Herbivorous insects and global change: potential changes in the spatial distribution of forest defoliator outbreaks

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Abstract. The geographical ranges and the spatial extent of outbreaks of herbivorous species are likely to shift with climatic change. We investigated potential changes in spatial distribution of outbreaks of the western spruce budworm, Choristoneura occidentalis Freeman, in Oregon, U.S.A. and the gypsy moth, Lymantria dispar (L.), in Pennsylvania, U.S.A. using maps of historical defoliation, climate and forest composition in a geographic information system. Maps of defoliation frequency were assembled using historical aerial reconnaissance data. Maps of monthly means of daily temperature maxima and minima and of monthly precipitation averaged over 30 years were developed using an interpolation technique. All maps were at a spatial resolution of $2 \times 2$ km. Relationships between defoliation status and the environmental variables were modelled using a linear discriminant function. Five climatic change scenarios were investigated: an increase of 2°C, a 2°C increase with an increase of 0.5 mm per day in precipitation, a 2°C increase with an equivalent decrease in precipitation, and equilibrium projections of temperature and precipitation by two general circulation models (GCMs) at doubled CO2. With an increase in temperature alone, the projected defoliated area decreased relative to ambient conditions for the budworm and increased slightly for the gypsy moth. With an increase in temperature and precipitation, the defoliated area increased for both species. Conversely, the defoliated area decreased for both when temperature increased and precipitation decreased. Results for the GCM scenarios contrasted sharply. For the Geophysical Fluids Dynamics Laboratory model, defoliation by budworm was projected to cover Oregon completely, whereas no defoliation was projected by gypsy moth in Pennsylvania. For the Goddard Institute for Space Studies model, defoliation disappeared completely for the budworm and slightly exceeded that under ambient conditions for the gypsy moth. The results are discussed in terms of potential changes in forest species composition.

Key words. Choristoneura occidentalis, Lymantria dispar, climatic change, insect outbreaks, geographic information system, discriminant analysis.

INTRODUCTION

Global mean annual temperatures are expected to rise as much as 3°C by the end of the 21st century as a result of anthropogenic increases in greenhouse gases (Houghton, Jenkins & Ephraums, 1990). A temperature change of such magnitude, with accompanying changes in precipitation, will have profound consequences for ecosystems, potentially affecting their compositions, functions and geographical distributions (Peters & Lovejoy, 1992; Kareiva, Kingsolver & Huey, 1993). As ecosystems change, herbivorous insects will be subject to indirect effects of climatic change on the trophic levels above and below, as well as to direct effects (Porter, Parry & Carter, 1991; Cammell & Knight, 1992). Acting together, these direct and indirect effects will affect the development, survival, reproduction and movement of insect populations, and changes in these life history parameters will have consequences for population dynamics that are difficult to anticipate. Climatic change may alter the temporal and spatial dynamics of outbreak species, changing the frequency of outbreaks and their spatial patterns, size and geographical range.

Speculations on the effects of climatic change on the spatial dynamics of insect species have been quite general to date; populations are expected to extend their ranges to higher latitudes and elevations as the climate warms (Porter et al., 1991; Sutherst, 1991). With increased overwintering survival, higher population growth rates and a longer growing season, outbreak areas of pest species are likely to shift.
in latitudinal range and may expand. Given this general hypothesis, we investigated potential changes in spatial pattern and extent for two outbreak species of forest defoliators, the western spruce budworm, *Choristoneura occidentalis* Freeman, and the gypsy moth, *Lymantria dispar* (L.), under several climatic change scenarios. To do so, we created detailed maps of outbreak areas, climatic variables and susceptible forest types with a geographic information system (GIS) and then estimated a functional relationship between outbreaks and the environmental variables. We used this relationship to extrapolate spatial redistributions of outbreak areas under several climatic change scenarios.

**METHODS**

**Development of maps**

Defoliation data were assembled, collated and analysed using IDRISI, a raster-based GIS (Eastman, 1989). Base maps of state boundary coordinates were used to define the study areas in Oregon in the northwestern United States and Pennsylvania in the northeastern United States. A grid cell size of 2 × 2 km was selected as standard for all map layers in the GIS because it represents the minimum dependable spatial resolution of the defoliation data. Each map layer comprised 240 × 327 cells in Oregon and 154 × 297 cells in Pennsylvania.

Defoliation was monitored annually in Oregon during 1947–79 and in Pennsylvania during 1969–89 using aerial sketch maps. Maps of western spruce budworm defoliation were sketched during low-level flights over forested areas of Oregon in July and August when defoliation was easily detected (Dolp, 1980). Maps of gypsy moth defoliation were made during flights over Pennsylvania in late July at peak defoliation. Thirty per cent defoliation was the lower threshold detectable from the air (Liebhold et al., 1994). When the cause of defoliation was in doubt, the presence of the pest species was verified on the ground. Annual maps of budworm defoliation were obtained from Dolp (1980), and those for gypsy moth were provided by the Pennsylvania Department of Environmental Resources (Liebhold et al., 1994).

A GIS allows investigation of multiple map layers, each of which is coordinated to the rest by means of georeference points. To create a uniform set of geographically referenced defoliation data, the annual maps were first transferred to mylar stable-base sheets. The maps were then scanned using a digital scanner at a resolution of 150 dots per inch. At least four georeference points were located accurately on intersections of state or county boundaries. The transformation of each map layer to a common base map resolution and projection was achieved through ‘rubber-sheeting’, a process by which a map is stretched mathematically to fit a base map given a set of common georeference points whose locations are defined on both maps (Antenucci et al., 1991).

Our basic data were defoliation frequency for individual grid cells. Because consistent measurements of defoliation intensity were lacking, annual defoliation was coded as a simple binary classification (i.e. 0 for undefoliated, 1 for defoliated). Frequency maps were created by overlaying the annual maps, adding up defoliation values for coincident grid cells and dividing the sum by the number of maps. For the budworm data, frequency for a single grid cell was computed by adding the annual values and dividing the sum by 33. For the gypsy moth data, a uniform computation of frequency was impossible because populations were not present throughout Pennsylvania from 1969–89. The gypsy moth, an invading species that was introduced into the United States in the 19th century, slowly extended its range southwestward across the state during this period (Liebhold, Halverson & Elmes, 1992). Therefore, the number of years used as the divisor in computing frequency varied among counties depending upon the length of time that each was at risk to defoliation (Liebhold et al., 1994). Western Pennsylvania was not included in the analysis because it was at risk for less than 10 years, and frequency computed over such a short period would probably be inaccurate.

Climatic data were 30-year averages of monthly means of daily temperature maxima and minima and of total monthly precipitation estimated at 1 km² grid cells (Russo, Liebhold & Kelley, 1993). Values were interpolated from averages for each variable over the period 1961–90 at weather stations across each state from climatological data published by the National Climatic Data Center (1990). Temperature data were obtained from 147 stations in Oregon and eighty-five stations in Pennsylvania, while precipitation data came from 170 stations in Oregon and 161 stations in Pennsylvania. The latitude, longitude and elevation of each station were obtained from the 30-second point elevation data published by the National Geophysical Data Center (U.S. Geological Survey, 1990). A multiple regression analysis was used to fit a linear model of each climatic variable as a function of latitude, longitude and elevation. Finally, the multiple regression equations were used to interpolate values of the variables for all map cells using their latitudes, longitudes and elevations as input (Russo et al., 1993). Rubber-sheeting was used to transform the climatic maps into the same registration as the defoliation map.

Forest type information came from a map published in Eyre (1980) that was digitized into the GIS. Many forest types were present in each state, and most had some defoliation by the pest species. For the western spruce budworm analysis, we extracted and combined maps of the Douglas fir, fir–spruce, larch and ponderosa pine forests, which are susceptible to defoliation (Carolin, 1987). Similarly, we combined maps of the oak–hickory and oak–pine forests for use in the gypsy moth analysis (Liebhold et al., 1994). Maps showed the presence or absence of susceptible forest types. They were transformed by rubber-sheeting to the same registration as the defoliation maps.

**Discriminant analysis**

We looked at potential changes in spatial distribution of outbreaks qualitatively, investigating changes in the simple presence or absence of defoliation and not in frequency.
Thus, we simplified each defoliation frequency map for analysis to one with grid cells that were never defoliated over the course of the study (i.e. defoliation state = 0) and those that were defoliated at least once (state = 1) (Fig. 1a, b).

A functional relationship between defoliation state and the environmental variables is necessary to extrapolate the effects of climatic change to changes in outbreak area. Discriminant analysis provides a powerful tool for separating data that are grouped in distinct classes (Manly, 1986). For binomial data such as ours, the analysis estimates a single function of the form Z:

\[ Z = a_1X_1 + a_2X_2 + \ldots + a_pX_p \]

in which the canonical variable, Z, is a linear combination of several independent variables, \( X_i \). This function is estimated such that it maximizes the ratio of the variation between the two groups to that within (Manly, 1986). An observation is classified into a group depending upon the distance and relationship of its Z value to the two group means. The discriminant function is especially useful for summarizing the effects of variables that are collinear, such as climatic variables (Johnston, 1978).

With up to thirty-seven variables available, we wanted to include only those most significant. To do so, we used a stepwise procedure that chose, at each successive step, that variable with the highest value of the likelihood ratio among those remaining.

**Extrapolation of climatic change effects**

Having estimated a linear discriminant function, we modified it to extrapolate climatic change effects as follows:

\[ D = a_1(T_1 + \Delta T_1) + a_2(T_2 + \Delta T_2) + \ldots + b_1(P_1 + \Delta P_1) + \ldots + CF \]

where D is the canonical variable for defoliation, \( T_i \) are the temperature variables, \( \Delta T_i \) are temperature changes for a climatic change scenario, \( P_i \) are the precipitation variables, \( \Delta P_i \) are precipitation changes and F is forest type. Using this relationship, we reclassified each grid cell, inserting ambient values and change values for the climatic variables. Climatic change was assumed to apply uniformly across each state; thus, the same change value for each variable was applied to every grid cell. Note that the forest type was not changed in these projections.

Climatic change scenarios included outputs of two general circulation models (GCMs): the Goddard Institute for Space Studies (GISS) (Hansen et al., 1983) and Geophysical Fluids Dynamics Laboratory (GFDL) (Manabe & Wetherald, 1987) models. The GCMs projected equilibrium changes in monthly temperature and precipitation after 100 years at doubled CO\textsubscript{2} levels. Besides using the
rather extreme GCM scenarios, we explored the range of responses in outbreak areas with smaller climatic changes. Additional scenarios included one with an increase in 2°C without change in precipitation and two others with a 2°C increase accompanied by an increase and a decrease of 0.5 mm precipitation per day.

RESULTS AND DISCUSSION
Discriminant analyses

The discriminant analysis for western spruce budworm defoliation produced a function of twenty-eight variables. The first six variables to enter the analysis, in descending order, were November minimum temperature, forest type, February minimum, January minimum, October precipitation and March precipitation. Mean daily minimum temperatures and monthly precipitation predominated. The only consistent relationship between defoliation and the climatic variables was for precipitation; canonical coefficients were positive in sign for August–December and negative for the other months. The squared canonical correlation (similar to the $r^2$ of a regression analysis) was 0.39. The discriminant function was highly significant (likelihood ratio = 0.627, $P = 0.0$, $n = 61809$) and classified 88.7% of the grid cells correctly. The function somewhat over predicted defoliation; 14% of all cells were actually defoliated, whereas 19.9% were classified as defoliated. The discriminant function fit the observed defoliation well (Fig. 1). Cells classified as defoliated were primarily in northeastern Oregon (1c), as were those observed (1a).

The analysis for gypsy moth produced a discriminant function of six variables. Forest type was chosen first by the stepwise procedure and explained over two-thirds of the variation in defoliation. Climatic variables entered next in the following order: April maximum temperature, September minimum, June precipitation, March minimum and September maximum. At 0.18, the squared canonical correlation was considerably less than that for the budworm analysis. However, this discriminant function also was highly significant (likelihood ratio = 0.822, $P = 0.0$, $n = 24952$) and classified 69% of the grid cells correctly. This model also overestimated defoliation; 49% of cells were actually defoliated, but 62.8% were classified as such. The areas classified as defoliated were similar to those observed and located primarily in the Allegheny Mountains of Pennsylvania (Fig. 1b, d).

Although both were highly significant, the discriminant analyses were very different in the number of variables included and the overall goodness of fit. These differences were probably a result of differences in climatic variability; temperature and precipitation were considerably more variable in Oregon than in Pennsylvania. For example, average annual precipitation over 30 years varied from 83–2474 mm across Oregon, but only from 1000–1204 mm in Pennsylvania. Such wide variation in Oregon probably enhanced the fit of the discriminant function.

In using a stepwise analysis, we sought a discriminant model to provide the best possible fit to the available climatic data. Thus, we did not select specific climatic variables a priori that might be important in explaining defoliation patterns and those selected are not necessarily ecologically relevant. Nevertheless, western spruce budworm defoliation was well correlated with climatic factors. Among the first three variables to enter the model were minimum temperature in November and February, which were inversely related to defoliation. Kemp, Everson & Wellington (1985) also reported an inverse relationship between budworm defoliation and fall and winter temperatures in the northwestern United States. The budworm hibernates during this period (Carolin, 1987) and increased temperature appears to reduce overwintering survival (Kemp et al., 1985). In addition, a consistent association between defoliation and precipitation was apparent; defoliation was correlated positively with precipitation during August–December and negatively otherwise. Average precipitation in Oregon increases during August–December and decreases during the rest of the year. Because larvae feed actively from May into July (Carolin, 1987), the inverse relationship between defoliation and precipitation during these months may reflect the effects of drought stressed host trees in promoting outbreaks (Mattson & Haack, 1987).

Early spring temperatures were important factors in gypsy moth defoliation. Defoliation was directly proportional to maximum temperature in April, during which period egg hatch often begins in Pennsylvania. Similarly, in a time series analysis of defoliation records from Connecticut and Massachusetts, Miller, Mo & Wallner (1989) reported defoliation to be directly related to daily maximum temperature in early April and daily minimum temperature during mid-April–mid-May. Defoliation in our study was inversely related to minimum temperature in March, suggesting that warm weather too early in spring may reduce the survival of eggs, perhaps through inducing hatch before host budbreak.

Climatic change effects

In the results that follow, areas projected as defoliated under the climatic change scenarios are compared with the areas classified as defoliated under ambient conditions (Figs 2a, 3a). For the analysis of budworm defoliation, an increase of 2°C without change in precipitation resulted in a decrease of the projected area defoliated to less than half that under ambient conditions (Table 1). Defoliation was confined to northeastern Oregon (Fig. 2b). When both temperature and precipitation increased, the projected area defoliated spread southwestward and increased 1.35 times over the area under ambient conditions (Fig. 2c). Conversely, a decrease in precipitation with increasing temperature resulted in a reduction of the area defoliated to a small area in northeastern Oregon (Fig. 2d).

An increase in temperature alone in Pennsylvania resulted in a slight increase in gypsy moth defoliation over that under ambient conditions (Table 1, Fig. 3a, b). Trends in projected defoliation with increased temperature and changed precipitation were qualitatively similar to those for the budworm. With the addition of 0.5 mm precipitation, the defoliated area increased relative to that with a simple

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FIG. 2. Potential outbreak areas of western spruce budworm in Oregon under climatic change scenarios. (a) Ambient temperature and precipitation. (b) 2°C increase. (c) 2°C increase with 0.5 mm precipitation per day increase. (d) 2°C increase with 0.5 mm precipitation per day decrease. (e) GISS model. (f) GFDL model.

because of their rapid reproduction and dispersal. In contrast, the response time of change in forest range may be on the order of centuries because trees are long-lived and their populations migrate slowly. Our projections represent distributions of defoliation that will be attained after a long period, probably in the same temporal range as the GCMs, which predict changes over 100–200 years. They represent the end points of change under the constant conditions of a scenario and give no indication of the transient distributions that may result from processes at shorter time scales.

It must be stressed that forest type was not changed in producing the defoliation projections. However, the changes in area of projected defoliation are interpreted in the following as due in part to possible changes in susceptible forest type. The general changes in geographical distribution of defoliation (Figs 2, 3) were increases and decreases relative to the current distributions of susceptible forest types. When the projected areas of defoliation were smaller than the current range of susceptible forest types, the projections probably resulted from both processes. For example, the restricted range of budworm defoliation under increased temperature (Fig. 2b) may have resulted from a shift in range of the budworm to higher elevation, a decrease in range of the susceptible forest types, or a combination of the two processes. On the other hand, expansion of the projected area beyond the current geographical range of susceptible forest (e.g. Figs 2c, 3c) must always involve at least an increase in range of the susceptible forest. Because range changes in susceptible forest types are a generally important component in explaining changes in the geographical distribution of defoliation, we consider the projections in more detail in this context. Under an increase in temperature alone, the area defoliated by the budworm decreased compared with areas defoliated under ambient conditions (cf. Fig. 2a, b). As temperature increases the potential growth and metabolism of plants increases, evapotranspiration increases and water availability becomes increasingly limiting. Franklin et al. (1992) projected large losses of forest area to juniper savanna, sagebrush steppe and grassland in Oregon under temperature changes of 2.5°C and 5°C without any change in precipitation. With reduced precipitation and increased temperature, our defoliation projections decreased appreciably in both Oregon and Pennsylvania (Figs 2d, 3d), presumably as a result of a further loss of forest area. Accepting this interpretation, many forested areas of Oregon may become savanna, steppe or grassland if temperature increases and precipitation decreases. Conversely, defoliated area increased with an increase in precipitation (Figs 2c, 3c). The increase was substantial in Oregon, suggesting that some of the central region, which is currently steppe, may potentially become forested with species susceptible to budworm. Using the GISS and GFDL scenarios, which project temperature increases more extreme than 2°C, Davis & Zabinski (1992) predicted potential ranges for four tree species currently found in Pennsylvania. In all cases, ranges shifted hundreds of kilometres northward and partially or completely out of the state.

Changes in defoliation by budworm projected under the two GCM scenarios were at opposite extremes. The GISS

scenario projected no defoliation (Fig. 2e), whereas the GFDL projected defoliation over the entire state (Fig. 2f). This was surprising given the apparently small differences in the seasonal averages of the climatic variables; temperature increased 4°C on average in the GFDL scenario and 5°C in the GISS, whereas precipitation increased by 0.42 mm and 0.63 mm per day, respectively. Like the scenario with small increases in temperature and precipitation (Fig. 2c), the combination of climatic factors in the GFDL presumably favoured a long-term increase in area of susceptible forest. In contrast, an average temperature increase of about 1°C in the GISS scenario with a small increase in precipitation resulted in a complete loss of defoliation in Oregon.

The trends for gypsy moth defoliation under the GCM scenarios were almost opposite those for budworm. Under the GISS scenario, the projected area of gypsy moth defoliation increased by about 6% over that under ambient conditions.

FIG. 3. Potential outbreak areas of gypsy moth in Pennsylvania under climatic change scenarios. (a) Ambient temperature and precipitation. (b) 2°C increase. (c) 2°C increase with 0.5 mm precipitation per day increase. (d) 2°C increase with 0.5 mm precipitation per day decrease. (e) GISS model. (f) GFDL model.

TABLE 1. Percentages of total areas and absolute areas of Oregon and Pennsylvania, U.S.A., projected as defoliated by western spruce budworm and gypsy moth, respectively, under five climatic change scenarios.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Oregon</th>
<th></th>
<th>Pennsylvania</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>km²</td>
<td>%</td>
<td>km²</td>
</tr>
<tr>
<td>Ambient temp. and precip.</td>
<td>19.9</td>
<td>49948</td>
<td>62.8</td>
<td>55182</td>
</tr>
<tr>
<td>Increase 2°C</td>
<td>7.7</td>
<td>19263</td>
<td>64.5</td>
<td>56676</td>
</tr>
<tr>
<td>Increase 2°C, + 0.5 mm/day</td>
<td>26.9</td>
<td>67561</td>
<td>77.7</td>
<td>68275</td>
</tr>
<tr>
<td>Increase 2°C, − 0.5 mm/day</td>
<td>0.9</td>
<td>2312</td>
<td>30.1</td>
<td>26449</td>
</tr>
<tr>
<td>GISS model</td>
<td>0.0</td>
<td>0</td>
<td>68.7</td>
<td>60367</td>
</tr>
<tr>
<td>GFDL model</td>
<td>100.0</td>
<td>251181</td>
<td>0.0</td>
<td>0</td>
</tr>
</tbody>
</table>

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conditions (Table 1, Fig. 3e), whereas no defoliation was projected under the GFDL scenario (Fig. 3f). Because temperatures were similar between the GCMs, the difference probably resulted from summer precipitation, which was considerably lower in the GFDL scenario for Pennsylvania than was that in the GISS scenario.

In conclusion, differences in projected defoliation among the scenarios were generally large given the relatively small changes in the climatic variables. Our results highlight the need for greater accuracy in projections of climatic change, such as those derived from GCMs, if they are to be useful in predicting effects on insect populations. Our results suggest profound changes for forest landscapes and the insect populations that inhabit them as the climate changes in the not-too-distant future.

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REFERENCES


