

# Forest Defoliators and Climatic Change: Potential Changes in Spatial Distribution of Outbreaks of Western Spruce Budworm (Lepidoptera: Tortricidae) and Gypsy Moth (Lepidoptera: Lymantriidae)

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**ABSTRACT** Changes in geographical ranges and spatial extent of outbreaks of pest species are likely consequences of climatic change. We investigated potential changes in spatial distribution of outbreaks of western spruce budworm, *Choristoneura occidentalis* Freeman, and gypsy moth, *Lymantria dispar* (L.), in Oregon and Pennsylvania, respectively, using maps of historical defoliation, climate, and forest type in a geographic information system. Maps of defoliation frequency at a resolution of  $2 \times 2$  km were assembled from historical aerial survey data. Weather maps for mean monthly temperature maxima and minima and precipitation over 30 yr were developed by interpolation. Relationships between defoliation status and environmental variables were estimated using linear discriminant analysis. Five climatic change scenarios were investigated: an increase of 2°C, a 2°C increase with a small increase and a small decrease in precipitation, and projections of two general circulation models (GCMs) after 100 yr at doubled carbon dioxide. With an increase in temperature alone, the projected defoliated area decreased relative to ambient conditions for budworm and increased slightly for gypsy moth. With an increase in temperature and precipitation, defoliated area increased for both species. Conversely, defoliated area decreased for both when temperature increased and precipitation decreased. Results for the GCM scenarios contrasted sharply. For one GCM, defoliation by budworm was projected to cover Oregon completely, whereas no defoliation was projected by gypsy moth in Pennsylvania. For the other, defoliation disappeared completely for budworm and slightly exceeded that under ambient conditions for gypsy moth. The results are discussed in terms of current forest composition and its potential changes.

**KEY WORDS** *Choristoneura occidentalis*, *Lymantria dispar*, climatic change

GLOBAL MEAN ANNUAL temperatures are expected to rise as much as 3°C by the end of the next century as a result of anthropogenic increases in greenhouse gases (Houghton et al. 1990). Such an increase in temperature, with accompanying changes in precipitation, will have profound consequences for ecosystems, potentially affecting their compositions, functions, and geographical distributions (Peters & Lovejoy 1992, Kareiva et al. 1993). In this context, 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 et al. 1991, Cammell & Knight 1992). Acting together, such 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 predict. Climatic change may alter the dynamics of outbreak species in time and

space, changing the frequency of outbreaks and their spatial patterns, size, and geographical range.

Current speculations on the effects of climatic change on the spatial dynamics of insect species are very general; populations are expected to extend their ranges to higher latitudes and elevations as the climate warms (Porter et al. 1991, Sutherst 1991). With higher overwintering survival, increased population growth rates, and a longer growing season, outbreak areas of some species are likely to shift in latitudinal range and may increase in size. Given this general hypothesis, we investigated potential changes in spatial pattern and extent in detail 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. In this study, we took an empirical approach, creating detailed maps of outbreak areas and climate patterns with a geographic information system (GIS) and then estimating a functional relationship between outbreaks and cli-

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matic variables. We used this relationship to extrapolate spatial redistributions of outbreak areas under several climatic change scenarios.

### Materials and Methods

**Map Development.** Defoliation data were assembled, collated, and analyzed using the IDRISI geographic information system (Eastman 1989). IDRISI is a raster-based GIS for capturing, storing, analyzing, and displaying geographical data. Base maps of state boundary coordinates were used to define the study areas in Oregon in the northwestern United States and in Pennsylvania in the northeastern United States. A  $2 \times 2$  km grid cell size was selected as standard for all map layers in the GIS because it represented the minimum dependable spatial resolution of the defoliation data. Each map layer comprised  $240 \times 327$  cells in Oregon and  $154 \times 297$  cells in Pennsylvania.

Defoliation was monitored annually in Oregon during the period 1947–1979 and in Pennsylvania during 1969–1989 using aerial sketch maps. Maps of western spruce budworm defoliation were sketched during a series of low-level reconnaissance flights over forested areas of Oregon in July and August when defoliation was easily detected (Dolph 1980). Maps of gypsy moth defoliation were sketched during flights over all of Pennsylvania in late July when defoliation was at its peak. Thirty percent defoliation was considered the lower threshold for detection from the air (Liebhold et al. 1994). When the cause of defoliation was questionable, the presence of pest life stages was verified on the ground. Annual maps of defoliation by western spruce budworm were obtained from Dolph (1980), and those for gypsy moth were provided by the Pennsylvania Department of Forest Resources (Liebhold et al. 1994).

Because procedures varied among regions and years, some errors in mapping were inevitable. Spatial errors are generated unavoidably in recording defoliation on sketch maps from aircraft (Talerico 1981); errors occur with respect to the exact location, degree, and areal extent of defoliation. In general, such errors are probably less than 1 km in magnitude (Talerico 1981). The relatively coarse resolution used for the data (i.e.,  $2 \times 2$  km) was intended to minimize such fine-scale spatial errors.

A GIS allows investigation of multiple layers of geographical data (i.e., 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. One inch represented 92 km on the Oregon maps and 50 km on the Pennsylvania maps. Use of relatively large grid cells (i.e.,  $2 \times 2$  km) and a fine scanner resolution minimized scanning error. Binary TIFF files from the scanner were converted to ASCII

files and saved as map layers in the GIS. 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*. Rubber-sheeting is a process by which a map is mathematically stretched to fit a base map given a set of common georeference points whose locations are defined on both maps (Antenucci et al. 1991).

In the analysis that follows, the 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 summing the annual values and dividing the total by 33. For the gypsy moth data, a uniform computation of frequency across Pennsylvania was not possible because populations were not present in all parts of the state from 1969 to 1989. The gypsy moth, an invading species that was accidentally introduced into the United States in the nineteenth century, slowly extended its range southwestward across the state during that period (Liebhold et al. 1992). Thus, the number of years used as the divisor in computing frequency varied among counties depending upon the length of time that each was potentially at risk to defoliation (Liebhold et al. 1994). The western part of Pennsylvania was not included in the analysis because it was at risk for <10 yr, and frequency computed over such a short period likely would be inaccurate because of the discontinuous spatial and temporal distributions of defoliation.

Climatic data were obtained from ZedX (Boalsburg, PA). The data were 30-yr averages of monthly means of daily temperature maxima and minima and of total monthly precipitation estimated at 1-km<sup>2</sup> grid cells (Russo et al. 1993). Values were interpolated from averages for each variable over the period 1961–1990 at weather stations across each state from the *Climatological Data* series published by the National Climatic Data Center (1990). Temperature data were obtained from 147 stations in Oregon and 85 in Pennsylvania, and precipitation data came from 170 stations in Oregon and 161 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 carried out to fit a linear model of each climatic variable as a function of latitude, longitude, and elevation at each station. Finally, the multiple regression equations were used to interpolate values of the variables for all grid cells using their latitudes, longitudes, and elevations as

**Table 1.** Proportions of area defoliated by western spruce budworm in Oregon in seven forest types (Eyre 1980)

Forest type	Proportion defoliated
Ponderosa pine	0.317
Fir-spruce	0.125
Douglas fir	0.102
Larch	0.059
Lodgepole pine	0.022
Pinyon-juniper	0.022
Nonforested	0.352

**Table 2.** Proportions of area defoliated by gypsy moth in Pennsylvania in six forest types (Eyre 1980)

Forest type	Proportion defoliated
Oak-hickory	0.788
Maple-beech-birch	0.120
Oak-pine	0.042
Pine	0.008
Aspen-birch	0.002
Nonforested	0.040

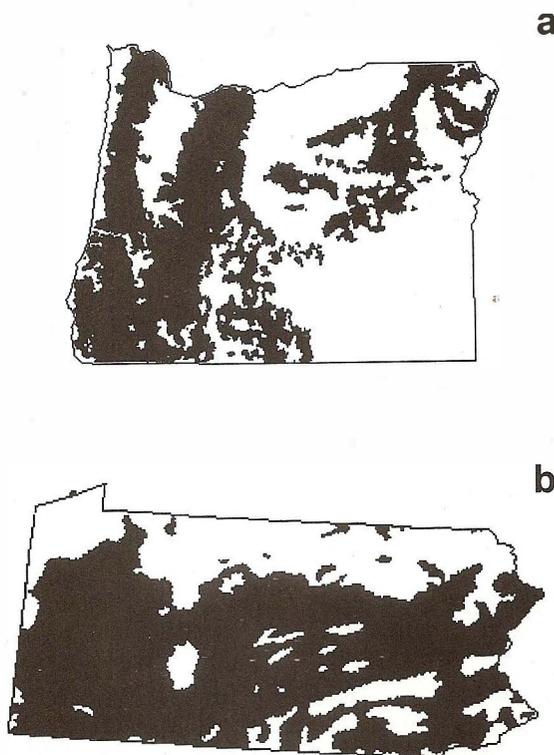
input (Russo et al. 1993). Rubber-sheeting was used to transform the climatic maps to the same registration as the defoliation map.

The accuracy of the interpolation technique may be assessed by comparing the mean absolute differences between values observed at the stations used in developing the regression equations and the values predicted by those equations. In Oregon the ranges of mean absolute differences of the weather variables among 12 months were 0.83–1.56°C for mean daily maxima ( $n = 147$ ), 0.72–1.28°C for mean daily minima ( $n = 147$ ), and 5.3–61.5 mm for total monthly precipitation ( $n = 170$ ). In Pennsylvania these ranges were 0.44–0.67°C for mean daily maxima ( $n = 85$ ), 0.72–0.94°C for mean daily minima ( $n = 85$ ), and 6.4–9.9 mm for total monthly precipitation ( $n = 161$ ).

Many techniques are available for interpolating spatial data, including various weighted averages, linear regression, and kriging and cokriging (Hevesi et al. 1992). In interpolating weather data over mountainous terrain, as required in our study, incorporation of elevation data may greatly improve fit (Hevesi et al. 1992, Phillips et al. 1992). Cokriging and multiple linear regression techniques, such as that used here, provide means of including elevation as an independent variable. From a statistical standpoint, cokriging is the preferable method of the two because it accounts for the spatial correlation of errors (Isaaks & Srivastava 1989). Although spatially correlated errors may be a problem in using regression for hypothesis testing, they are probably less so for interpolation, and regression has been employed successfully for this purpose (Pielke & Mehring 1977, Russo et al. 1993). In a comparison of several techniques, Hevesi et al. (1992) reported linear regression using elevation as an independent variable to be second in accuracy only to cokriging with elevation for interpolating precipitation over mountainous terrain. In the regression technique used here, the additional stratification of weather data by physiographic region likely enhanced the accuracy of the interpolation (Russo et al. 1993).

Forest-type information came from a forest-type group map published in Eyre (1980) that was digitized into the GIS. Many forest types were present in each state, and map overlays indicated that most types had some defoliation by the pest species (Ta-

bles 1 and 2). 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 budworm defoliation (Brooks et al. 1985). Although ponderosa pine is not a preferred host, considerable defoliation may occur on the true fir and Douglas fir that are often prevalent in the understory of ponderosa pine stands because of fire suppression. 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 (Fig. 1). They were transformed by rubber-sheeting to the same registration as the defoliation maps.



**Fig. 1.** Distributions of susceptible forest types for western spruce budworm and gypsy moth, respectively. (a) Combined Douglas fir, fir-spruce, larch, and ponderosa pine forests. (b) Combined oak-hickory and oak-pine forests.

**Statistical Analysis.** As a first approach, we chose to look at potential changes in spatial distribution of outbreaks qualitatively. We investigated potential 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). Note that observed frequency of defoliation ranged from 0.0 to 0.45 for the budworm and from 0.0 to 0.80 for the gypsy moth.

Extrapolating the effects of climatic change to changes in outbreak area requires a functional relationship between defoliation state and the environmental variables. Linear discriminant analysis provides a powerful tool for distinguishing data that are grouped in distinct classes (Manly 1986). For binomial data such as ours, the analysis estimates a single function of the form

$$Z = a_1X_1 + a_2X_2 + \dots + a_nX_n \quad (1)$$

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 (i.e., the  $F$  ratio) (Manly 1986). An observation is classified into one group or the other depending upon the distance and relationship of its  $Z$  value to the two group means. The discriminant function is particularly good for summarizing the effects of variables that are collinear, such as the climatic variables used here (Johnston 1978).

In estimating a discriminant function with up to 37 variables, we wanted to include only those most significant. Thus, we used a stepwise procedure that chose, at each successive step, the variable that contributed most to the discriminatory power of the model as measured by Wilks's lambda (PROC STEPDISC [SAS Institute 1990]). The significance threshold for a variable to enter or remain in the model was 0.15. The models were validated by running 10 stepwise analyses using subsets of 50% of the entire data set selected at random.

#### Extrapolating the Effects of Climatic Change.

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

$$D = a_1(T_1 + \Delta T_1) + a_2(T_2 + \Delta T_2) + \dots \quad (2) \\ + b_1(P_1 + \Delta P_1) + \dots + cF$$

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. The same climatic change value for each

**Table 3. Discriminant function for western spruce budworm defoliation in Oregon, with 28 environmental variables ordered by their entry into the model using a stepwise procedure (the squared canonical correlation and Wilks's lambda are for the entire model at each successive step)**

Variable	Order	Raw canonical coefficient	Squared canonical correlation	Wilks's lambda
Nov. minimum <sup>a</sup>	1	-0.072	0.062	0.938 <sup>b</sup>
Susceptible forest <sup>c</sup>	2	-0.992	0.090	0.910
Feb. minimum	3	-0.073	0.151	0.849
Jan. minimum	4	0.067	0.206	0.794
Oct. precipitation	5	0.025	0.206	0.794
Mar. precipitation	6	-0.051	0.260	0.740
Oct. minimum	7	-0.027	0.264	0.736
Oct. maximum	8	0.074	0.361	0.639
Aug. minimum	9	0.053	0.368	0.632
Nov. precipitation	10 <sup>d</sup>	0.060	0.369	0.631
June maximum (all variables)	28	0.022	0.385	0.627

<sup>a</sup> Climatic variables are 30-yr averages of daily maximum and minimum temperatures by month and of total monthly precipitation.

<sup>b</sup>  $P(>F) = 0.0$  for all analyses ( $n = 61,809$ ).

<sup>c</sup> Presence/absence of Douglas fir, fir-spruce, larch, and ponderosa pine forests.

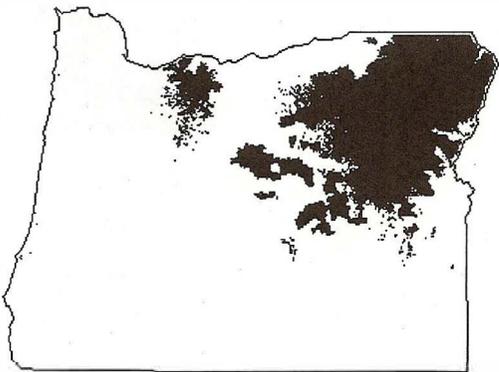
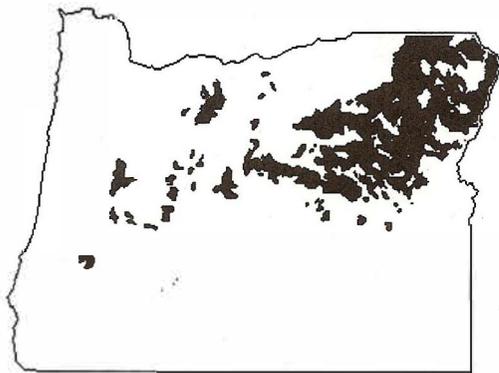
<sup>d</sup> The remaining 18 variables (and canonical coefficients) in order of entry were Jan. precipitation (-0.023), Apr. precipitation (-0.040), Sept. minimum (0.060), Jan. maximum (0.062), Dec. maximum (-0.037), July precipitation (-0.073), Sept. precipitation (0.037), Aug. precipitation (0.057), July minimum (0.081), June minimum (-0.110), Apr. minimum (0.058), May minimum (-0.054), Aug. maximum (-0.037), May precipitation (-0.015), Feb. precipitation (-0.035), Dec. precipitation (0.028), Nov. maximum (-0.028), and June maximum (0.022).

variable was applied to every grid cell; that is, climatic change was assumed to apply uniformly across each state.

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 yr at doubled carbon dioxide levels. Besides using the GCM scenarios, which were rather extreme, we explored the range of responses in outbreak areas with smaller changes in the climatic variables. Three additional scenarios included one with an increase of 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

**Discriminant Analyses.** The discriminant analysis for western spruce budworm defoliation yielded a function of 28 variables (Table 3). Because they explained the most variation, only the first 10 variables are shown in detail. Improvement in the



**Fig. 2.** Area of Oregon defoliated by western spruce budworm. (a) Actually defoliated. (b) Classified as defoliated by the linear discriminant function under ambient conditions.

fit of the model through the successive steps is apparent. The first variables to enter the analysis were primarily mean daily minimum temperatures, followed by forest type and monthly precipitation. The only consistent pattern between defoliation and the climatic variables was for precipitation; canonical coefficients were positive in sign for the months August through December and negative for the other months. The squared canonical correlation, which is analogous to the  $r^2$  of a regression analysis, was 0.39. The discriminant function was highly significant and classified 88.7% of the grid cells correctly. The error rate for defoliated cells (i.e., the rate of misclassification of defoliated cells as undefoliated) was lower (2.7%) than that for undefoliated cells (8.6%). Thus, the function somewhat overpredicted defoliation; 14% of all cells were actually defoliated, whereas 19.9% were classified as defoliated. The goodness of fit of the discriminant function is apparent in Fig. 2. Cells classified as defoliated were primarily in north-

**a** **Table 4.** Discriminant function for gypsy moth defoliation in Pennsylvania, with six environmental variables ordered by their entry into the model using a stepwise procedure (the squared canonical correlation and Wilks's lambda are for the entire model at each successive step)

Variable	Order	Raw canonical coefficient	Squared canonical correlation	Wilks's lambda
Susceptible forest <sup>a</sup>	1	2.083	0.142	0.858 <sup>b</sup>
Apr. maximum <sup>c</sup>	2	0.095	0.155	0.845
Sept. minimum	3	0.057	0.174	0.826
June precipitation	4	0.015	0.175	0.825
Mar. minimum	5	-0.092	0.178	0.822
Sept. maximum	6	-0.058	0.178	0.822

<sup>a</sup> Presence/absence of oak-hickory and oak-pine forests.

<sup>b</sup>  $P(>F) = 0.0$  for all analyses ( $n = 24,952$ ).

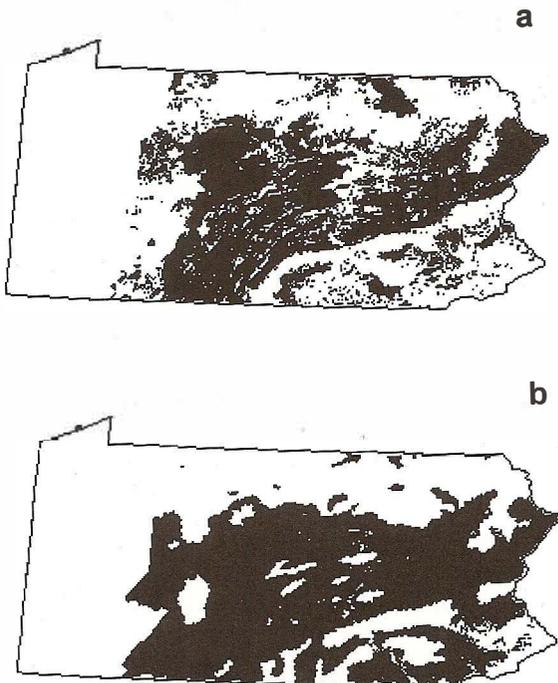
<sup>c</sup> Climatic variables are 30-yr averages of daily maximum and minimum temperature by month and of total monthly precipitation.

**b**

eastern Oregon (Fig. 2b), as were those observed (Fig. 2a). Note that the projections are also shown as binomial data to simplify comparison with observations. Defoliated cells have a probability  $>0.5$  of belonging to the defoliated class.

The analysis for gypsy moth yielded a discriminant function of six variables (Table 4). Forest type was chosen first by the stepwise procedure and explained over two-thirds of the variation in defoliation state. Four of the five remaining variables were mean monthly maximum and minimum temperatures. At a value of 0.18, the squared canonical correlation was considerably less than that for the budworm analysis. However, this discriminant function also was highly significant and classified 69% of the grid cells correctly. As in the budworm analysis, the error rate for defoliated cells was lower (8.8%) than that for undefoliated cells (22.2%). This model also overpredicted 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 were located primarily in the Allegheny Mountains of Pennsylvania (Fig. 3).

**Effects of Climatic Change.** In the following, results of the climatic change scenarios are compared with the areas classified as defoliated under ambient conditions by the discriminant function (Figs. 4a and 5a). For the analysis of budworm defoliation, an increase of 2°C without change in precipitation resulted in a diminishing of the projected area defoliated to less than half that under ambient conditions (Table 5). The defoliated area was localized in northeastern Oregon (Fig. 4b). When both temperature and precipitation increased, the projected area of defoliation spread southwestward and increased 1.35-fold over the area under ambient conditions (Fig. 4c). Conversely, a decrease in precipitation with increasing temperature resulted in a reduction of the area defo-



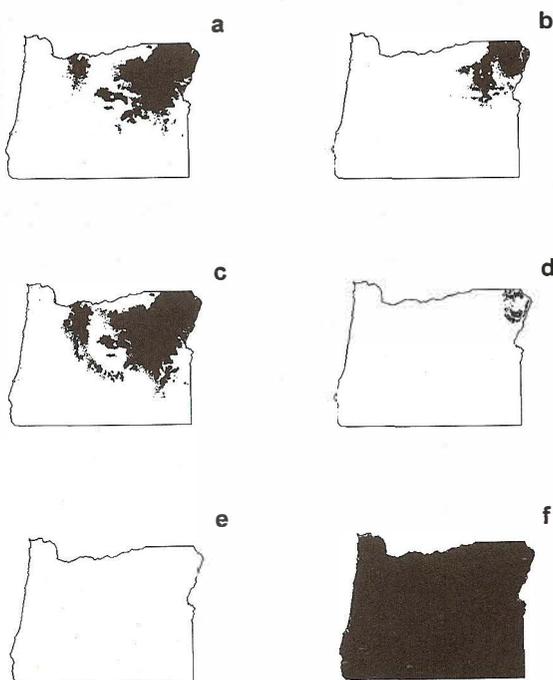
**Fig. 3.** Area of Pennsylvania defoliated by gypsy moth. (a) Actually defoliated. (b) Classified as defoliated by the linear discriminant function under ambient conditions.

liated to a tiny area in the extreme northeast of the state (Fig. 4d). The GCM scenarios produced opposite extremes: the GISS scenario projected no defoliation (Fig. 4e), whereas the GFDL projected defoliation over the entire state (Fig. 4f).

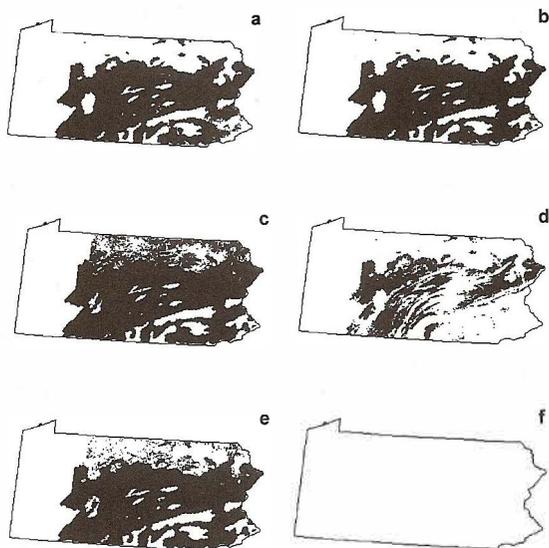
In contrast to the budworm results, an increase in temperature alone in Pennsylvania resulted in a slight increase in gypsy moth defoliation over that under ambient conditions (Table 5; Fig. 5 a and b). Trends in projected defoliation with temperature increase and precipitation changes were qualitatively similar to those for the budworm. With the addition of 0.5 mm precipitation, the defoliated area increased relative to that with a simple temperature increase (Fig. 5c), and with a loss of

**Table 5.** Percentages of total areas and absolute areas of Oregon and Pennsylvania projected as defoliated by western spruce budworm and gypsy moth, respectively, under five climatic change scenarios

Scenario	Oregon		Pennsylvania	
	%	km <sup>2</sup>	%	km <sup>2</sup>
Ambient temperature and precipitation	19.9	49,948	62.8	55,182
Increase 2°C	7.7	19,263	64.5	56,676
Increase 2°C, +0.5 mm/day	26.9	67,561	77.7	68,275
Increase 2°C, -0.5 mm/day	0.9	2,312	30.1	26,449
GISS model	0.0	0	68.7	60,367
GFDL model	100.0	251,181	0.0	0



**Fig. 4.** 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.



**Fig. 5.** 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.

0.5 mm, it decreased (Fig. 5d). Under the GISS scenario, the projected area of gypsy moth defoliation increased by  $\approx 6\%$  over that under ambient conditions (Table 5; Fig. 5e), whereas no defoliation was projected under the GFDL scenario (Fig. 5f).

## Discussion

**Effects of Climate on Defoliation.** 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 yr varied from 83 to 2,474 mm across Oregon, but only from 1,000 to 1,204 mm in Pennsylvania. Such wide variation in Oregon likely enhanced the fit of the discriminant function.

In using a stepwise correlation approach, we were seeking a discriminant model to provide the best possible fit to the available climatic data. Thus, we made no a priori selections of specific climatic variables that might be most important in explaining defoliation patterns, and there is no necessary ecological relevance to those selected. Nevertheless, western spruce budworm defoliation was clearly 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 (Table 3). Similarly, Kemp et al. (1985) reported an inverse relationship between budworm defoliation and fall and winter temperatures in the northwestern United States. During that period, the budworm hibernates as a diapausing second instar (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 in August through December and negatively otherwise. Average precipitation in Oregon increases in the period August through 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 those months may reflect the effects of drought-stressed host trees in promoting outbreaks (Mattson & Haack 1987). Swetnam & Lynch (1993) also reported a statistical association between budworm outbreaks and precipitation. Unlike our results, outbreaks in their study were most strongly associated with spring precipitation. However, it must be emphasized that they analyzed temporal patterns of outbreaks whereas we analyzed spatial patterns. We expect factors that explain year-to-year variation in defo-

liation to be different from those explaining stand-to-stand variation.

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 in Connecticut and Massachusetts, Miller et al. (1989) found defoliation to be directly related to daily maximum temperature in early April and daily minimum temperature during mid-April to mid-May. Hunter (1993) observed that warm, dry weather was important in host finding by newly hatched larvae. 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 premature hatch before host budbreak.

**Effects of Climatic Change.** Although entomologists focus on defoliation as a manifestation of insect population dynamics, the dynamics and distribution of defoliation depend upon the complex interaction of a defoliator species, its hosts, and the host habitats. Thus, climatic change may alter defoliation through both direct effects on an insect population and indirect effects on its habitat. Habitat factors may include host stand composition, stand stress, and the composition and activity of the natural enemy guild. Climatic change potentially may alter the geographical distribution of defoliation through changing two components of the defoliation process: the range of a defoliator species and the ranges of its host tree species. The most general range changes projected for insect populations under increasing temperature are movements toward higher latitudes and elevations (Porter et al. 1991, Sutherst 1991). With climatic change, the geographical ranges of many tree species may shift and alter the forest landscape substantially as trees die out in some regions and populations migrate to others with more favorable conditions (Leverenz & Lev 1987, Davis & Zabiniski 1992, Franklin et al. 1992).

Because the range shift processes operate simultaneously, it may be difficult to partition their separate effects in explaining changes in the distribution of defoliation. Another problem is that the processes work at different time scales. The response time of the first process is relatively short, perhaps on a scale of years, because of the rapid reproduction and movement of insect populations. 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 yr. They represent the results of long-term change under the constant conditions of a scenario and, thus, give no indication of the intermediate, *transient* distribu-

tions that may result from processes at shorter time scales.

The general changes in geographical distribution (Figs. 4 and 5) were increases and decreases relative to the current distributions of susceptible forest types (Fig. 1). 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. 4b) 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, cases in which the projected area extended beyond the current geographical range of susceptible forest (e.g., Figs. 4c and 5c) 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. The scenarios involving small changes in temperature and precipitation suggest the importance of range changes in forest types. Under a simple increase in temperature, the area defoliated by the budworm diminished compared with areas defoliated under ambient conditions (Fig. 4 a and b). As temperature increases, the potential growth and metabolism of plants increase, 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 and 5°C without any change in precipitation. The slight increase in projected defoliation by gypsy moth with increasing temperature probably reflected the lower climatic variability in Pennsylvania and thus, the decreased sensitivity of the analysis to small temperature changes. With reduced precipitation and increased temperature, defoliation diminished appreciably in both states (Figs. 4d and 5d), 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. 4c and 5c). 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 climatic change scenarios from the GISS and GFDL GCMs, which project temperature increase 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 kilometers northward and partially or completely out of the state.

Changes in defoliation by western spruce budworm projected under the two GCM scenarios were at opposite extremes. 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 and 5°C in the GISS scenario, whereas precipitation increased by 0.42 and 0.63 mm per day, respectively. As in the scenario with small increases in temperature and precipitation (Fig. 4c), the combination of climatic factors in the GFDL presumably favored 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. Defoliation exceeded that for ambient conditions under the GISS scenario and disappeared under the GFDL scenario. Because temperatures were similar between the GCMs, the difference likely resulted from summer precipitation, which was considerably lower in the GFDL scenario for Pennsylvania than that in the GISS scenario.

Overall, differences in projected defoliation among the scenarios were great given the relatively small changes in the climatic variables. Our results, like those of Rogers & Randolph (1993) for tsetse fly prevalence in Africa, stress that projections of climatic change, such as those derived from GCMs, need to be more accurate if they are to be useful in anticipating effects on insect populations. Our results suggest that profound changes in forest landscapes and the insect populations that inhabit them will occur as the climate changes in the not too distant future.

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