Landscape Framework To Predict Phenological Events for Gypsy Moth (Lepidoptera: Lymantriidae) Management Programs

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ABSTRACT Ability to predict the timing of phenological events (herein termed target events) is an important component of gypsy moth, *Lymantria dispar* (L.) management programs and integrated pest management programs in general. Several simulation models have been developed that, in part, demonstrate their validity for predicting events at individual locations. The framework described in this article extends the use of these models to be able to make predictions (i.e., create maps) for heterogeneous landscapes. An algorithm is presented that can predict the time that a target event will occur anywhere in a landscape using temperature, a digital elevation model, linked egg hatch and larval development models, and a linear function that relates elevation to the Julian date when a given target event will occur. The algorithm was validated with four data sets collected from Virginia, West Virginia/Pennsylvania, and Utah. Model predictions were satisfactory for the Virginia data sets and differed significantly from those for West Virginia/Pennsylvania and Utah data sets. Potential sources of error are discussed. Target event maps are presented that demonstrate how this landscape framework can be used in gypsy moth management programs.

KEY WORDS *Lymantria dispar*, phenological model, landscape

IN THE EASTERN UNITED STATES, and particularly the Appalachian Mountains, gypsy moth, *Lymantria dispar* (L.) populations are distributed over areas that are topographically and ecologically complex. Variability in the elevation, slope, and aspect of ridges and valleys of these mountainous regions creates temperature gradients that change the timing of biological events (e.g., bud break and egg hatch) by as much as 2–3 wk (Carter et al. 1992). The resulting mosaic of events creates difficulties for gypsy moth managers because monitoring egg and larval development for control programs at many locations is prohibitively expensive and time-consuming. This forces managers to monitor only a few locations and, based on their experience, extrapolate their findings to other locations in, often times, several adjoining ecosystems. The term "landscape" has been used to describe land areas composed of clusters of adjoining or interacting ecosystems (Forman & Godron 1986). Because gypsy moth populations are not restricted to a particular ecosystem type integrated pest management (IPM) programs must usually be pursued at the landscape level to be successful.

Even if gypsy moth managers accept the landscape concept, this acceptance will not inherently produce better IPM programs unless decision-support tools, such as developmental models and geographic information systems (GISs), are designed to be applied to landscapes and are accessible to managers (Roberts et al. 1993). Insect development models (i.e., models that predict when biological events will occur) have been used in IPM programs for many years (Croft & Welch 1984, Ravlin 1991), but have been capable only of making predictions for individual locations. With reference to the gypsy moth, there are two egg-hatch models developed by Lyons & Lysyk (1989) and Johnson et al. (1983) and three larval development models, GMPHEN (Sheehan 1992), GymTime (Logan et al. 1991), and an unnamed model by Casagrande et al. (1987). Each of these models uses different functional forms to model temperature-developmental rate relationships and different algorithms to model variability in development times. They all, however, are only capable of predicting phenological events for individual locations and have not been applied to the landscape level.

The objectives of this study were to produce a framework to integrate developmental models with GISs and produce landscape-level predictions of important biological events for gypsy moth man-

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agement programs. This landscape framework should be accessible to managers and flexible enough to accept new or more complex models as they become available.

Materials and Methods

Our method of predicting gypsy moth phenological events across a landscape (Page County, Virginia, in this study) is based on three elements: (1) a landscape representation of temperature, (2) temperature-driven egg hatch and larval development models, and (3) a function that facilitates the production of landscape maps by relating the predicted date of a phenological event to one or more factors (e.g., elevation) that modify temperature across a landscape.

Landscape Representation of Temperature. Temperature data for the Page County landscape were taken from a weather monitoring station in Luray, VA (1960–1990). Daily maximum and minimum temperatures of individual years (1960–1990) and 30-yr average daily maximum and minimum temperatures were used in this study. Average daily minimum and maximum temperatures were calculated from the 30 yr of daily minimum and maximum temperatures, respectively.

A 1-degree digital elevation model (DEM) (U.S. Geological Survey 1990) was used to obtain elevations at 100-m horizontal intervals and a vertical lapse rate (i.e., the change in temperature as a function of the change in elevation) of 0.5°C per 100 m elevation was multiplied by daily maximum and minimum temperatures for each of the 810 square grid (100 by 100 m) cells. This lapse rate was chosen because it is an appropriate value for April to June when gypsy moth larvae occur in the eastern United States (Landsberg 1943, Lee 1969, Forbes 1970, Leffler 1981, Boyer 1984). For a more complete discussion of lapse rates see Birch 1950, Blackwell et al. 1980, Geiger 1965, Henderson-Sellers & Robinson 1986, and Tabony 1985. Hourly temperatures, used to drive the gypsy moth egg and larval development models, were computed using the modified sine wave method of Allen (1976). Because our study focused on developing a framework to predict target events across a landscape and because temperature prediction is a large research area in itself, no attempt was made to validate temperature predictions.

Egg Hatch, Larval Development Models, and Target Events. The degree-day (DD) model (Johnson et al. 1983) was used to predict the mean time that egg hatch occurs for each grid cell (282 DD, base 3°C). The relationship between the standard deviation of egg hatch (in days) and the cumulative number of days after 1 January when the temperature was below 5°C was taken from Masaki (1956) and used to model variability in egg hatch. Output from the egg-hatch model (i.e., the proportion of a population that hatched during each 1-h time step) was used to initialize the cohort-based larval development model, GymTime of Logan et al. (1991). Like the egg-hatch model, GymTime calculates the proportion of a population that occurs in each instar for each time-step. Model output was restricted to the date on which a user-selected *target event* was predicted to occur. Target events are biological occurrences (e.g., 50% second-instar emergence or first adult emergence) that dictate the time and place that critical management activities must occur. Target events are defined by the characteristics of control tactics, the biology of the organism to be managed, the biology of the host plant, and practical considerations associated with field implementation.

T-Function. Predicting when a target event will occur for each grid cell (100 by 100 m) in Page County would require 810 model runs and a corresponding temperature file for each cell. These runs would require a tremendous amount of computing time and disk space that may not be available on computers that are commonly used in gypsy moth management programs. To make landscape modeling feasible for management situations, a mathematical function was developed that describes the relationship between the variables that affect temperature and the Julian date on which a target event is predicted to occur (a T-function). For the purpose of developing the landscape modeling framework in this study, the T-function describes only the Julian date-elevation relationship.

The T-function was developed by simulating larval development at 100 m intervals of elevation. From these simulations, we derived a linear function that describes the relationship between elevation and a simulated date for 50% second-instar emergence (i.e., a target event). To capture the complete range of elevations and temperatures found throughout the mid-Atlantic region, simulations were run using elevations ranging from −1,000 to 3,000 m. This range of elevations also provided a more complete picture of how the model would behave using temperatures from different parts of the United States.

To determine if T-functions derived from historical temperature data differ from those derived from data from an individual year, larval development for 39 individual years (1950–1989) was simulated to predict Julian dates for 50% second-instar emergence. T-functions were fit to output data from each of the 39 simulations, and a *t*-test (SAS Institute 1985) was used to compare the means of the 39 slopes and intercepts with the slope and intercept of the T-function derived from a simulation using the 30-yr average temperatures.

Because the T-function is linear over the range of elevation that is biologically realistic for gypsy moth populations in the eastern United States (0–2,000 m above sea level) (Fig. 1) and this linearity is maintained for both average and single-year temperature inputs, the following method can be

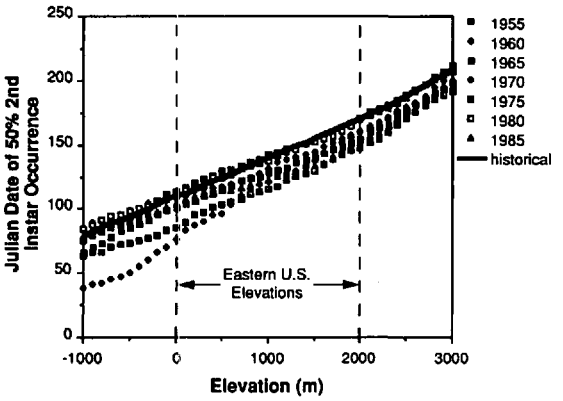

Fig. 1. Examples of simulated 50% cumulative second-instar gypsy moth occurrence at 100-m elevation intervals using historical temperature data from Luray, VA.

used to predict the date of a target event across a landscape (Fig. 2).

1. Simulate gypsy moth development at a location that has recorded temperature data.
2. Estimate temperatures at a higher elevation (e.g., 1,000 m higher) using the 0.5°C lapse rate.
3. Simulate development and predict when a target event will occur (e.g., 50% egg hatch) for the higher elevation using the lapse rate-adjusted temperature.
4. Use the two simulated points to define a T-function (i.e., Julian date as a function of elevation for our example).
5. Based on a digital elevation model, apply the T-function to all cells of the landscape to create a target event map that shows the date of an event for each cell of the map. The T-function can be applied directly to the elevation maps within the GIS. Calculations and production of the target event map were done using GRASS (U.S. Army Corps of Engineers 1991), a raster-based GIS.

Thus, only two simulations, one temperature record, and a digital elevation model are needed to simulate larval development across any landscape and predict the date of any target event in the gypsy moth life cycle.

Model Validation. Field observations of gypsy moth egg hatch from Virginia (1991, 1992), West Virginia/Pennsylvania (1990), and Utah (1991) provided four data sets to validate our landscape-level development model. The Virginia and West Virginia/Pennsylvania data sets provided a direct validation of our approach because parameters such as the vertical lapse rate were selected specifically for the mid-Atlantic region. The Utah data set was used to explore the geographic robustness of the approach without making parameter modifications.

Egg hatch was observed every 2 d on 75 egg masses in each of five sites in 1991 and four sites in 1992 in the Shenandoah National Park (Virginia) and every 3–4 d on six egg masses in each of the nine sites in the Salt Lake City, UT, area of the Wasatch Mountains. Data from north-central West Virginia/Pennsylvania were obtained from Russo et al. (1993). The date on which 50% cumulative egg hatch occurred was estimated for each site and year and used as a target event for the validation runs. The mean date of initial egg hatch from 20 egg masses for each of 15 sites in West Virginia and southwestern Pennsylvania was obtained from Russo et al. (1993) and was used as the starting point for validation runs on those sites. Elevations for the validation sites are 445–853 m and 530–853 m for the Virginia 1991 and 1992 sites, respectively, 1,357–2,220 m for Utah and 439–829 m for the West Virginia/Pennsylvania sites.

Simulation runs for each of the four validation data sets were driven by temperature data provided by the National Climatic Data Center (1990–1992a, b, c, d). Weather station elevations were also obtained from the National Climatic Data Center. The weather stations are located in Luray,

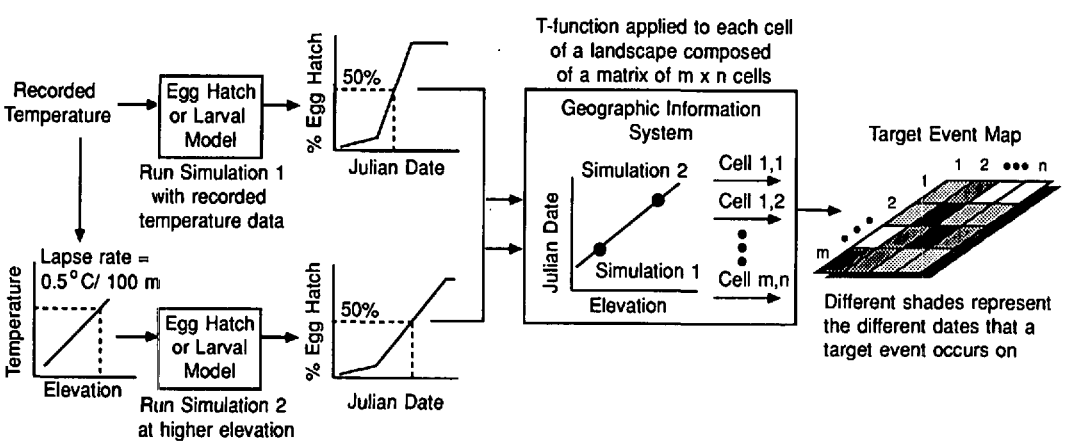

Fig. 2. Computation sequence to derive target event maps from a single temperature-recording site.

VA, Morgantown, WV, and Salt Lake City, UT. Validation of the landscape model was accomplished by deriving T-functions from the simulation runs and comparing those functions (differences in Julian dates) with corresponding T-functions derived from each of the four validation data sets.

Planning with a Target Event Map. In management situations, the dates that a target event occurs among different locations are different only when the timing of management activities (e.g., insecticide applications) are affected. Because insecticides are effective for a given number of days and gypsy moth larvae are most susceptible during the early instars, managers have a window of time (target window) available when applications will be most successful. The type of insecticide used will influence the size of the target window. The persistence of insecticides such as diflubenzuron would produce target windows of up to 30 d after bud break (Dubois 1991). However, at 30 d, trees would be at full leaf expansion, and defoliation already would have occurred because gypsy moth larvae would have progressed beyond the most susceptible early instars. Hence, a target window for diflubenzuron applications is ≈14 d. Conversely, the target window for microbial insecticides such as *Bacillus thuringiensis* Berliner is much smaller because of three constraints: (1) leaves need to be almost fully expanded to intercept the insecticide, (2) it is essential that applications are well synchronized with the occurrence of early instars to be most efficacious and early larval instars are only present for 1–2 wk, and (3) *B. thuringiensis* is persistent on foliage for only ≈1 wk (Dubois 1991).

The target window concept can also be used to define the spatial extent of treatment blocks across landscapes based on whether or not areas (grid cells) are the same or different with respect to a target event. Starting with an arbitrary date, the days of the year are divided into classes with the class width defined by the target window. Cells in a target event map that fall within the same class are phenologically homogenous and can be aggregated. Treatment blocks can be combined when the means of the target event dates fall into the same class defined by a target window. A treatment block should be divided when the variability of the dates of the target event in a block is likely to diminish the effectiveness of a control tactic or other management activity (e.g., counting moths in pheromone-baited traps). For this study we assumed that variability is too high when the standard deviation of target event dates exceeds half the size of a target window. In an actual management program, treatment blocks probably would be divided based on the preferences and level of risk aversion for an individual manager, cost considerations, and unforeseen events (e.g., rain or high winds) that occur during the treatment application period.

Results and Discussion

The landscape framework to predict phenological events for gypsy moth management programs is based on topographic and temperature representations of a landscape, and linked egg and larval development models. Each of these elements could be made more complex, and each is the focus of extensive research. We refrain from increasing the complexity until the simple framework presented here is fully evaluated. In this section we discuss some of the problems associated with simplicity and suggest some possible solutions. We also elaborate on some potential management applications of our approach.

Temperature and Model Considerations. Accurate prediction of target events requires accurate measurement and forecasting of temperature, a reliable model of larval development, and accurate timing of model initialization (egg hatch). Weather forecasts are generally reliable for <6 d. Current attempts to predict egg hatch through simulation are unsuccessful, and only the very simplistic egg hatch model based on work by Johnson et al. (1983) and Masaki (1956) and the model of Lyons & Lysyk (1989) are available. Moreover, a rigorous validation of these models has not been done. Research is being conducted better to understand egg development and diapause and to formulate a better egg hatch model (Tauber et al. 1990; Gray et al. 1991, 1994). Without a reliable egg-hatch model, larval development models are best initialized with observed egg hatch to synchronize simulations with real-world events (Casagrande et al. 1987). For these situations, we developed a method to initialize the landscape-wide development model with observed egg hatch data. It cannot be assumed that egg-hatch observations will be available at two elevations; thus, the same methods used to develop the T-function cannot be used. An observation of 50% cumulative egg hatch (or any other percentile) at only one elevation can be used to initialize the egg hatch–larval development model. This can be done by developing an egg-hatch–elevation function for 50% cumulative egg hatch by simulating egg hatch at two elevations. However, there probably will be a difference between the observed and simulated dates at the elevation of observed egg hatch. In this case, the two simulations of egg hatch should be shifted by the difference of observed and simulated 50% cumulative egg-hatch dates. The adjusted egg-hatch distributions can then be used to initialize simulations of larval development at the two elevations that are the basis for the T-function.

The larval development model used in this study also needs to be extensively validated. The observations that were used to parameterize the model are the same used by Sheehan (1992). However, Sheehan's GMPHEN was never formally validated.

T-Function. A visual examination of the relationship between the date of a simulated target event and elevation indicated that the relationship was linear in the elevation range over which gypsy moth occurs in the eastern United States. This linearity occurred as a result of simulations that were

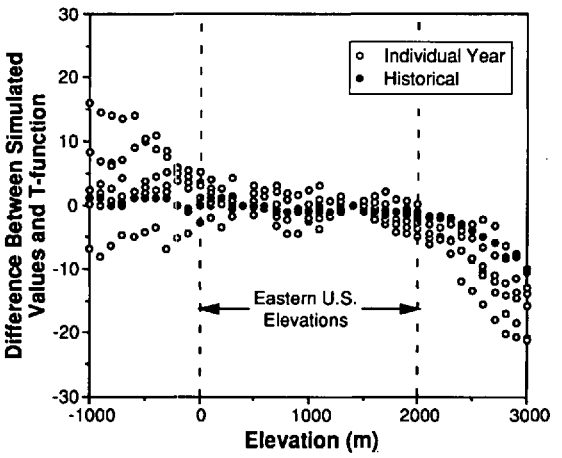

Fig. 3. Differences between Julian dates of 50% cumulative second-instar gypsy moth emergence derived from simulations at individual elevations and the T-function. Larval development was simulated using temperatures of individual years (1960, 1965, 1970, 1975, 1980, 1985) and historical temperatures.

driven by temperatures from individual years and those driven by historical average temperatures (Fig. 1). A linear relationship over this elevation range describes the variability well (Table 1). When Julian dates of a target event were estimated using this relationship and compared with the Julian dates of target events derived from simulation at each 100-m interval, differences were <6 d. When historical average temperatures were used to drive the model, differences were <2 d (Fig. 3).

Our estimated relationship between development and elevation is in good agreement with Hopkins' bioclimatic law (Hopkins 1919), which states that a 122-m change in elevation will result in a 4-d difference in development time. The mean estimated difference in ontogeny is 3.7 d per 122-m elevation (Table 1).

The linear relationship between simulated date of a target event and elevation should be expected because of the linear character of lapse rate, the linear function used in the egg-hatch algorithm, and the near linearity of the larval development algorithm over a portion of the temperature range. This relationship should be reevaluated if a more accurate model of egg hatch includes nonlinear development functions.

The T-function was moderately sensitive to the year of temperatures selected to derive the function. Comparison of the slopes and intercepts from seven randomly selected years resulted in significant differences in slope or intercept or both, among years. Similarly, the mean intercept from the 39 individual relationships was significantly different from the intercept of the relationship using historical average temperatures. However, the mean slope from the 39 individual relationships was not significantly different from the slope of the relationship estimated from the historical average temperature (Table 1).

Table 1. T-function slopes, intercepts, and Julian dates (50% second-instar emergence) derived from simulation runs for Luray, VA

Year[a]	Slope	Intercept	Julian date
1955	0.0270	90.1	100
1960	0.0270	106.1	116
1965	0.0270	101.1	111
1970	0.0390	78.7	93
1975	0.0250	115.8	125
1980	0.0290	109.4	120
1985	0.0210	103.3	111
Mean[b]	0.03008	101.7	112.7
SD[b]	0.00623	12.4	11.00
Historical[c]	0.0300	111.0	122
P[d]	0.94	<0.001	<0.001

[a] Seven individual years of temperature data.
[b] Thirty-nine individual years (mean).
[c] Daily average minimum and maximum temperatures from 39 yr (historical).
[d] Significance (P) of a t-test for the null hypothesis that the mean of 39 yr = the mean of an average year.

Historical average temperature affected model output in two ways. First, average temperatures lack the extremes of individual years and on a given day may not exceed the temperature threshold required to simulate egg and larval development. Second, the nonlinear dependence of larval development on temperature means that simulated development as a result of temperature extremes is not equivalent to that resulting from the mean of the extremes. Despite these effects, for practical reasons we use historical average temperatures when actual temperatures are lacking.

Advantages of using the T-function as opposed to individual simulations for each raster cell of a digital landscape relate principally to computer time and memory requirements. Russo et al. (1993) estimated daily minimum and maximum temperatures for each 1-s map cell using vertical and horizontal lapse rates estimated from 30 yr of daily maximum and minimum temperatures from 240 weather stations and the latitude, longitude, and elevation of the stations. Target events were then simulated for each cell. Although this technique is potentially very powerful, it requires very large disk storage capability and numerous simulations involving lengthy computer time. Our technique requires significantly less memory and only two simulations. For these reasons we recommend applying a T-function to grid cells in a raster-based GIS.

Validation. Simulated 50% egg hatch did not differ greatly from that observed in Virginia in 1991 or 1992. Simulated 50% emergence was 5 d earlier than that observed at the low-elevation site and 1 d later than that observed at the high-elevation site in 1991. In 1992, simulated 50% emergence was 2 d earlier than observed at the low-elevation site and <1 d later than observed at the high-elevation site (Fig. 4). In each case, discrep-

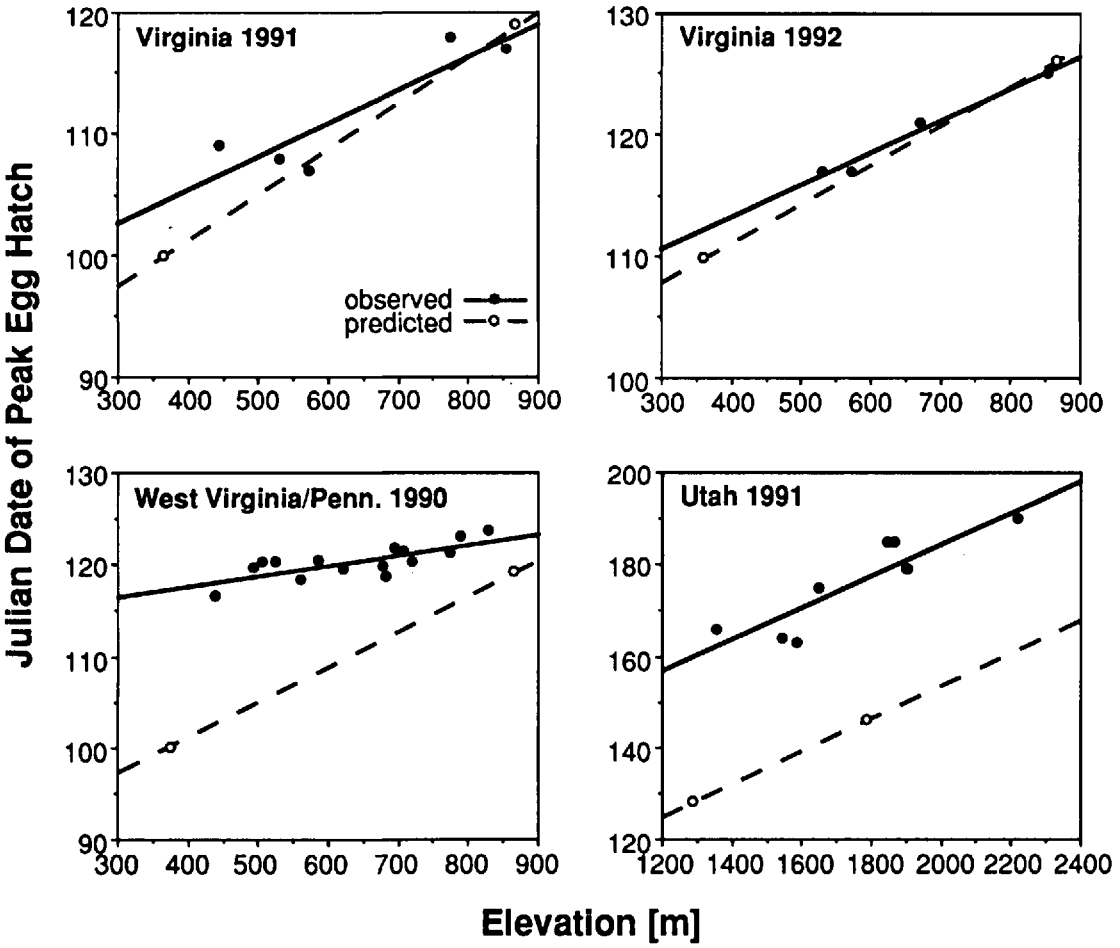

Fig. 4. Comparison of predicted (using the T-function) and observed 50% cumulative gypsy moth egg hatch in Virginia 1991, 1992; West Virginia/Pennsylvania, 1990 (data from Russo et al. 1993); and Utah, 1991.

ancies between model prediction and observation may be caused by a failure of the egg-hatch model to predict accurately initial egg hatch and subsequent distribution (at any elevation), an excessive lapse rate, or a combination of these factors. Temperature measurement is also, of course, a source of error.

Model predictions did not correspond closely to observations in West Virginia/Pennsylvania or Utah. Predicted 50% egg hatch was 15 d earlier than observed at the low-elevation site in West Virginia/Pennsylvania and 33 d earlier than observed in Utah. Predicted 50% emergence was 11 and 35 d earlier than observed in the high-elevation sites of West Virginia/Pennsylvania and Utah, respectively. As in Virginia, discrepancies between model prediction and observation in West Virginia/Pennsylvania may be a result of a failure of the egg-hatch model to predict accurately initial egg hatch and subsequent distribution (at any elevation), an excessive lapse rate, or both. Discrepancies in Utah may be caused solely by a failure of the egg-hatch model to predict accurately initial egg hatch and subsequent distribution at any elevation. Attempts to predict gypsy moth egg hatch in Utah with GMPHEN using on-site temperature records resulted in predicted egg hatch preceding observed egg hatch by 1–3 wk (S. L. Smith, personal communication). The uniform error between predicted and observed 50% emergence over the range of elevation suggests a valid lapse rate; however, it also suggests (not surprisingly) that T-functions are region-specific.

Russo et al. (1993) produced satisfactory predictions of the same West Virginia/Pennsylvania observations using the Johnson et al. (1983) egg-hatch model, as was used in this study. However, they artificially increased the egg-hatch heat-accumulation requirements to 317 degree-days. Reliable prediction of landscape-wide gypsy moth development will probably require a biologically based temporally and geographically comprehensive egg-hatch model to eliminate the need to adjust arbitrarily degree-day requirements and to arrive at more accurate predictions.

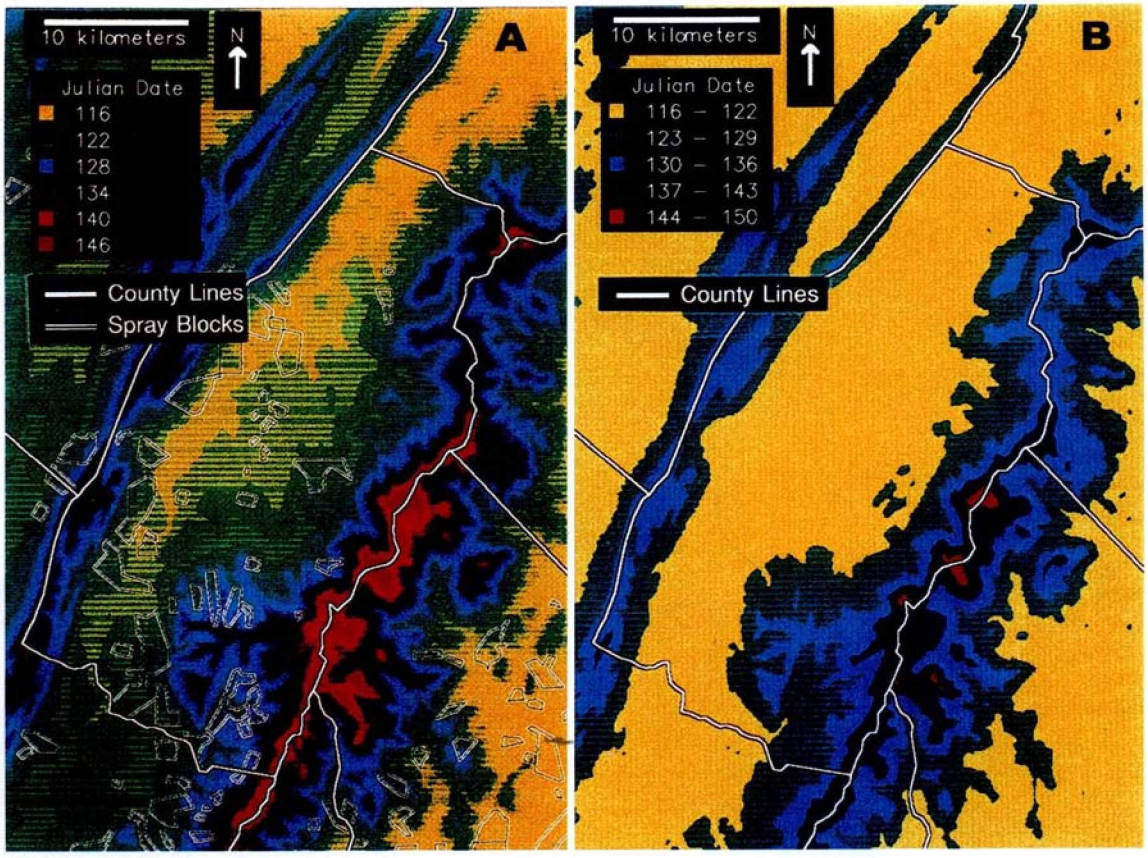

Fig. 5. (A) Target event map showing predicted Julian dates of 50% cumulative second instar occurrence. (B) Target event map showing predicted Julian dates of 50% cumulative second-instar occurrence with areas grouped from Map 5A using a 7-d target window.

The effect of elevation on observed 50% egg hatch varied among the three locations but remained similar between 1991 and 1992 in Virginia (Fig. 4). This suggests that a region-specific selection of vertical lapse rate may be necessary or that egg hatch may be better described by a nonlinear temperature-dependent function than the linear function used in our model. Other improvements may be obtained by using different lapse rates for minimum and maximum corrections (Boyer 1984) or for different months (Lee 1969, Pielke & Mehring 1977, Leffler 1981). Predicting temperatures across a topographically diverse landscape may be improved using mountain climate models (e.g., MTCLIM [Hungerford et al. 1989]) that include factors such as slope, aspect, and leaf area index in addition to elevation. This would, of course, complicate the calculation of the T-function but is probably necessary to achieve more accurate results. We assumed that the selected weather stations accurately measure temperature and that temperature is not affected by local factors such as water bodies or urban areas that do not affect the rest of the landscape in a similar manner. The use of multiple weather stations would reduce this risk at the expense of an increase in data requirements.

Planning with Target Event Maps. Maps produced by the landscape-wide gypsy moth development model can be used by pest managers in many ways. Areas that are predicted to have similar target event dates (Fig. 5A) can be aggregated into a single class (Fig. 5B). Simplifying the predicted landscape-wide target event dates to a few meaningful classes will facilitate sampling and control activities. Managers can then use these maps as a guide to determine the range of life stages present on a given date for a given area.

Spray blocks can be displayed with a corresponding prediction of the date when a target event will occur (Fig. 6A). In this example, the predicted range in recommended treatment dates (based on peak occurrence of second instars) over the entire landscape is 16 d. Assuming a 7-d target window, spray blocks with the target event predicted to occur on days 119 through 129 (green, light blue, dark blue, pink in Fig. 6A) could be treated during the same time period.

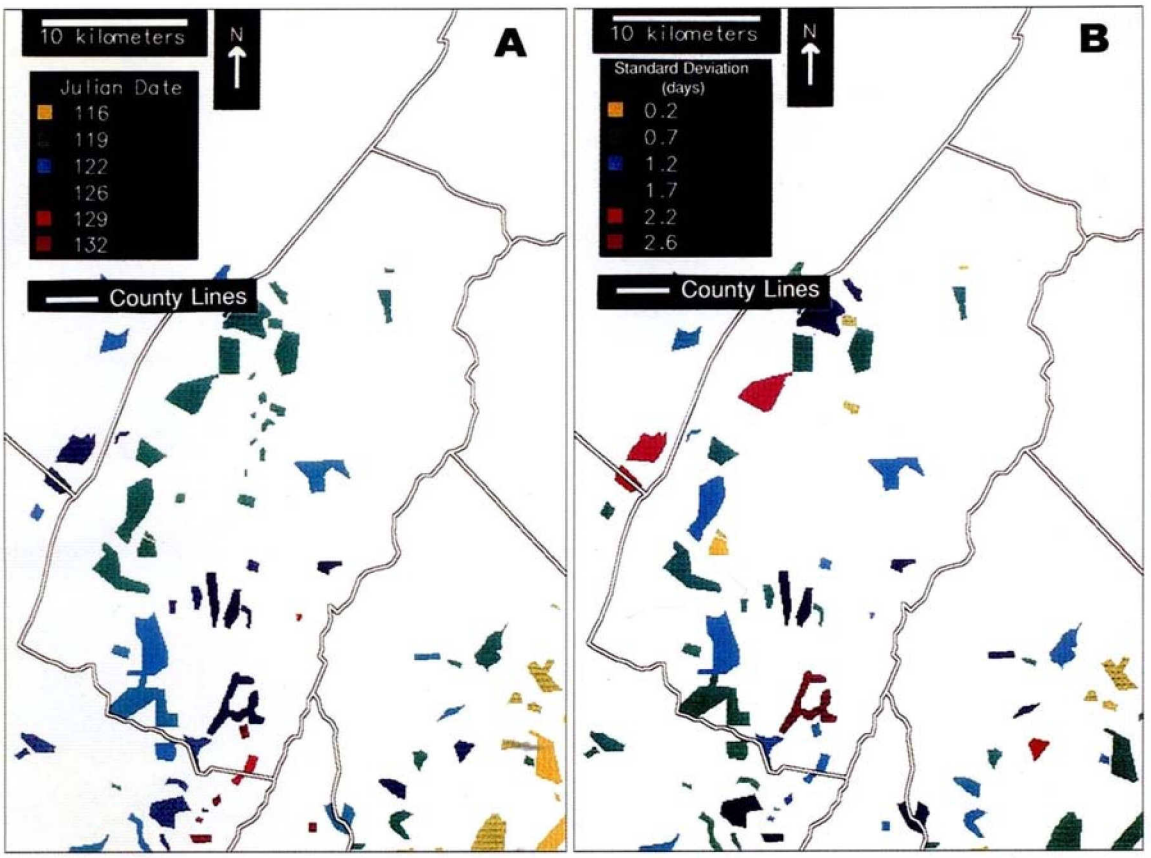

Fig. 6. (A) Target event map showing predicted Julian dates of 50% cumulative second-instar occurrence within spray blocks. (B) Target event map showing predicted standard deviation of Julian dates of 50% cumulative second-instar occurrence within spray blocks.

Spray blocks can also be displayed with the predicted variability of a target event date. Spray blocks in which the variability is predicted to be excessive can be divided into smaller blocks. For this example, we arbitrarily required that the standard deviation in the predicted target event date across a spray block be less than one-half of the target window. Fig. 6B shows the standard deviation for each spray block. With the maximum standard deviation of 2.6 d and a target window of 7 d none of the blocks should be subdivided.

Throughout this article we used the example of insecticide application for gypsy moth management. However, the landscape framework presented here is applicable to any control tactic or management action that is distributed over heterogeneous land areas. The adaptation of the procedures to other geographic regions or other insect systems requires only that valid parameters for developmental models and temperature modification algorithms be available. In addition, this framework can be implemented on many computers that are currently being used in IPM programs, and it is not restricted to the software used in this study.

Acknowledgments

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