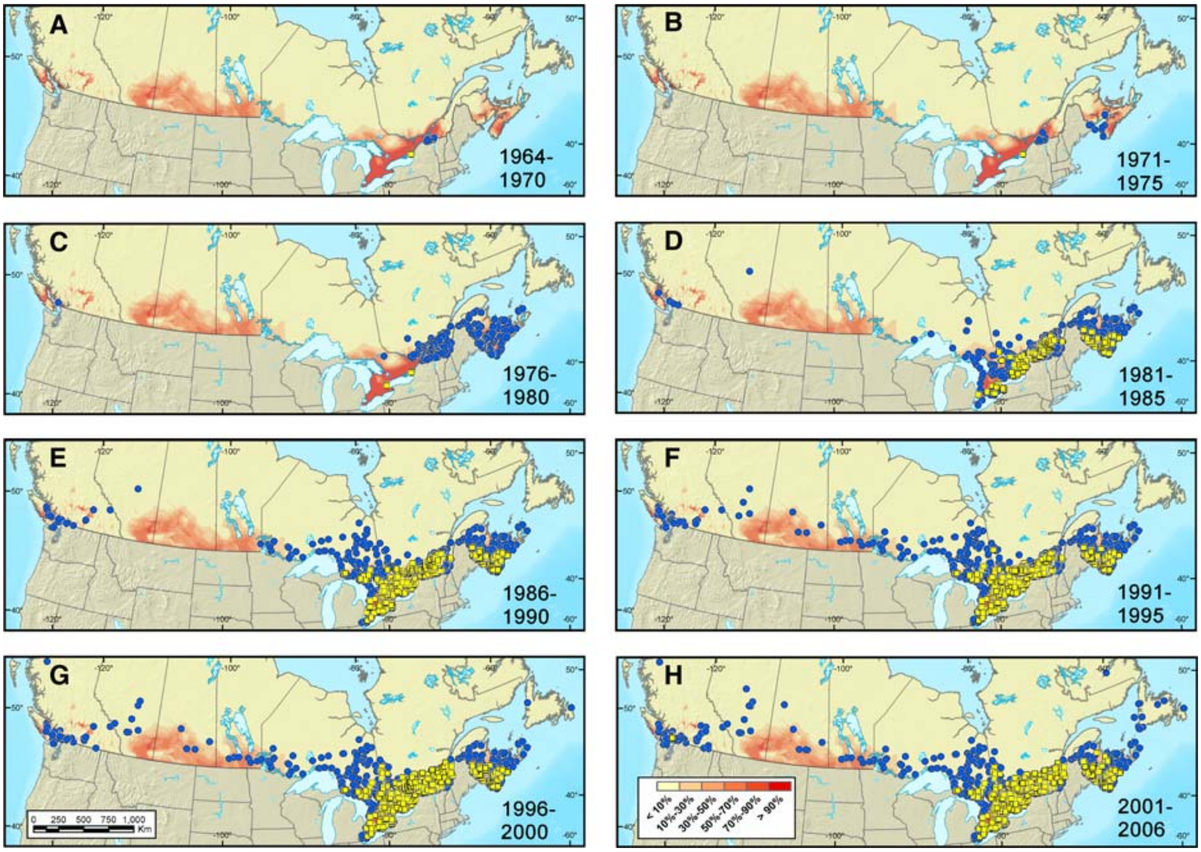


Fig. 2 Historical distribution of gypsy moth recoveries from pheromone traps (blue ●) and from sampling of other life stages (yellow ■) in Canada between 1964 and 2006. Background: probability of establishment based on climate suitability for an adaptive life cycle using climate normals for 1971–2000. (**a**) 1964–1970; (**b**) 1971–1975; (**c**) 1976–1980; (**d**) 1981–1985; (**e**) 1986–1990; (**f**) 1991–1995; (**g**) 1996–2000; (**h**) 2001–2006

defoliation by the gypsy moth in Quebec exceeded 5,000 km^2 (Fig. 3a). By the early 1980s, the insect had become widely distributed in southeastern Ontario (Fig. 2d) with nearly 3,000 km^2 of forest defoliated in 1985 (Fig. 3a).

It seems likely that the rapid invasion of Ontario by the gypsy moth was driven by spread west from outbreak populations in Quebec into eastern Ontario as well as by northward expansion of the very large outbreak of 1980–1982 in the northeastern USA (Fig. 3b). In 1989, the CFIA determined that the area generally infested with the gypsy moth in eastern Canada covered 151,000 km^2 between southeastern Ontario and Nova Scotia (Fig. 1). By 1990, with a second defoliation episode covering 4,000 km^2 in Ontario (Fig. 3a), the insect was already occupying most of the area of medium to high climatic suitability in eastern Canada (Fig. 2e). There has been little change in its geographical distribution since then (Fig. 2f, g, h). The CFIA-regulated area in 2006 covered 326,000 km^2 from the eastern tip of Lake Superior to Nova Scotia (Fig. 1).

Adult gypsy moths have been recovered regularly in pheromone traps from northwestern Ontario to British Columbia since the late 1980s, but so far there is no evidence of established populations. This situation is partly the result of numerous successful eradication campaigns as well as the fact that areas of climate suitability in the west are fragmented (Fig. 2), as is the distribution of host plants (see later).

The change over time in the range of coordinates at which moths and other life stages of the gypsy moth have been recovered in pheromone traps or other samples suggests a rapid invasion of the climatically suitable parts of Canada followed by a

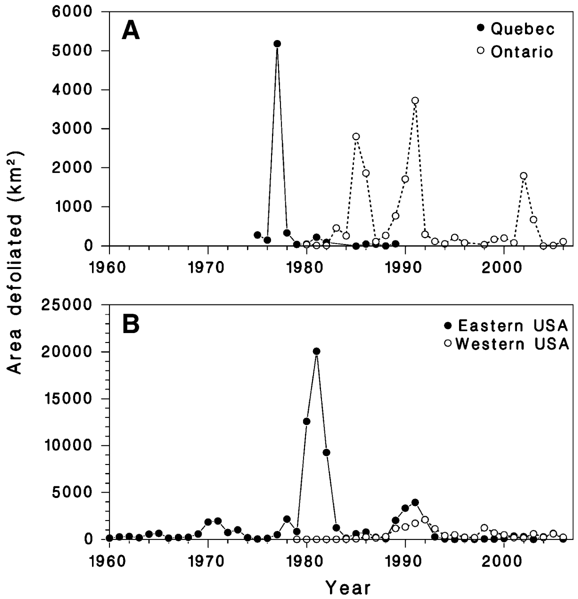
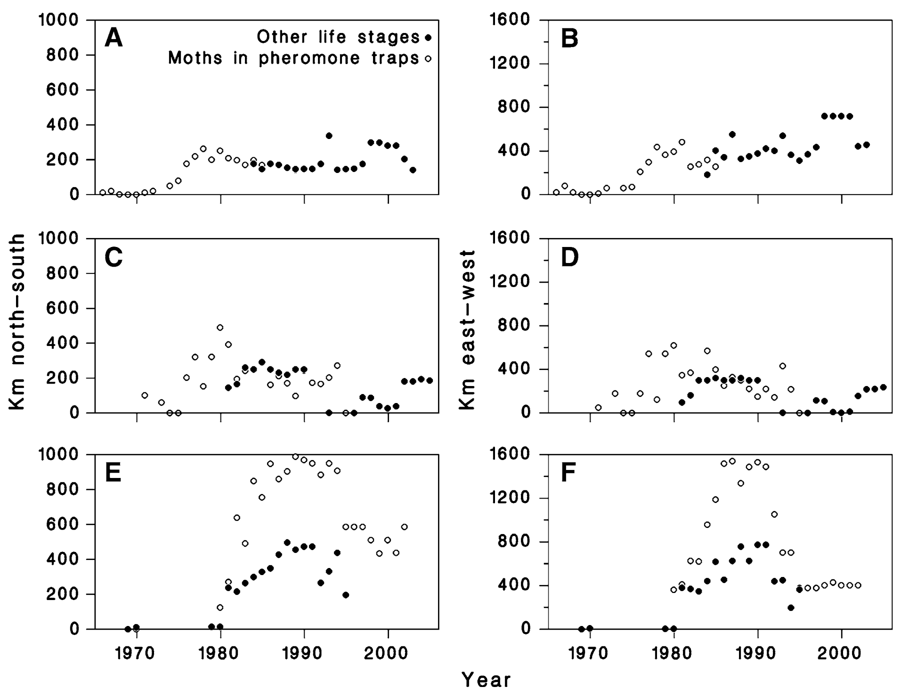


Fig. 3 Area (km^2) with moderate to severe defoliation by the gypsy moth in (**a**) Ontario (○) and Quebec (●) and (**b**) the bordering areas infested in the United States (eastern: from Maine to New York, ●; western: from Ohio to Wisconsin, ○) between 1960 and 2006

period of relative stasis (Fig. 4). In Quebec, the spread northward and from east to west occurred very rapidly prior to 1980 at the time of the widespread defoliation episode depicted in Fig. 3a, and has since stopped (Fig. 4a, b). Nor has there been a resurgence of defoliation in the Maritime Provinces of New Brunswick and Nova Scotia. This spatio-temporal pattern of invasion has an interesting additional feature: there is a marked reduction in both the north-south and east-west ranges from a maximum in the early 1980s (Fig. 4c, d) such that the range of the gypsy moth has become “compressed” over time. This compression was most dramatic in Ontario, where the gypsy moth spread rapidly between 1980 and 1990 to reach a maximum north-south and east-west range between 1000 km and 1600 km, respectively. A significant compression of the gypsy moth’s range then occurred in the early to mid-1990s (Fig. 4e, f).

This apparent compression pattern could, for example, be an artifact if sampling effort was reduced in the outlying areas where risk was considered low. However, in both the Maritimes and Ontario, pheromone trapping intensity actually increased during the 1990s as a result of the sharp increase in positive finds in the late 1980s. There is better evidence that the distribution of the gypsy moth was indeed very broad following the initial outbreak phase as potential migrants were abundant (1977–1979 in Quebec and New Brunswick, and 1984–1992 in Ontario), and the

Fig. 4 North-south (left column) and east-west (right column) range (km) of gypsy moth recovered in pheromone traps by FIDS (○) and various other life stages (●) found over time. (**a**, **b**) Quebec. (**c**, **d**) Maritime Provinces. (**e**, **f**) Ontario



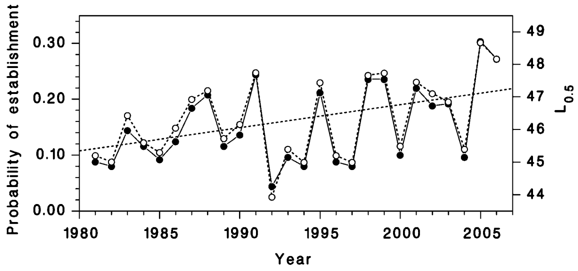


Fig. 5 Annual fluctuations of P, the probability of gypsy moth establishment (●), and of the latitude $L_{0.5}$ at which $P = 0.5$ (○) as determined by Eqs. 1 and 2 (straight dotted line: regression of $L_{0.5}$ over time)

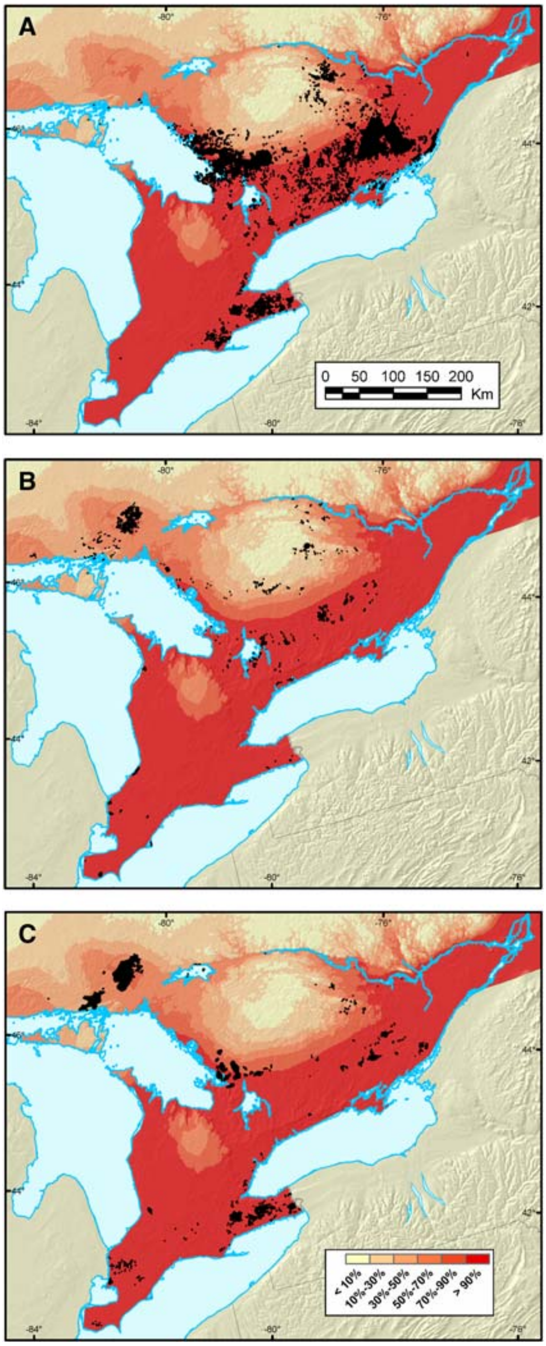


Fig. 6 Geographical distribution of moderate to severe defoliation by the gypsy moth in Ontario. Background: probability of establishment based on climate suitability for an adaptive life cycle using climate normals for 1971–2000. (**a**) 1981–1991; (**b**) 1992–1997; (**c**) 1998–2003

risk of long-distance transport, even to inhospitable areas, increased. Positive traps in northern Ontario, for example, are all associated with campgrounds. As outbreaks in favorable areas waned, the abundance of migrants decreased, and the apparent range of the gypsy moth as determined from pheromone trap catches compressed as depicted in Fig. 4.

There is also evidence of a strong association between these historical patterns of the gypsy moth distribution and historical patterns of climatic suitability in Ontario, as defined by the probability of completing its life cycle. First, there has been a steady increase in the area of climatic suitability for the gypsy moth across Ontario since 1980 (regression of $L_{0.5}$ against time, $F_{1,24} = 4.82$, $P = 0.038$; Fig. 5). This trend would have been more pronounced had it not been for a sharp decrease in suitability for five of the six years between 1992 and 1997. These years also correspond to a pronounced reduction in the area of defoliation in Ontario (710 km^2 compared to the 8,491 km^2 defoliated in the previous 10 years) and before the resurgence of defoliation (2,873 km^2) since 1998 (Fig. 6). The temporary decline in climatic suitability across Ontario between 1992 and 1997 (Fig. 5), led to a reduction in population density and therefore in potential migrants in the formerly favorable climatic zones, and reduced even further the likelihood of persistence in marginal climatic zones. Recovery of the trend in increasing climatic suitability since 1998 (Fig. 5) has been correlated with resurgence in defoliation (Fig. 6c) and increased frequency of moths in pheromone traps to the north and west in Ontario (Fig. 2).

Reductions in population densities within the established range of the gypsy moth may also have involved the belated arrival of natural enemies. The fungal pathogen *Entomophaga maimaiga* Humber, Shimazu and Soper spread across the North American range of the gypsy moth, including Ontario, during

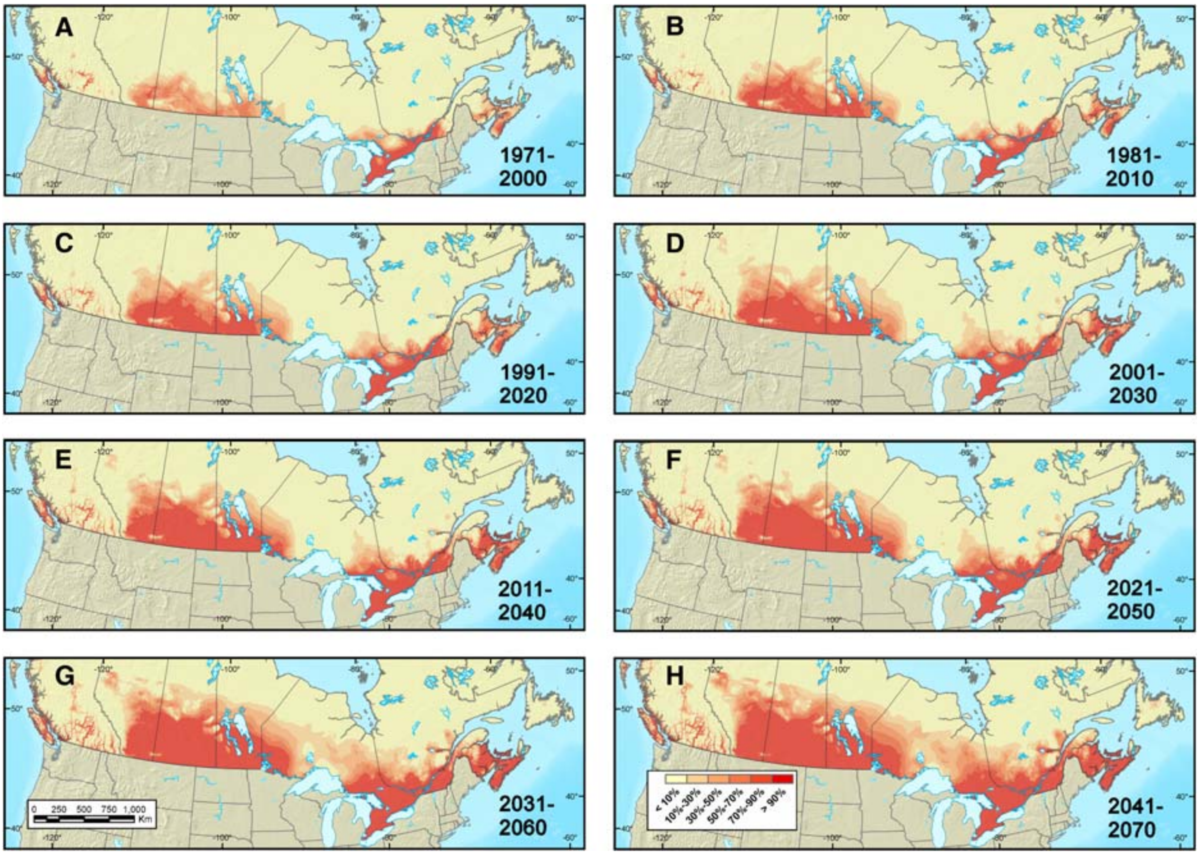


Fig. 7 Potential distribution of the gypsy moth in Canada based on its probability of establishment as a function of climate. Prepared by applying the output of the Canadian Global Circulation Model (version I) under a 1%/year increase in atmospheric CO_2. Normals updated each decade, from (**a**) 1971–2000 to (**h**) 2041–2070

the first half of the 1990s (Nealis et al. 1999; Villedieu and van Frankenhuyzen 2004). Natural enemies may dampen the amplitude of outbreaks in favorable areas and therefore reduce the risk of migrants but will have no effect on the likelihood of establishment in new areas.

The northern and western expansion of the gypsy moth in Ontario in the 1990s is reflected in the spatial distribution of defoliation in that province. From 1970 to 1991, most of the defoliation occurred in the southeastern portion of the province near the area of original introduction (Fig. 6a). Since that time, defoliation has been farther north and west (Fig. 6b, c). These sequences of defoliation correspond to the familiar pattern of severe defoliation on the "leading edge" of the invasion process (Elkinton and Liebhold 1990; Liebhold and Tobin 2006).

This historical information shows that the gypsy moth has spread rapidly throughout the area in eastern Canada where the climate is suitable for its establishment and that the most severe defoliation occurred in a wave that followed shortly after the insect first invaded and became established in Quebec and then in Ontario. In Quebec, the gypsy moth has not caused damage of concern since the late 1980s but in Ontario, defoliation has occurred in a series of waves (Fig. 3a).

Climate change is expected to increase the future area of suitable climate for gypsy moth establishment throughout Canada as increasingly warm summers allow the insect to complete its univoltine life consistently in areas that are now marginal for an adaptive life cycle (Fig. 7). The change in suitable area for the gypsy moth over the next 50 years will be greatest in western Canada, especially the Prairie Provinces. In British Columbia, the steep topography and the cold climate of the mountains and central plateau restrict the total area of climatic susceptibility

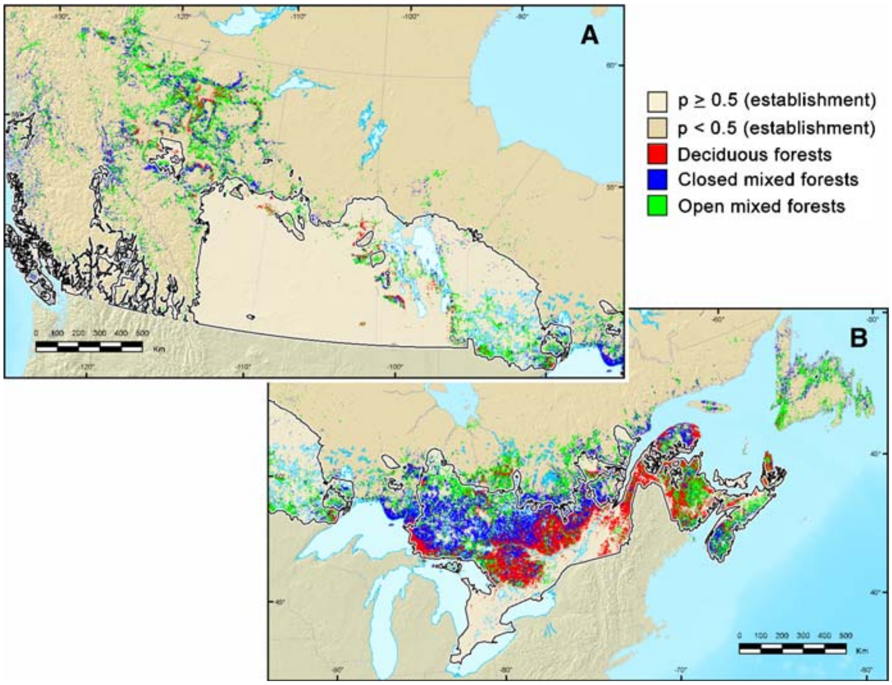


Fig. 8 Overlap between high climatic suitability for the gypsy moth (pale shading: probability of establishment >0.5 calculated from climate-changed normals 2041–2070) and susceptible forest types in Canada (red: deciduous; blue: closed mixed; green: open mixed). (**a**) Western Canada (note the patchy distribution of high climatic suitability in BC). (**b**) Eastern Canada

to gypsy moth invasion over the period considered here.

The overlap between the area of climatic suitability for the gypsy moth (where the probability of establishment >0.5) and the area of distribution of the most susceptible forest types in Canada (deciduous, closed) represents the potential ecological and economic risks posed by invasion of this species. This risk (Fig. 8), depicted here as a surface area of forested landscape, has been relatively low historically, mostly because the portion of eastern Canada that was climatically suitable to the insect was also the least forested as the result of human occupation (e.g. southwestern Ontario in Fig. 8). However, this area at risk is expected to double or triple over the next 50 years as areas with susceptible forest species become more climatically suitable for the gypsy moth as a result of climate change (Fig. 9).

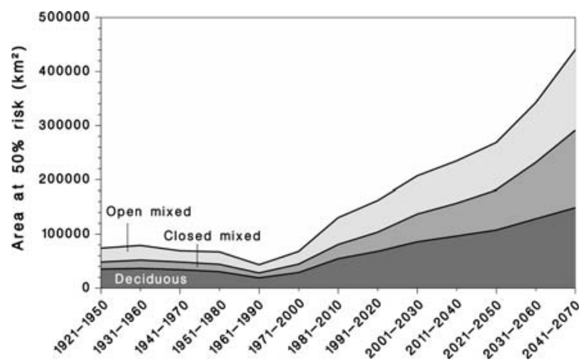


Fig. 9 Change in area of overlap between high climatic suitability for the gypsy moth (probability of establishment >0.5) and susceptible forest types in Canada, in response to climate change. Dark tone: deciduous forest type (most susceptible). Medium tone: closed mixed forests; Light tone: open mixed forests (least susceptible)

Much of this increased risk will occur in eastern Canada, as a result of the vast extent of susceptible forest types in that part of the country that have so far been protected from the gypsy moth by unfavorable climate (Fig. 8). In western Canada, a large proportion of the climatically suitable area will remain dominated either by prairie vegetation or coniferous forests (spruce, pine) that are not expected to support significant gypsy moth populations or suffer much damage. Nonetheless, the trees that will constitute the future hosts for the gypsy moth in an infested prairie region are trees in shelter belts, river valleys and urban settings. These trees are highly valued and they occupy areas associated with humans and are therefore at a greater risk of receiving the gypsy moth. At the most distant reaches of our projections (after 2010 in Fig. 7), the area of climatic suitability for the gypsy moth in the Prairies will overlap with the southern range of several suitable hosts in the birch (*Betula*) and poplar (*Populus*) genera. Although sustained outbreaks of the gypsy moth in forest stands dominated by these species may be, at present, uncommon, the congruence of suitable climate and suitable hosts will surely result in a native forest sustaining an alien insect species with proven potential for damage.

Discussion

The gypsy moth repeatedly invaded eastern Canada from adjacent infested areas of the northeastern USA. Once established in the upper St. Lawrence River region in the 1960s, the gypsy moth rapidly spread through suitable habitats in Quebec, Ontario and the Maritime Provinces until its distribution in eastern Canada stabilized in the mid-1990s. Our seasonality-based modeling indicates that this apparent stability of range of the past 10 years in eastern Canada corresponds to the area where the climate most suitable for completion of the gypsy moth life cycle overlaps with susceptible forest types. To the north and west of the current established range in Canada (i.e. eastern shore of Lake Superior near the city of Sault Ste. Marie, ON), the natural spread of gypsy moth has been limited by a combination of unsuitable climate and lack of susceptible forest types. The relative contribution of these two factors in limiting the insect's northern spread has been controversial (Sullivan and Wallace 1972; Williams and Liebhold 1995; Sharov et al. 1999). The GMLS model used here predicts closely the current distribution of the insect in eastern Canada on the basis of climate suitability alone indicating climate plays the dominant role. Aggressive management of the gypsy moth associated with the Slow the Spread program in Wisconsin and Minnesota (Reardon et al. 1998; Sharov et al. 2002; Thorpe et al. 2006) contributes to the slow rate of spread in adjacent northwestern Ontario. Eradication of spot infestations in Pacific coastal regions in both the USA and Canada have kept that region free of established gypsy moth populations despite the presence of areas with both suitable climate and host species (Nealis 2002).

Where the area of greatest climate suitability (i.e. probability of establishment >0.5) overlaps with areas of high host abundance in Quebec and Ontario, extensive and severe defoliation has occurred. A distinct warming trend since the mid-1980s in Canada is expanding this zone of climatic suitability both in eastern and western Canada. There is evidence that gypsy moth populations are invading these new areas further north and causing severe defoliation (Fig. 7). We now consider the consequences of these patterns in terms of future risk and possible management options.

Risk to forest resources from the gypsy moth in Canada is a function of two factors: (1) the risk of introduction and (2) the overlap between the area of climate suitability and the geographical distribution of host trees.

Areas already infested by the gypsy moth meet both of these conditions and will remain sources of future invasions. As zones immediately adjacent to these infested areas become more suitable because of climate change, invasion will be rapid if suitable hosts are present. The impact will be dependent upon the actual nature of the host plant distribution in these areas, with closed forests dominated by preferred hosts experiencing the greatest impacts. Given the broad host range of the gypsy moth, including abundant northern hardwoods such as birches, aspens and a variety of ornamental plants, defoliation is likely but the ecological and economic impacts are less predictable. On the one hand, the historical pattern in Ontario and elsewhere suggests that leading-edge populations can reach damaging levels quickly. On the other hand, the apparent rapid movement of significant mortality agents, especially the pathogens Nuclear Polyhedrosis Virus (NPV) and *Entomophaga maimaiga*, that accompany the invasion of the gypsy moth (Nealis et al. 1999; Hastings et al. 2002; Villedieu and van Frankenhuyzen 2004; Dwyer et al. 2004) could dampen those damaging effects.

Regardless of the dynamic behaviour in this expanding distribution, the source area for gypsy moth invasions further west will continue to increase in eastern Canada and in the USA (Williams and Liebhold 1995) by a factor of two to three times in the next 50 years as will the area of suitable climate and susceptible host plants in the potential receiving areas further west. With the ever-increasing movement of people and commodities, movement of gypsy moth life stages across otherwise inhospitable habitats into susceptible areas is inevitable. These circumstances have several important implications for the management of the forest resources at risk. Our analysis suggests that distinct but complementary management strategies are required in different parts of Canada. First, the potential for damaging outbreaks will persist for most of the deciduous forest east of the Great Lakes. Climate change will result in those areas currently at the margin of the range to become more suitable and the gypsy moth can be expected to invade quickly in spite of regulatory efforts. Accordingly, management priorities in eastern Canada should address resource protection. Areas at greatest risk of damaging defoliation will be those for which models such as the one used here show that climate is most suitable and for which inventories show that host plants are most abundant. Monitoring gypsy moth populations in these areas will permit resource managers to identify regions of potential damage and implement effective suppression options. This monitoring will also identify zones where the risk of transport of life stages outside the regulated area is greatest as there are strong correlations between extensive eastern outbreaks and the frequency of trap captures in the west (Phero Tech Inc. 1994). Identification of increased risk resulting from elevated populations in source areas will trigger increased focus on the well-known pathways for gypsy moth transport; movement of people and their associated goods. Regulation of these pathways then becomes feasible via existing regulations pertaining to transportation of goods within Canada.

In western Canada, information from monitoring gypsy moth in source areas will trigger monitoring efforts to detect new invasions. The risk factors with respect to pathways and susceptible host plants are well known. This analysis adds the capability of adding climate suitability to the assessment to provide an optimal monitoring scheme that balances cost and risk (Logan et al. 2007).

While the expanded potential distribution of the gypsy moth in the Prairie Provinces appears largely contiguous under climate change, the potential distribution in British Columbia will continue to be discontinuous because of topographical and forest heterogeneity. In fact, the actual susceptible area in both western regions may be mostly fragmented because in the Prairies, most of the area at risk (based on climate) will remain agricultural or natural grassland with trees mostly isolated near urban centres, river bottoms and windbreaks. Thus, it should be possible to prevent establishment of the gypsy moth in all of western Canada by maintaining a strategic monitoring network and undertaking occasional eradication programs where the climate profile indicates that immigrant populations threaten to persist in an area.

There are several sound reasons to maintain the gypsy moth-free status of western Canada. The first and most obvious is that the gypsy moth is a demonstrably destructive insect in North America. Wherever it has become established, significant damage has occurred to native and to high-value amenity trees. Infested areas then become subject to regulation with the associated negative economic impacts on trade. Further, this damage leads to the expensive and unpopular use of pesticides, often in urban areas or in habitats that are, ironically, set aside for conservation purposes and that are now at risk of a biological invasion.

A less obvious reason for maintaining as large a gypsy-moth free area in Canada as possible is the additional threat of invasion by the Asian strain of the gypsy moth. Female moths of this strain are capable of flying and the larvae have a much broader host plant range, including conifer species, than does the European strain. The Asian strain of the gypsy moth is not currently present anywhere in Canada but constitutes a much higher risk to conifer forests, especially on the Pacific coast. At present, it is monitored with the same pheromone lure as the European gypsy moth. Captured male moths are distinguished as European or Asian only by subsequent DNA analysis. As long as western areas remain free of the gypsy moth, the few male moths trapped there each year can all be screened using molecular technology. However, if the European gypsy moth becomes established and common in western regions, the necessity of sub-sampling trap catches could severely compromise the ability of phytosanitary measures to detect the Asian gypsy moth invasion in Canada.

The management of risk of invasion by alien species has far-reaching socio-economic and environmental benefits. An effective policy and response can be greatly aided by the application of scientific knowledge to interpret historical patterns and then to model likely future scenarios. Such an approach allows us to identify variability in the risk profile associated with different factors in different areas and thereby to determine variable and appropriate policies and responses. In our case, extensive knowledge of gypsy moth biology and ecology enabled us to design an effective management strategy to achieve realistic objectives based on the analysis of the risk factors discussed in this paper.

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References

Allen JC, Foltz JL, Dixon WN, Liebhold AM, Colbert JJ, Régnière J, Gray DR, Wilder JW, Christie I (1993) Will the gypsy moth become a pest in Florida? Fla Entomol 76:102–113

Beaubien J, Latifovic R, Cihlar J (2002) Land cover of Canada 1998. Special Publication, NBIOME Project. Produced by the Canada Centre for Remote Sensing and the Canadian Forest Service, Natural Resources Canada, available from the Canada Centre for Remote Sensing, Ottawa

Brown GS (1975) Gypsy moth. In: Prebble ML (ed) Aerial control of forest insects in Canada. Department of the Environment, Ottawa, pp 208–212, Catalogue No. Fo23/19/1975

Doane CC, McManus ML (1981) The gypsy moth: research toward integrated pest management. USDA Forest Service, Technical Bulletin 1584

Dwyer G, Dushoff J, Yee SH (2004) The combined effects of pathogens and predators on insect outbreaks. Nature 430:341–345

Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North America. Annu Rev Entomol 35:571–596

Fosberg MA, Peterson M (1986) Modeling airborne transport of gypsy moth (Lepidoptera: Lymantriidae) larvae. Agric For Meteorol 38:1–8

Gray DR (2004) The gypsy moth life stage model: landscape-wide estimates of gypsy moth establishment using a multi-generational phenology model. Ecol Model 176:155–171

Gray DR, Logan JA, Ravlin FW, Carlson JA (1991) Toward a model of gypsy moth egg phenology using respiration rates of individual eggs to determine temperature-time requirements of prediapause development. Environ Entomol 20:1645–1652

Gray DR, Ravlin FW, Régnière J, Logan JA (1995) Further advances toward a model of gypsy moth (*Lymantria dispar* (L.)) egg phenology: Respiration rates and thermal responsiveness during diapause, and age-dependent developmental rates in postdiapause. J Insect Physiol 41:247–256

Gray DR, Ravlin FW, Braine JA (2001) Diapause in the gypsy moth: a model of inhibition and development. J Insect Physiol 47:173–184

Hastings FL, Hain FP, Smith HR, Cook SP, Monahan JF (2002) Predation of gypsy moth (Lepidoptera: Lymantriidae) pupae in three ecosystems along the southern edge of infestation. Environ Entomol 31:668–675

Isaaks EH, Srivastava RM (1989) An introduction to applied geostatistics. Oxford University Press, New York

Jobin L (1995) Gypsy moth, *Lymantria dispar*. In: Armstrong JA, Ives WGH (eds) Forest insect pests in Canada. Natural Resources Canada, Canadian Forest Service, Ottawa, pp 133–139, Fo24-235/1995E

Liebhold AM, Tobin PC (2006) Growth of newly established alien populations: comparison of North American gypsy moth colonies with invasion theory. Popul Ecol 48:253–262

Liebhold AM, Halverson JA, Elmes GA (1992) Gypsy moth invasion in North America: a quantitative analysis. J Biogeogr 19:513–520

Liebhold AM, Gottschalk KW, Muzika R-M, Montgomery ME, Young R, O'Day K, Kelley B (1995) Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. USDA Forest Service, Northeastern Forest Experiment Station, General Technical Report NE-211

Logan JA, Casagrande RA, Liebhold AM (1991) Modeling environment for simulation of gypsy moth (Lepidoptera: Lymantriidae) larval phenology. Environ Entomol 20:1516–1525

Logan JA, Régnière J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. Front Ecol Environ 1:130–137

Logan JA, Régnière J, Gray DR, Munson AS (2007) Risk assessment in face of a changing environment: Gypsy moth and climate change in Utah. Ecol Appl 17:101–117

Lyons DB, Liebhold AM (1992) Spatial distribution and hatch times of egg masses of gypsy moth (Lepidoptera: Lymantriidae). Environ Entomol 21:354–358

Mayo JH, Straka TJ, Leonard DS (2003) The cost of slowing the spread of the gypsy moth (Lepidoptera: Lymantriidae). J Econ Entomol 96:1448–1454

Nalder IA, Wein RW (1998) Spatial interpolation of climatic normals: test of a new method in the Canadian boreal forest. Agric For Meteorol 92:211–225

Nealis VG (2002) Gypsy moth in Canada: case study of an invasive insect. In: Claudi R, Nantel P, Muckle-Jeffs E (eds) Alien invaders in Canada's waters, wetlands, and forests. Natural Resources Canada, pp 151–159, Fo42-329/2002E

Nealis VG, Erb S (1993) A sourcebook for management of the gypsy moth. Canadian Forestry Service, Great Lakes Forestry Centre, Fo42-193/1993E

Nealis VG, Roden PM, Ortiz DA (1999) Natural mortality of the gypsy moth along a gradient of infestation. Can Entomol 131:507–519

Phero Tech Inc (1994) A risk assessment of European gypsy moth in British Columbia. Prepared by Deloitte and Touche Management Consultants, Guelph, Ontario

Pitt JP, Régnière J, Worner S (2007) Risk assessment of gypsy moth, *Lymantria dispar* (L), in New Zealand based on phenology modeling. Int J Biometeorol 51:295–305

Power JM (1986) FIDSINFOBASE: the forest insect and disease survey information system. Canadian Forest Service, Petawawa National Forestry Institute, Information Report PI-X-65

Price DT, McKenney DW, Caya D, Côté H (2001) Transient climate change scenarios for high resolution assessment of impacts on Canada's forest ecosystems. Report to Climate Change Action Fund (CCAF) and CCIS

Reardon RC, Leonard DS, Mastro VC, McLane W, Leonhardt BA, Talley S, Thorpe K, Webb RE (1998) Using mating distruption to manage gypsy moth: a review. USDA Forest Service, Forest Health Technology Enterprise Team, FHTET-98-01

Régnière J (1996) Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environ Entomol 25:869–881

Régnière J, Nealis VG (2002) Modelling seasonality of gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), to evaluate probability of its persistence in novel environments. Can Entomol 134:805–824

Régnière J, Sharov A (1998) Phenology of *Lymantria dispar* (Lepidoptera: Lymantriidae) male flight and the effect of moth dispersal in heterogeous landscapes. Int J Biometeorol 41:161–168

Régnière J, St-Amant R (2007) Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. Int J Biometeorol 51:415–430

Sharov AA, Liebhold AM (1998a) Bioeconomics of managing the spread of exotic pest species with barrier zones. Ecol Appl 8:833–845

Sharov AA, Liebhold AM (1998b) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. Ecol Appl 8:1170–1179

Sharov AA, Liebhold AM, Roberts EA (1998) Optimizing the use of barrier zones to slow the spread of gypsy moth (Lepidoptera: Lymantriidae) in North America. J Econ Entomol 91:165–174

Sharov AA, Pijanowski BC, Liebhold AM, Gage SH (1999) What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility? Agric For Entomol 1:37–45

Sharov AA, Leonard D, Liebhold AM, Roberts EA, Dickerson W (2002) "Slow the Spread": a national program to contain the gypsy moth. J For 100:30–36

Sheehan KA (1992) User's guide for GMPHEN: gypsy moth phenology model. USDA Forest Service, Northeastern Forest Experiment Station, General Technical Report NE-158

Sullivan CR, Wallace DR (1972) The potential northern dispersal of the gypsy moth, *Porthetria dispar* (Lepidoptera: Lymantriidae). Can Entomol 104:1349–1355

Thorpe K, Reardon R, Tcheslavskaia K, Leonard D, Mastro V (2006) A review of the use of mating distruption to manage gypsy moth, *Lymantria dispar* (L.). USDA Forest Service, Forest Health Technology Enterprise Team, FHTET-2006-13

Villedieu Y, van Frankenhuyzen K (2004) Epizootic occurrence of *Entomophaga maimaiga* at the leading edge of an expanding population of the gypsy moth (Lepidoptera: Lymantriidae) in north-central Ontario. Can Entomol 136:875–878

Weseloh RM (1997) Evidence for limited dispersal of larval gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae). Can Entomol 129:355–361

Weseloh RM (2003) People and the gypsy moth: a story of human interactions with an invasive species. Am Entomol 49:180–190

Williams DW, Liebhold AM (1995) Forest defoliators and climatic change: potential changes in spatial distribution of outbreaks of western spruce budworm (Lepidoptera: Tortricidae) and gypsy moth (Lepidoptera: Lymantriidae). Environ Entomol 24:1–9