Range of gypsy moth in British Columbia: a study of climatic suitability

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ABSTRACT

The potential range of gypsy moth in British Columbia is predicted from climatic comparisons to its native range in Eurasia and by using temperature-dependent phenological models of the life stages. The cool and wet coastal areas, northern B.C., and high elevations are predicted to be unsuitable for gypsy moth. Southeastern Vancouver Island, parts of the lower mainland, and southern interior valleys appear to have suitable climates. However, the availability of preferred hosts may limit establishment in some of these areas. Habitats with Garry oak are of particular concern, since it is the most suitable native tree species and is already threatened by urban development.

Keywords: *Lymantria dispar*, Lymantriidae, discriminant function analysis, life stage, biogeoclimatic zones, development modelling

INTRODUCTION

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), a native of Eurasia, was introduced to North America in 1869 from France (Montgomery and Wallner 1988). Despite the inability of females of the European strain to fly, it has since expanded its range from the initial foothold in Massachusetts to the entire eastern forest region from southern Quebec and Ontario to Georgia, and to Wisconsin in the west. Individuals have been caught in western North America since the late 1970s, when pheromone traps were first developed and used. Moths have been trapped in Oregon, Washington, Utah, California, and British Columbia. An outbreak in Oregon in 1984, and local populations in Oregon, Washington and Utah, were all controlled with *Bacillus thuringiensis*. In B.C., all introductions so far have died out naturally or been controlled by spraying.

Its potential to become established in B.C. is a controversial but pressing question. The major mode of introduction is as egg masses, for example on recreational vehicles and trailers from infested areas in eastern North America. With increasing immigration and tourism from the east to B.C. and the abandonment of control efforts in Quebec and Ontario, introductions may continue at high levels in the future. The range of gypsy moth depends on adequate climate for the annual cycle of development and synchronization

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with hosts, and on the availability of suitable hosts. The gypsy moth is remarkably polyphagous, but its best development is on oaks and some poplars or aspen. The suitability of many of the woody plants of B.C. for gypsy moth has not been assessed. However, Garry oak, quaking aspen, and red alder are all favourable (Lechowicz and Mauffette 1986, Miller *et al.* 1991a). Larvae develop successfully on Douglas-fir, lodgepole pine and ponderosa pine in the laboratory, although development is slow, and larval survival is highly dependent on temperature and foliage age (Miller and Hanson 1989, Miller *et al.* 1991b). First instar larvae were unable to establish on Douglas-fir in another laboratory study (Jobin 1981).

The objective of this paper is to predict the potential range of gypsy moth in B.C., and identify areas of high susceptibility. We have used several approaches to accomplish this, but we have limited the analysis mostly to climatic factors. Hosts are considered only briefly.

The life cycle of the gypsy moth

The gypsy moth is univoltine, with an obligate winter diapause (Montgomery and Wallner 1988). The moths emerge in mid-summer (July in eastern North America and Europe). Females from Europe are flightless and emit a pheromone to attract males. Eggs are laid near the site of pupation which is usually on tree trunks or the undersides of branches, but also on rocks or man-made structures. All eggs are laid in a single mass covered with short hairs from the female's body. The embryos develop for about two weeks (depending on temperature), and the larvae overwinter within the eggs. In spring, around the time of budburst of the favoured oak hosts, the larvae hatch. Newly-hatched larvae climb upwards to locate food; if they are unsuccessful they will spin silk strands to be wind-blown (ballooning) to another tree. Early instar larvae feed during the day but the later instars feed at night, seeking sheltered spots to hide during the day. They may move between trees, especially if their original host tree is defoliated. Typically, larval development takes from six to eight weeks, with five instars in males, and six in females. Mature larvae seek protected spots for pupation, usually in crevices near the tree base, in the litter, or on rocks or structures, and emerge as adults about two weeks later.

Range of gypsy moth in Eurasia and eastern North America

The gypsy moth is native to most of Europe, northern Asia, Japan and China (Giese and Schneider 1979). In Europe, it occurs from the west coast to the Urals; extending north to a line from about central Sweden, east to Moscow, roughly corresponding to the northern limit of the range of oaks, its favoured hosts (Giese and Schneider 1979). In altitude it is found also as high as oaks will grow (Grijpma, 1989). The southern limit is in northern Africa and the islands of Corsica and Sardinia. Grijpma (1989) noted that gypsy moth is most abundant in the broadleaved forests of southern and southeastern Europe.

MATERIALS AND METHODS

We used several methods to predict the suitability of the regions of B.C. for establishment of gypsy moth, focusing on climatic parameters. First, we studied the climates in regions of Europe and Japan where the gypsy moth occurs, and those of neighbouring areas where it is absent, and compared them to the climates of British Columbia. We analysed the climatic limits in Eurasia with two-dimensional plots, and also used multivariate analyses. As well, we ran temperature-dependent models of gypsy moth development on climatic data from selected sites in B.C., to see whether gypsy moth can complete all its life stages in these climates.

Plotting of climatic limits

The gypsy moth ranges in Europe and Japan were extracted from the maps of Giese and Schneider (1979). Distribution records in Asia other than those of Japan were not considered to be reliable, so data for Asia were not included in the analysis. Climatic normals (30 year means) were obtained from Muller (1982) for stations in Europe, Japan, and North America, and from Environment Canada, Atmospheric Environment Service, for B.C. The normals for stations where gypsy moth occurs and those bordering on the range were plotted. Temperature and precipitation data for weather stations, in areas with and without gypsy moth, were plotted for comparison with B. C. weather stations.

Mapping of biogeoclimatic sub-zones

The biogeoclimatic classification system in British Columbia combines vegetation, soil, and climatic data to characterize forest and range ecosystems (Pojar *et al.* 1991). Climatic summaries (mean temperatures for warmest and coldest months, mean annual temperature, and mean annual precipitation) for biogeoclimatic sub-zones were matched with climatic limits for the gypsy moth as determined by Giese and Schneider (1979). Biogeoclimatic subzones with climatic characteristics where the gypsy moth might become established (precipitation >100 mm/year; mean Jan. temperature -18 to +12 °C; and mean July temperature +15 to +27 °C), and where the potential for outbreaks may exist (precipitation 250 - 1000 mm/year; mean Jan. temperature -18 to + 5 °C; mean July temperature +15 to + 23 °C), were plotted to outline potential climatic boundaries in B.C.

Discriminant functions

The above method can consider only two variables at a time, but climate is composed of many variables. We used discriminant functions to get a better idea of the multivariate influence of climate on the range of the gypsy moth. The discriminant function technique finds the best linear combination of variables for discriminating between two or more classifications, in this case the presence vs. absence of gypsy moth. The function can then be used to classify new observations, in this case sites in B.C. Variables used were Jan. and July mean monthly temperatures, average annual precipitation and temperature, July minus Jan. temperature (an index of continentality), and precipitation divided by July temperature (an index of dryness). The DISCRIM procedure of SAS was used (SAS Institute, 1985). The discriminant functions based on 139 European, Japanese and eastern North American stations in and around the current range of gypsy moth distribution were used to classify 55 sites in B.C. and the Pacific Northwest as to their climatic suitability for gypsy moth.

Life stage development modelling

The rate of growth of an insect depends on various factors, including food quality, population density, pathogen infection, and humidity (e.g. Lance *et al.* 1986, 1987), but temperature is the major determinant. As a minimum requirement for establishment, temperatures must be warm for long enough for the insect to complete all life stages from egg to adult. In B.C., climatic conditions vary considerably from the wet and cool coastal climate, to the hot and dry summers and cold winters of the interior. These temperature variations may define the potential range of the gypsy moth in B.C.

The timing of spring emergence is crucial because it is the starting point for the other stages. We predicted spring emergence using the biophysical model of Hunter (1993), which gave the most accurate prediction of hatch phenology in 3 out of 4 years of data from Quebec, out of three models tried (Hunter 1993). The program of Sheehan (1992) was used to simulate gypsy moth larval and pupal development.

We ran these models for Victoria, Vancouver, Castlegar, Williams Lake, Prince Rupert, Smithers, Prince George and Fort St. John. These sites had relatively complete

30-year weather records and are representative of east-west and north-south gradients in the province. The model was run for five years, chosen as follows: 1) The years with the lowest and highest average temperatures in the months Jan. to May were determined. Out of these, the years having the earliest and latest hatch were chosen based on the egg hatch model of Hunter (1993). 2) In addition, the years having the warmest and coldest average May temperatures were chosen, and 3) the year 1992, which was frequently among the warmest years, was chosen to give a standard across sites that was near to a best case for the gypsy moth. These years represented the best and worst years for gypsy moth development. Since the rate of development varies with host species, the model has several host plant options. We ran the model with all larvae feeding on red oak, a common Vancouver street tree. The rate of development on this host is slightly less rapid than on white oak, but more rapid than on most other hosts (Casagrande *et al.* 1987).

To validate the model, we compared predicted adult emergence times with available data on the timing of adult male moth catches in traps in the Vancouver area in 1991-1993, and in the east Fraser Valley in 1994. We used records of live moths found in detection traps by Agriculture Canada, with the assumption that moths would not survive for more than a few days once captured in a trap.

RESULTS

Plotting climatic limits

Plots of climate data showed that mean annual temperatures of 3 °C (Fig. 1) and Jan. temperatures of -15 °C (not shown) appear to limit the gypsy moth in the north. Only two stations with gypsy moth "present" had a mean July temperature below 15 °C (Brocken, Germany, and Botrange, Belgium; Fig. 2). The resolution of the maps of Giese and Schneider (1979) is not fine enough to determine whether or not these cold pockets (which are surrounded by warmer areas) actually have gypsy moth.

There are some areas where gypsy moth does not occur although it occurs at sites with similar climates (mean annual temperatures of 3 - 10 °C, Fig. 1; mean July temperatures of 15 - 18 °C, Figure 2). These sites are in the United Kingdom, Norway, Sweden and Finland, beyond the range of oaks, but within the ranges of aspen and alder which are potential hosts. The European distribution of gypsy moth closely matches the range limits of oaks. Most B.C. sites fall into this climatic range, in which the presence of oaks seems as important as climate. All of the sites in eastern North America with gypsy moth are within the same range of temperature and precipitation as the areas in Eurasia where gypsy moth occurs (Fig. 1 and 2). However, B.C. stations with low temperatures, and extremely high or low rainfall, are outside this range.

Few places receive as much precipitation as coastal B.C. (>1000 mm per year). Similar amounts occur on the Atlantic coast of Europe (Ireland and Norway), in some coastal areas of former Yugoslavia, and in Japan. The gypsy moth has not been recorded from Ireland or Norway. Outbreaks have occurred in Yugoslavia, but the resolution of Giese and Schneider's (1979) map is not high enough to determine whether these have occurred in the wet areas or in the dry Mediterranean climates of the coast. The gradient of precipitation is very steep in this area. Japan receives at least as much precipitation as coastal B.C. (Fig. 2), and the gypsy moth is present in the south of Japan, with outbreaks in the northwest and on Hokkaido. However, compared with coastal B.C. the climate in Japan is much warmer in the summer (Fig. 2), and oaks occur as important forest elements throughout the Japanese archipelago. Another difference is that this is the Asian strain of the gypsy moth, which has slightly different development rates and hosts.

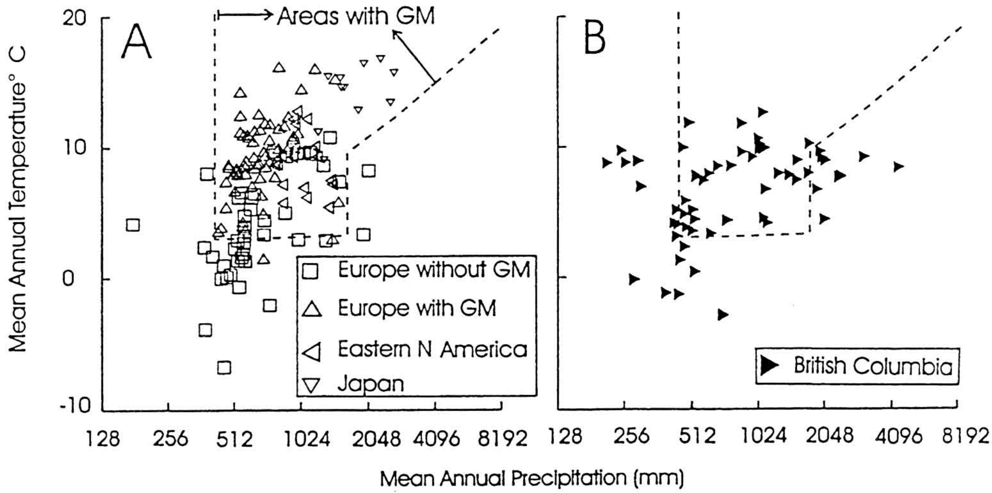

Figure 1. Annual mean temperature versus total precipitation for sites: A) with gypsy moth in Europe, Japan and North America, and without gypsy moth in Europe; and B) at 51 sites in British Columbia and 4 sites in the Pacific Northwest United States. The dashed line in A) encloses sites with gypsy moth in Europe, Japan, and North America (two cold outliers in Europe excepted, see text). The same lines have been superimposed on the data in B) for reference.

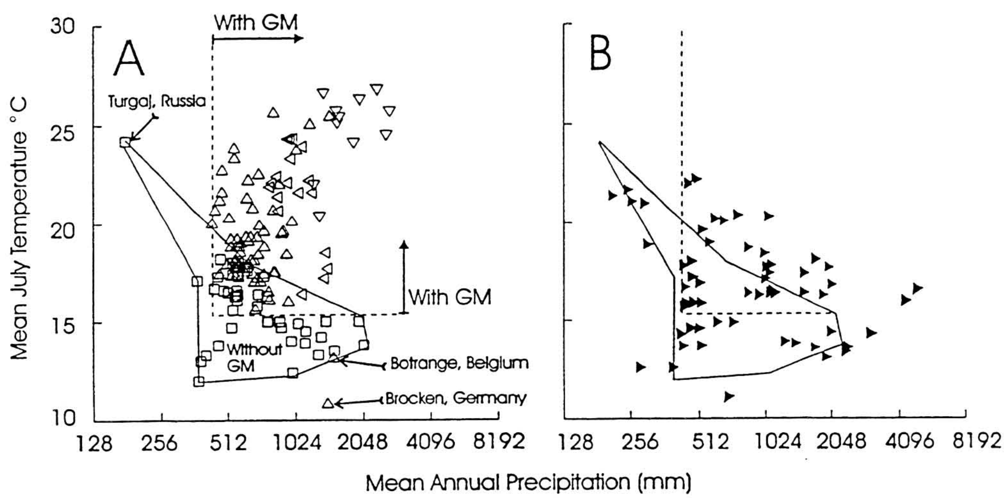

Figure 2. July mean temperature *vs* total precipitation for sites: A) with gypsy moth in Europe, Japan, and North America, and without gypsy moth in Europe; and B) at 51 sites in British Columbia and 4 sites in the Pacific Northwest United States. The solid line in A) encloses sites without gypsy moth in Europe. Areas with gypsy moth in Europe, Japan, and North America (two cold outliers in Europe excepted) are above and to the right of the dashed line. The same lines have been superimposed on the data in B) for reference.

Biogeoclimatic sub-zone

Figure 3 shows the results of mapping biogeoclimatic sub-zones with suitable climate based on Giese and Schneider's (1979) climatic limits for gypsy moth. This analysis shows that gypsy moth can establish in most of the southern part of British Columbia, with the exception of higher elevations and the wet coastal areas. Climatic conditions conducive to outbreaks exist in the Lower Mainland and the dry coastal areas immediately to the north of Vancouver, B.C. (the Sunshine Coast), the dry areas (east coast) of southern Vancouver Island, and the dry and warm valleys of the southern interior (Okanagan Valley and the Kootenay areas).

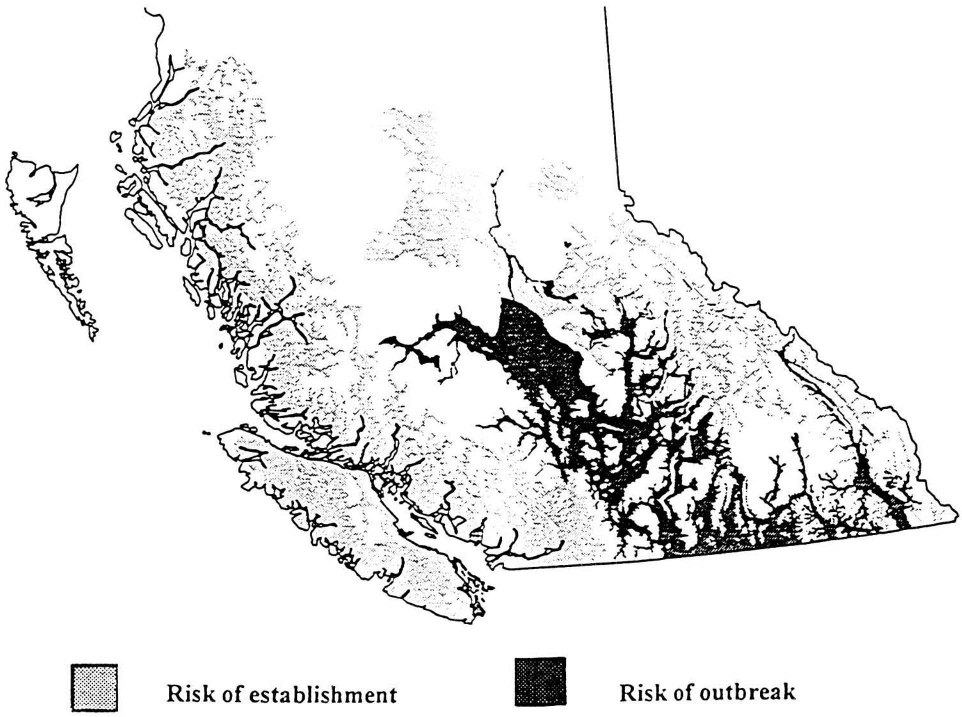

Figure 3. Areas at risk for establishment, or outbreak, respectively, of gypsy moth in B.C., based on plotting of biogeoclimatic subzones of B.C. and climatic range limits for the gypsy moth reported in the literature (Giese and Schneider 1979). Map courtesy of Forest Insect and Disease Survey, Pacific Forestry Centre, Canadian Forest Service, Victoria, B.C.

Discriminant function analysis

Discriminant function analysis showed that many areas of southern and central B.C. have climates very similar to those of Europe and Japan where gypsy moth is present (Fig. 3). Figure 4 shows a graphical representation of the results of this analysis, so that each weather station is represented as a dot, the size of which represents the discriminant function prediction of its climate's relative suitability for gypsy moth. In addition, Fig. 4 shows geographic locations where gypsy moth has been detected using pheromone trapping (triangles). Northern sites in B.C., and cool, wet sites of central and western B.C. are similar to sites in Europe that lack gypsy moth.

The functions misclassified 26 (17%) of the original 156 sites, including Brocken, Germany; Botrange, Belgium; and Turgaj, north of the Aral Sea in the former USSR

(Fig. 2). Thus, we can expect a similar error rate in B.C. Three of the four sites classified in the Pacific Northwest United States had a climate very suitable to gypsy moth. These were Medford, OR (similarity index of 0.99), Portland OR (0.96), and Seattle, WA (0.93). The fourth site (Tatoosh Island, at the extreme northwest tip of the Olympic Peninsula, WA) was classified as unsuitable (0.37).

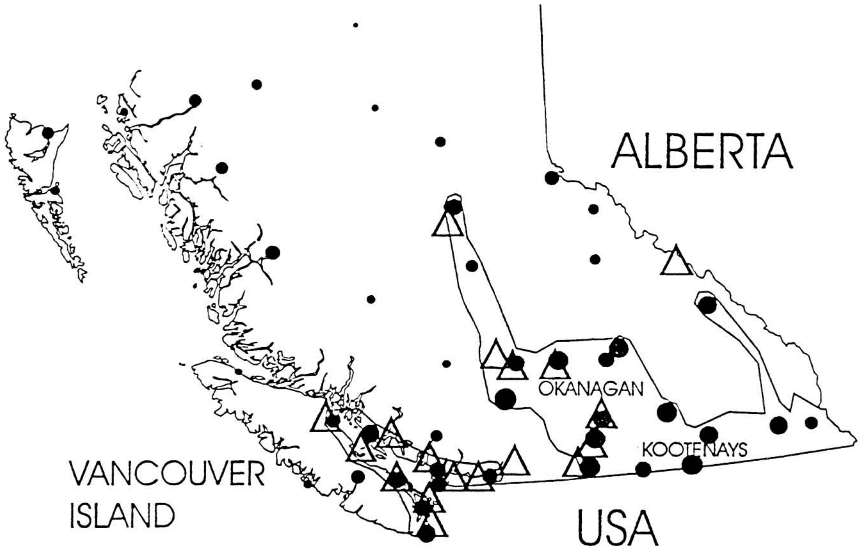

Figure 4. Graphical representation of the discriminant function analysis. Each weather station is represented by a dot, the size of which represents the discriminant function prediction of its climate's suitability for gypsy moth. The solid line encloses the subset of weather stations with climates very suitable for gypsy moth at lower elevations (cf. Figure 3, biogeoclimatic subzones with climate suitable for outbreaks). The triangles show locations where gypsy moth life stages have been found in B.C.

Life stage development modelling

Validation of Lower Mainland trap catch data. The models predict when adults emerge from pupae, and adults can be expected to live for several days. Thus, the actual catches can be expected to lag a couple of days or so behind the predicted emergence period. The model gave a remarkably good correspondence between predicted and observed phenologies, given that the flight time varies by up to a month among years, and considering the very small numbers of live moth catches (Table 1).

Ability to complete development. The temperature-dependent models predict that gypsy moth will be able to reach the adult stage in all years at the more southern locations, but not in every year in the northern ones. In northern B.C. few individuals complete development even in the warmest years (Table 2).

These models do not provide for the requirement that there must be sufficient warmth between the time that eggs are laid and winter begins for the embryos to develop into larvae. This is an additional constraint, so even if adults could emerge and mate in the fall, there may well be insufficient warmth for this embryonic development.

Table 1

Comparison of timing of catches of male gypsy moths found alive in traps on the Southern Mainland of British Columbia to predicted time of emergence of adults using 2 models (Sheehan 1992, Hunter 1993). Adults live for a few days after emergence.

		Period of gypsy moth flight	
Location	Year	Observed from trap catches	Predicted emergence
Vancouver	1991	7 Aug. - 4 Sept. (N=20)	5 Aug. - 31 Aug.
Vancouver	1992	9 July - 10 Aug. (N=26)*	17 July - 10 Aug.
Vancouver	1993	3 Aug. - 25 Aug. (N=13)	29 July - 24 Aug.
Chilliwack	1994	27 July, 5 Aug., 10 Aug. (N=3)	19 July - 12 Aug.
Hope	1994	3 Aug., 5 Aug. (N=2)	21 July - 14 Aug.

*One additional live moth was caught on 25 Aug.

Table 2

Predicted ability of gypsy moth to complete development at selected sites in B.C. in years with extreme climatic conditions and in 1992, which was among the warmest years at all sites. The table lists the most advanced stages attainable (A = Adult, P = Pupa), and the date when moths begin to emerge from pupae. All individuals did not necessarily achieve the most advanced stage before the onset of winter.

	Development Stage Reached and Date of First Flight in Year (with)				
Location	Coldest May	Warmest May	Earliest hatch	Latest hatch	1992
Victoria	A - Aug 28	A - Jul 20	A - Jul 22	A - Aug 27	A - Jul 22
Vancouver	A - Aug 28	A - Jul 10	A - Jul 29	A - Aug 28	A - Jul 17
Castlegar	A - Aug 3	A - Jul 22	A - Jul 14	A - Aug 2	A - Jul 14
Williams Lake	A - Oct 2	A - Sep 12	A - Aug 14	A - Sep 16	A - Aug 14
Smithers	P	A - Aug 12	A - Aug 30	A - Sep 25	A - Aug 31
Prince Rupert	P	A - Oct 8	A - Oct 8	P	P
Prince George	P	A - Aug 13	A - Aug 13	P	A - Aug 13
Fort St. John	P	A - Aug 21	P	P	A - Aug 21

In summary, Castlegar, Victoria, and Vancouver are suitable for complete development; Williams Lake, Smithers, and perhaps Prince George, are marginal; while Prince Rupert and Fort St. John would probably not permit complete gypsy moth development.

DISCUSSION

The results of the climatic analysis, the multivariate comparisons of the weather in European and Japanese sites, and the gypsy moth development models gave similar predictions: southern and central B.C. have climates suitable for the gypsy moth; northern areas, high elevations, and the cool, wet coastal areas are unsuitable. However, climate is not the only factor affecting the establishment of gypsy moth in B.C. Hosts are important, and the largely coniferous forests of B.C. may be quite resistant. Our analyses indicate that gypsy moth may not become established where there are no oaks, even if the climate is suitable, as seems to be the case in north-western Europe. The only native oak in B.C., Garry oak or western white oak (*Quercus garrayana*), is limited to the Gulf Islands and southeastern coastal Vancouver Island from the southern tip to Comox, plus two small patches in the lower mainland (Lyons 1991). Ornamental oaks are common in urban and suburban areas, where introductions are most likely to occur.

Areas in the southern mainland, eastern Vancouver Island and Gulf Islands with preferred hosts and suitable climate and large numbers of people moving through them are probably at the greatest risk for gypsy moth establishment. Most catches of gypsy moth have been made in these areas (Figure 4). This pattern is also evident in Oregon and Washington: most catches are made in suburban areas or places with a large component of oak (Dreistadt and Dahlsten 1989).

We have included areas in Japan in the climatic analysis, although the Asian strain of the gypsy moth probably has different thermal requirements. We included these areas because it is more conservative to do so than to exclude them; including them gives the gypsy moth a larger potential range. However, the models of development are based on the European strain only.

Some other influences not examined here are: synchrony with plant phenology; negative effects of rain after hatch; and freezing after the breaking of winter dormancy. Gypsy moth larvae emerge from winter dormancy around the time of leaf emergence of oaks (Hunter and Lechowicz 1992; Hunter 1993). New foliage is preferred, since it is higher in nitrogen and water, and less tough (Hunter and Lechowicz 1992). Emergence at the correct time is important because there is a brief window between budburst and the time when foliage becomes unacceptable. Gypsy moth host-seeking activities (crawling up tree trunks, ballooning) are inhibited by cool and wet weather (Leonard 1971). Phenological models for tree budburst have not been developed for hardwoods of the Pacific Northwest, and there are few data on budburst for B.C., so we could not test whether gypsy moth would be well synchronized with leaf emergence in this region. Preliminary analyses using tree phenology models from eastern North America which we applied to climatic data from B.C. indicated good synchrony (Hunter, unpublished). However winter dormancy is the least well understood life stage of the gypsy moth and of the host trees. New models are being developed that encompass the entire diapause period and should yield better predictions of gypsy moth emergence times (Gray *et al.* 1991). However, using a "pre-release" version of this new model altered hatching dates by only one or two days, if at all, and did not have a dramatic impact on the predictions here (Hunter, unpublished).

Some further research may be worthwhile on host suitability for the most common B.C. forest and urban trees. Development rates are often slower on hosts other than oak, so the interaction between climate and host needs to be considered, particularly in marginal areas where the time available for development is limited. Also, although gypsy moth can survive on many species in the lab, they may avoid feeding or do much more poorly on these hosts in the field. This may be due to factors such as: unacceptably low quality of foliage during the host-seeking stage (Hunter and Lechowicz 1992); differential susceptibility to disease (Keating and Yendol 1987); mortality from predators on hosts where growth is slow, and lack of suitable day-time resting sites (Liebhold *et al.* 1986).

This is not the first effort to predict where gypsy moth will be able to establish. Giese and Schneider (1979) developed climatic limits in Europe and Asia using a cartographic comparison between isotherms and isohyets with the range of gypsy moth. Allen *et al.* (1993) developed predictions for Florida and for the entire world. Their world predictions, based on climate matching, seemed to indicate the potential for establishment of gypsy moth in southwestern B.C., but not northern Vancouver Island or Prince Rupert, and thus matched our more detailed projections for B.C. Sullivan and Wallace (1972) examined the cold tolerance of overwintering gypsy moth eggs. They found that eggs can withstand several weeks exposure to -18 °C, and a few days below -24 °C with no reduction in survival. Snow cover provides effective insulation for egg masses laid close to the ground, so they can survive much lower air temperatures. Sullivan and Wallace (1972) predicted that the distribution of host plants would be more significant in determining northern range limits than would low winter temperatures. The range of the gypsy moth in eastern North America is apparently still expanding northward in Ontario (but not in Quebec, as far as is known) and it remains to be seen whether they will persist beyond the range of oaks.

In B.C. the most vulnerable area will be the range of Garry oak. Since this area is already threatened by urbanization, and Garry oak populations are declining, the potential impact of gypsy moth, should it establish itself there, is of great concern. Monitoring and education of landowners should be greatest in this area.

Two additional areas are of less certain susceptibility to gypsy moth. The southern mainland has suitable climates, particularly in the drier parts, and a variety of ornamental hardwoods that may provide suitable hosts. However, gypsy moth populations may not be able to persist in urban settings with little input from surrounding continuous hardwood forests. For persistence, Allen *et al.* (1993) estimated that a gypsy moth population requires a minimum patch size of 1.06 km diameter of continuous, suitable forest. Diffusion from smaller patches would be greater than reproduction within the patch, so populations would decline. In any case, in urban and suburban areas, gypsy moth would mostly be a "picnic problem" and is unlikely to threaten forestry or conservation. The other suitable areas, the dry interior valleys, should be monitored carefully, although lack of favoured hosts and spraying in orchards are likely to limit the impact of the gypsy moth.

We hope that these predictions will provide a useful guideline for determining areas where monitoring and protection efforts should be concentrated.

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