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Jacques Régnière, Daniel Lavigne, Robert Dickison and Andrew Staples

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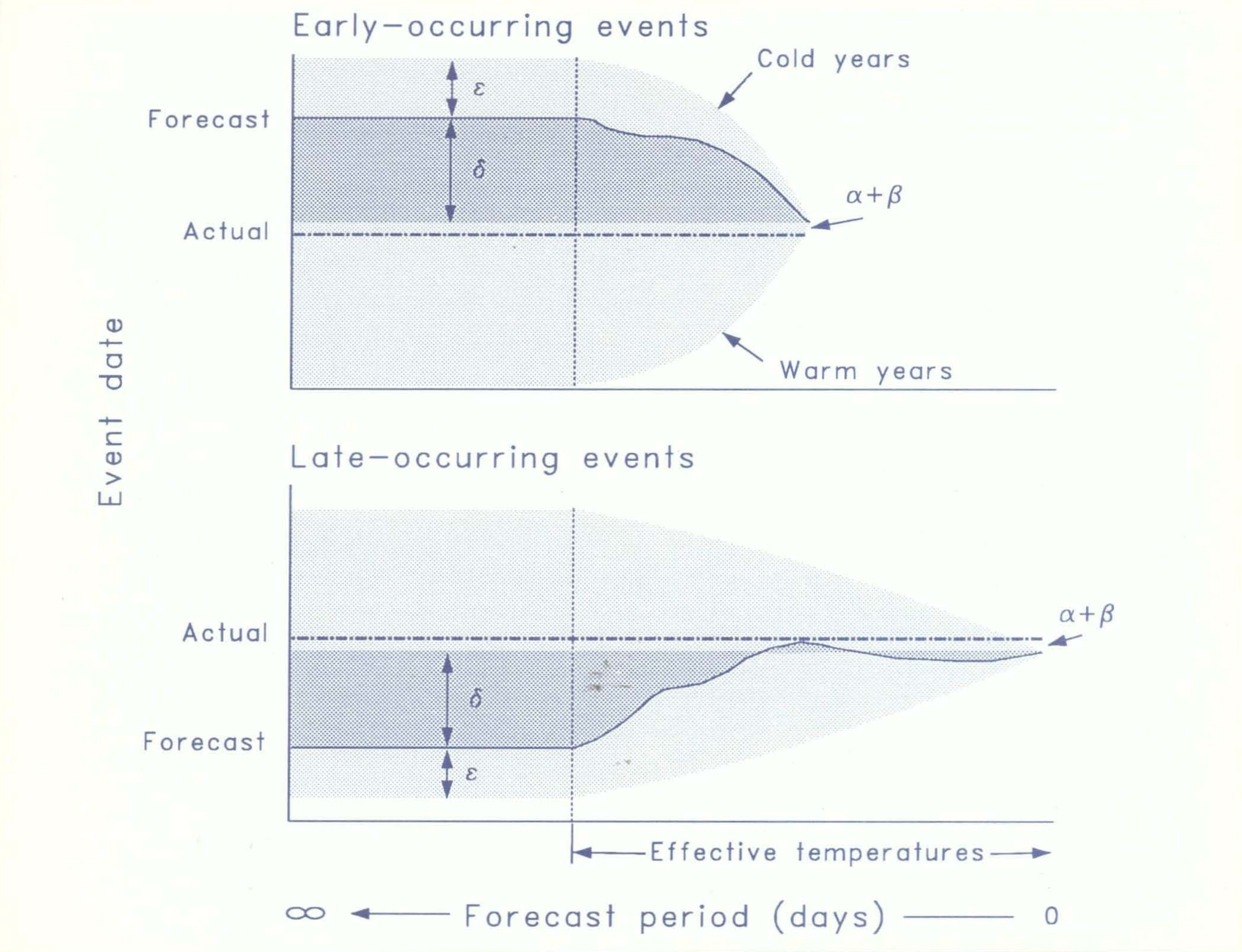

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Jacques Régnière, Daniel Lavigne[1],
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Information Report LAU-X-115
1995

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ABSTRACT

BioSIM is a software tool for use in forecasting events in the seasonal biology of insect pests. Forecasts are made by simulation models provided by the system and are based on regional air temperature databases. The accuracy and usefulness of BioSIM in forecasting the development of the spruce budworm, *Choristoneura fumiferana* (Clem.), in New Brunswick was assessed using development data collected in 1992 and 1993 in the northern portion of the province. It was found that both available models of budworm phenology (the Régnière and the Lysyk models) were highly accurate (± 3 days) in predicting the insect's development. It was also found that BioSIM's compensation for vertical and latitudinal lapse rates produced adequate air temperature regimes for sites that are remote from weather-recording stations, and that the vertical gradients of insect phenology generated by the system reflected observations accurately. This indicates that the system can be used to generate phenology maps for use in pest management decision support systems. The accuracy and precision of phenology forecasts generated by BioSIM depended on the length of the forecast period and on the target life stage. As a rule, early-occurring phenological events (e.g. peak L_3) are far more difficult to predict than late-occurring events (e.g. peak L_6). Model calibration, using recent phenology observations, can be used to reduce prediction error.

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RÉSUMÉ

BioSIM est un outil logiciel qui a été conçu pour prévoir l'évolution saisonnière des insectes ravageurs. Les prévisions sont établies à partir des modèles de simulation fournis avec le système et de bases de données régionales sur la température de l'air. Nous avons évalué la précision et l'utilité de BioSIM comme outil de prévision du développement de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clem.), au Nouveau-Brunswick, à partir de données sur le développement recueillies en 1992 et 1993 dans le nord de cette province. Nous avons constaté que les deux modèles disponibles sur la phénologie de la tordeuse, à savoir les modèles de Régnière et de Lysyk, sont très précis pour prédire le développement de l'insecte (± 3 jours). Nous avons également remarqué que la compensation, par le système BioSIM, des gradients thermiques verticaux et latitudinaux produisait des régimes de température adéquats pour les sites éloignés des stations météorologiques, et que les gradients verticaux de la phénologie de l'insecte établis par le système étaient fidèles aux observations. Nous en concluons que BioSIM peut être utilisé pour établir des cartes phénologiques qui pourront ensuite servir comme éléments d'outils d'aide à la décision pour les programmes de lutte antiparasitaire. L'exactitude et la précision des prévisions phénologiques établies par le système BioSIM ont varié en fonction de la durée de la période de prévision, ainsi que du stade de l'insecte à l'étude. De façon générale, les événements phénologiques précoces (p. ex. le stade 3) sont beaucoup plus difficiles à prévoir que les manifestations tardives (p. ex. le stade 6). Enfin, l'étalonnage du modèle, sur la base des observations phénologiques récentes, peut réduire l'erreur de prévision.

INTRODUCTION

Spruce budworm (*Choristoneura fumiferana* [Clem.]) is a major North American insect pest of conifer trees such as balsam fir (*Abies balsamea* L.), red, white and black spruce (*Picea rubens* Sarg., *P. glauca* [Moench.] Voss. and *P. mariana* [Mill.] B.S.P.), though other species are also attacked during epidemics (Harvey 1985). Outbreaks of spruce budworm are recurring phenomena that pose a severe threat to industrial wood supply (Brown 1970; Kettela 1983). Because of a considerable increase in their extent and severity over the past century (Blais 1983), these outbreaks may also constitute an environmental threat. Control programs based on aerial spraying against populations of spruce budworm have been carried out in New Brunswick almost every year since 1952. Early programs relied on DDT, a highly toxic and long-lasting insecticide. Because it represented a considerable environmental hazard, DDT was replaced by less persistent chemical insecticides such as fenitrothion and aminocarb in the 1970's and 1980's. The biological insecticide *Bacillus thuringiensis* var. *kurstaki* Berliner (hereafter, *B.t.*) was introduced as an operational control tool more recently.

In New Brunswick, the primary objective of the spruce budworm control program has been to keep the forest alive through foliage protection. It has not been population suppression. Foliage protection is achieved by applying insecticide to targeted areas after larvae have emerged from overwintering and before too much feeding damage has occurred. Experience has shown that adequate timing at the seasonal level is a critical element of the success (efficiency, efficacy or innocuousness) of spruce budworm management activities. These include treatments or control operations as well as population monitoring and damage assessment. Efficient deployment of human and material resources assigned to these activities requires forecasting the occurrence of the target life stages or "susceptibility windows". Plans must be developed on the basis of these forecasts and must be updated regularly as target events near. Furthermore, timing is only one aspect that must be taken into consideration in conducting pest management activities on a seasonal basis. These forecasts must be integrated with forest resource, risk and land-use patterns in the development of protection plans. So-called "new generation" pesticides (narrow-spectrum, low residual toxicity insecticides such as *B.t.*) are often used at ultra-low application volumes and often have a narrower window of opportunity requiring very precise timing and targeting (Schaub et al. 1995). This implies a flexible, integrated approach to seasonal planning taking into consideration more variables at a faster rate.

Insects are poikilotherms and their developmental responses to temperature are often complex (Precht 1973). For this reason, their seasonality is highly dependent on ambient temperature (Janisch 1932) and other meteorological conditions that determine the microclimate in their immediate environment. Thus, the timing of events in the spruce budworm's life cycle varies considerably from year to year and from location to location.

Considerable effort has been devoted in the past to developing methods of forecasting the course of events in seasonal development of spruce budworm. Aerial observations of leaf flushing and the occurrence of ice break-up in New Brunswick were used to establish phenological zones representing early, intermediate and delayed development. These traditional zones are generally used from a logistical standpoint to plan sampling activities for spruce budworm control operations in New Brunswick (Webb 1958; MacDonald 1963). More specific timing of surveys and treatments is now done through routine monitoring of insect and host-tree development (Carter and Lavigne 1994). Prior to the onset of field surveys, conventional forecasting of seasonal development for first block openings is based on current and historical records of degree-day summation (base: 3°C) for various weather stations within the province. Where forecasts of first block openings are needed, observed and predicted degree-day sums for the nearest weather station(s) are examined in relation to degree-day sums noted for the same station(s) in previous years. Years with similar degree-day sums are identified, and historical block opening information for these years is combined. Ground and aerial observations of insect and tree development are then made to provide updated forecasts of expected first opening dates. A good history of block openings exists for much, but not all, of the province.

However, the need for rapid updating of geographically specific phenology forecasts and for their integration with other information involved in the decision-making process, implies the use of computerized models. Two such models for predicting spruce budworm phenology have been published. The first is a very detailed mathematical description of the insect's seasonal biology including development, mortality, feeding (defoliation), reproduction and moth flight. It is a process-oriented model based mostly on laboratory experiments and nonlinear descriptions of developmental responses to temperature, including several sources of population-level variability. Various aspects of this model were developed and validated over a number of years (Régnière 1982, 1983, 1984, 1987, 1990; Régnière and You 1991). The second model is empirical in nature (Lysyk 1989). It outputs expected frequencies of the active life stages of spruce budworm from emerging second instar larvae (L_2) in the spring to adult emergence in late summer. It is based on a series of nonlinear functions describing the relative frequency of successive life stages as functions of accumulated degree-days above 8°C. As such, it is a "distributed" model that realistically simulates the age structure of the population. Lysyk (1989) compared his model with that of Régnière and found it to be more accurate. In particular, earlier versions of Régnière's model were consistently and considerably biased (late) in predicting early larval development (2^{nd} and 3^{rd} instars). Part of this problem was addressed in a revision of the method used to simulate postdiapause development (Régnière 1990). However, significant bias still existed. An analysis and correction of this bias was completed in 1991 on the basis of an extensive set of population development data collected in 20 sites in Quebec over the period from 1985 to 1990. These data were part of the same data set used by Régnière and You (1991) to model spruce budworm feeding damage. The corrections made to Régnière's model (unpublished) involved modifying the development rates of second, third and fourth instars in such a manner as to accelerate early larval development without affecting the total length of development beyond the fifth instar.

Given the availability of suitable phenology models, forecasting seasonal events for integrated pest management (IPM) also requires the availability of adequate temperature data, running large numbers of simulations, and interpreting and representing the results in a form suitable for decision making. BioSIM, a software product developed by the Canadian Forest Service, was designed to perform these tasks (Régnière et al. 1995). This report is an analysis of BioSIM's performance in forecasting the phenology of spruce budworm populations in New Brunswick in 1992 and 1993, using the Régnière and the Lysyk models.

BioSIM OVERVIEW

BioSIM is a software tool that uses various sources of geographically referenced temperature data and a collection of simulation models to generate location-specific forecasts of selected seasonal processes. These forecasts can be used directly in planning pest management activities or can form the basis of landscape-wide projections. BioSIM is composed of four modules. The first of these is designed to develop and maintain weather databases and the simulation model-base. The second module controls the execution of various simulation models in the model-base, allowing the user to run large numbers of simulations while systematically controlling parameters such as geographical location and elevation. It integrates the tasks of assembling temperature regimes and running simulations (Fig. 1). The third module is a set of analytical tools that can interpret model outputs to extract particular features. For example, the module can be used to determine dates at which a given output variable reaches a specific critical feature (e.g. values of minimum, mid-point or maximum frequency of a target life stage), or the value of a variable on a given date. Features extracted from model output are hereafter referred to as "events". This module can also compile summary tables or fit regression equations relating these events to controlled parameters (the so-called t-functions of Schaub et al. 1995). The fourth module is an interface between analysis results and geographical information systems (GIS) for further integration into the decision-making process.

Temperature-regime assembly

The central task carried out by BioSIM is the assembly of a suitable temperature regime for input to the seasonal simulation model (Fig. 1). The system assembles a complete series of daily minimum and maximum air temperatures for a specified period of time and location (latitude, longitude and elevation) from information contained in three weather databases: monthly normals (historical temperature data), real-time (current year) temperature data and 5-day temperature forecasts. Monthly normals are used to fill in periods where real-time temperature data are missing or to generate temperature predictions. Five-day forecasts, routinely produced by weather service agencies, can also be used to improve on these predictions. Three functions are performed during temperature regime assembly for a given location: (1) find the "best" sources of temperature data in the three weather databases; (2) adjust these data for latitude and elevation differences between the source and the specified location; and (3) generate daily minimum and maximum air temperatures from monthly normals. In the resulting time series of air temperatures, real-time temperature data, when available, supersede normals or 5-day forecasts.

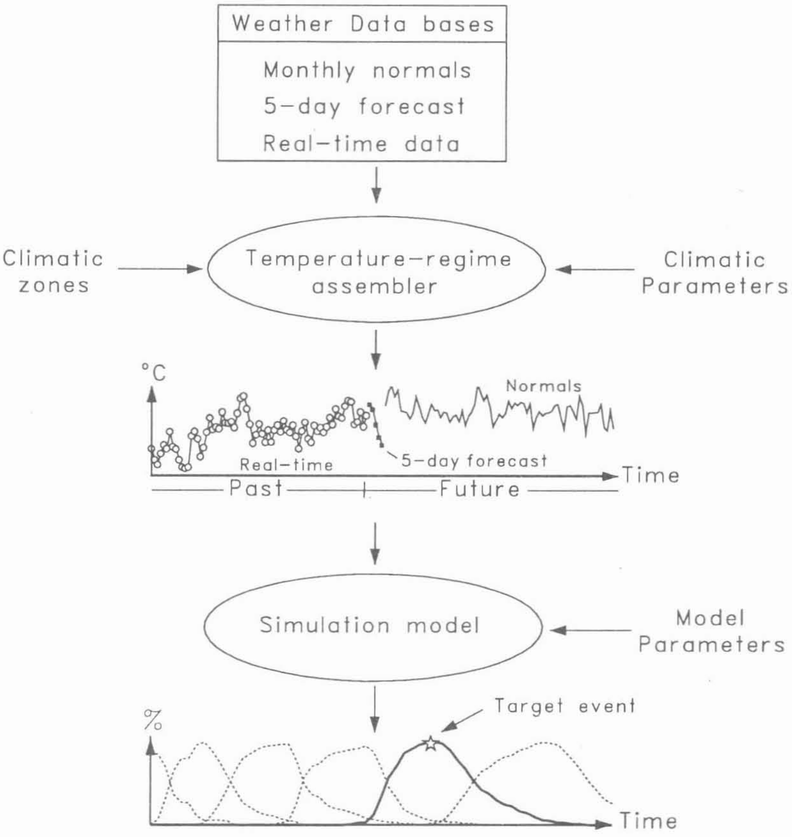

Figure 1. Diagram of the core functions of BioSIM: (1) temperature-regime assembly from three weather databases (monthly normals, 5-day forecast, real-time minima and maxima), location coordinates and search criteria such as climatic zones and elevation differences; (2) control of simulation model parameters and input; and (3) interpretation of model output to extract target event information.

The "best" source of temperature data for a specified location is defined as the nearest station among the subset of stations belonging to the same climatic zone and within a specified elevation range from that location (hereafter, the elevation tolerance criterion). Climatic zones are a partition of the relevant geographical area along ecological, geological or climatological lines. These zones are specific to a particular implementation of the system, and are defined by the user in an accessory database. The idea behind these geographical zones is that weather stations from a given area may not adequately describe temperature patterns observed in a nearby location because of overriding geographical or geomorphological factors, such as the proximity of a significant body of water (hereafter, the maritime effect). Under such circumstances, it may be preferable to use temperature data from a more distant source located in a similar geographical area (zone) than from a nearer source located in a markedly different context. The elevation tolerance criterion is used to give some weight to elevation in addition to cartesian distance in the station selection process. Considerable trial and error testing of BioSIM conducted during the system's development and installation in Quebec led to the selection of 250 m as an appropriate default value of the elevation-tolerance criterion. Whenever a source of temperature data in one of the databases cannot be found using the specified criteria (empty subset), the limiting criterion is dropped (i.e. climatic zones are no longer considered or the elevation tolerance is set to a very large value) and the search is repeated. The sequence of search criterion relaxation for elevation and climatic zones is (1) on-on, (2) off-on, (3) on-off and (4) off-off.

Temperature data obtained from the three databases are adjusted automatically for differences in elevation and latitude between the source and the specified location, using lapse rates (Régnière and Bolstad 1994). These lapse rates are different for minima and maxima, and vary with time of year in a sinusoidal pattern (Régnière and Bolstad 1994, their Fig. 5). Latitudinal lapse rates range from -1.35° or -1.45°C/°N (minima, maxima) in January to -0.55° or -0.30°C/°N in July. They were obtained from an array of eastern seaboard weather stations ranging from Miami (Florida) to Bangor (Maine). Vertical lapse rates range from -0.65° or -0.45°C/100 m (minima, maxima) in January to -0.9° or -0.7°C/100 m in July, and were estimated from a set of weather stations in a narrow latitude band in the Appalachian Mountains of western North Carolina, where there is no maritime influence.

After selecting the best station in the normals database, BioSIM generates a series of daily air temperature minima and maxima for an entire year. However, as discussed by Régnière and Bolstad (1994), normals cannot be used directly as input in most insect or plant development models. Indeed, threshold temperatures and other sources of non-linearity in developmental responses to temperature imply that natural daily temperature fluctuations tend to accelerate development. This effect is particularly pronounced in the spring, as temperatures warm up and frequently cross development-rate inflection points (e.g. thresholds). Normals, being averages, do not fluctuate this way. Stochastic daily minima and maxima are generated on the basis of extreme monthly and mean monthly minimum and maximum air temperature normals obtained by linear interpolation between monthly values. Daily deviations are distributed normally around the daily normal, with a certain amount of correlation between minimum and maximum on a given day and between minima or maxima on successive days (autocorrelation).

BioSIM can run simulation models using normals exclusively, to simulate the "normal" course of events, or in combination with real-time temperature data either from past years (for historical reconstruction) or from the current year (for actual forecasting). The system can also control the amount of real-time temperature data incorporated into a temperature regime to simulate the progression of a season's forecast as more and more real-time data become available to predict the occurrence of a given event. This allows the analysis of the relationship between the length of the forecast period (defined as the number of days for which temperatures generated from normals are used to forecast an event) and the accuracy of the prediction.

Sources of error in seasonal forecasting

In this discussion, we assume a negligible amount of error associated with observed events that are compared with model predictions. In practice, this is often questionable as various sources of sampling error and biases exist. There remain four sources of error that can affect the accuracy of seasonal forecasts made by temperature-driven simulation models (Fig. 2). The first two, α and β, can cause deviations between model predictions and observed events when the model is used in historical reconstruction mode (no forecasting, when the entire temperature regime used as model input is real-time in nature). Error-source α represents the inaccuracy of the simulation model itself, caused by inadequate or incomplete descriptions of the processes being modeled. Few models describe the influence of all factors involved. These influences can cause random (imprecision) or systematic (bias) deviations between model predictions and observed phenomena. Model validation runs, using on-site temperature data and comparing simulation results with observations taken in the same site, can provide information on the magnitude of α error. The second source of error, β, is caused by differences between actual on-site temperature and the real-time temperatures used as model input. Several factors can lead to β error: inadequate weather-data source matching (e.g. maritime effect), erroneous lapse rates or other landscape effects such as cold-air drainage or terrain shading. To determine the magnitude of β, α must be known.

The other two sources of error, δ and ε, are related to the use of normals when a model runs in forecasting mode. The simpler of these two is ε error, which is due to the stochastic nature of temperature regimes generated from normals by BioSIM. This error can theoretically be eliminated by running a sufficiently large number of replicates of simulations and obtaining average model predictions. How much replication is needed depends on several factors, particularly on the amount of synthetic temperature data relative to real-time data (i.e. the length of the forecast period), the degree of precision required of the model's output, and the specific process being simulated. The last source of error, δ, is due to the systematic deviation of actual temperature in any given year from normals, which may persist for prolonged periods. The resulting model predictions can deviate correspondingly. Thus, in a "cold" year, predicted events will tend to be earlier than observed, and vice versa. Such periodic deviations vanish gradually during a season as the amount of "effective" real-time temperature data available increases. Here, the term effective refers to those temperatures that can induce significant development, and is therefore specific to the exact temperature-dependent responses involved in the prediction. These sources of error, especially δ, can only be known in retrospect.

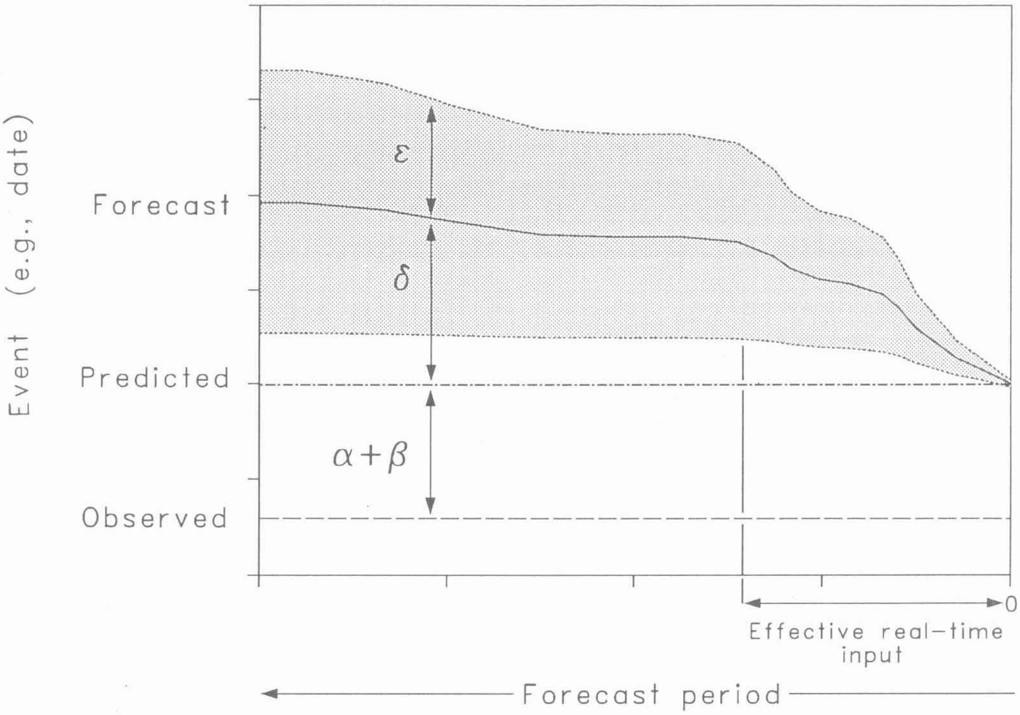

Figure 2. Illustration of the four sources of forecasting error: α is a model error (precision and bias); β is temperature-data projection (lapse-rate adjustment) error; δ is forecast error due to systematic deviation between a season's temperature patterns and normals; and ε is random error caused by the use of stochastic normals.

MATERIALS AND METHODS

Temperature information

Weather databases

The first major step in implementing BioSIM is the elaboration of the three main weather databases. By international agreement, temperature normals are calculated for Standard Normal Periods (SNP) of 30 years. Data for the current SNP (1961-1990) were obtained from the Canadian Atmospheric Environment Service (AES). Inspection of the current versus the previous (1951-1980) normals showed a decrease in the number of available stations for New Brunswick. Stations that had been abandoned since 1980 did not have an adequate length of record within the current SNP to meet AES standards. Obviously it is important to have a broad database; on the other hand, because it is important to use the same SNP for the basis of geographical analysis, old and new normals cannot be arbitrarily mixed. We therefore created a composite database by adjusting the old normals from stations dropped during the last SNP as described below and adding them to the normals database.

The purpose of the composite database was to make it possible to use BioSIM to predict block opening dates. Most of the insect and tree development involved in spray scheduling for spruce budworm control in New Brunswick depends on temperatures during May. Differences between the old and new normal temperatures were thus only determined for May. The new normals were up to 0.6°C warmer. These temperature differences were mapped, and the resulting patterns were used to adjust, for May only, old normals in the BioSIM database. The adjustments were applied equally to mean, minimum and maximum daily temperatures. However, extreme minimum and maximum values were not adjusted. This procedure allowed the inclusion of an additional 10 stations from the 1951-1980 SNP to the 1961-1990 set of normal-generating stations for the province.

The real-time temperature database (daily maximum and minimum air temperature) used in 1992 (25 stations) and 1993 (15 stations) was obtained from the New Brunswick Department of Environment - Flood Forecast Centre, the AES and other collaborators such as New Brunswick Power, the Canadian military and private sources.

In the present test, no 5-day forecast temperature data were used. We reasoned that having access to accurate 5-day forecasts of air temperature for a given location would be equivalent to advancing the forecast period by 5 days.

Climatic zones

New Brunswick was divided into three large climatic zones (Fig. 3) to account for significant maritime influences near the Gulf of St. Lawrence (East Shore zone) and Bay of Fundy (Bay of Fundy zone). The extent of these zones inland was determined arbitrarily, with the recognition that these boundaries could be changed when appropriate analysis of this influence has been done. Water temperatures in June are near 8°C in the Gulf of St. Lawrence, compared with daily mean minimum and maximum temperatures of 8.7°C and 22.8°C in Fredericton, N.B. Attenuation of the maritime influence is controlled by both distance from the coast and topographic barriers. As a preliminary criterion, the margin of the East Shore climatic zone was placed at a distance of about 60 km inland or at a land elevation of about 150 m, whichever was narrower.

The importance of the maritime influence on coastal temperatures is demonstrated by comparing the mean monthly air temperatures in June at Bathurst (elevation 12 m), in the East Shore climatic zone, with those at Nipisiguit Falls (106 m) and Little River Mine (341 m), both in the Inland climatic zone. The 94 m difference in elevation between Bathurst and Nipisiguit Falls gives rise to a 0.5°C increase in temperature. The difference in mean temperature for the same period between Nipisiguit Falls and Little River Mine (a 246 m difference in elevation) is -0.7°C. Vertical lapse rates generated by BioSIM for June at these latitudes are -0.9°C/100 m and -0.7°C/100 m for minimum and maximum temperature (Régnière and Bolstad 1994).

On-site temperature data

On-site temperature monitoring equipment (SmartReader data loggers, Young Environmental Systems, Vancouver, B.C.) was installed in all 1993 sites in accordance with Fire Weather Station Standards recommended by the World Meteorological Organization for agro-meteorological observations in forested areas (as cited by Turner and Lawson 1978). Temperature was measured electronically every 15 s, averaged and logged every 2 min. Data were recorded from April 1 to July 15. Daily minimum (AM) and maximum (PM) temperatures were determined from these records.

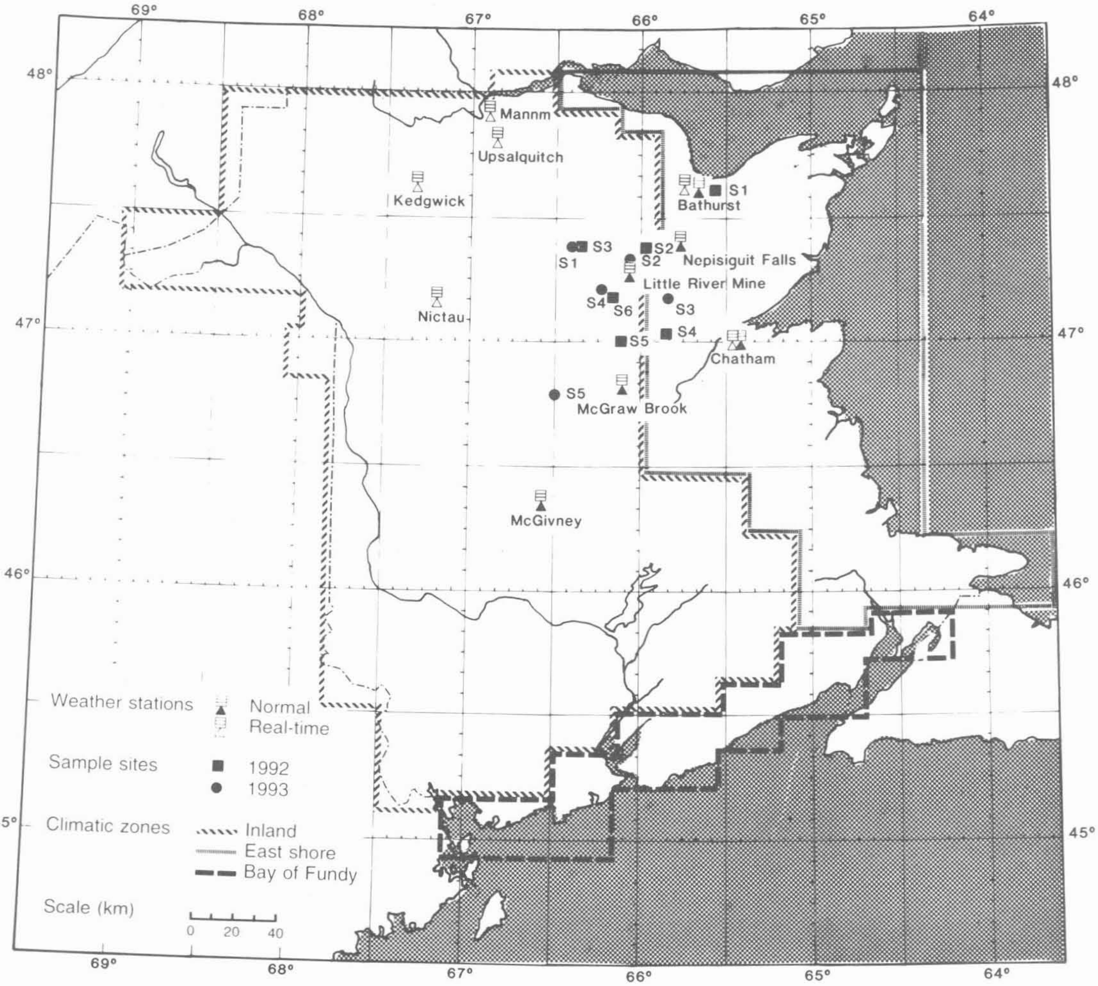

Figure 3. Map of New Brunswick showing the boundaries of the three climatic zones (Inland, East Shore and Bay of Fundy), as well as the locations of the 1992 and 1993 sample sites and normals or real-time weather stations associated with them. Tables 2 and 4 detail the various station-site associations.

Spruce budworm development information

Population sampling

In 1992 and 1993, sample sites were selected on the basis of two criteria: (1) the presence of moderate to high overwintering populations of spruce budworm and (2) the geographic and phenological distribution of potential locations. Sites were evenly distributed to cover a wide range of latitudes and elevations within the budworm-infested area of the province. In 1993, site selection was further restricted to locations adjacent to (< 200 m) open areas meeting national weather station location standards (Turner and Lawson 1978).

Spruce budworm and host-tree development were determined every 2-3 days at all sites in both years from the time of peak larval emergence in the spring to pupation and moth emergence. Foliage samples (45-cm branch tips) were collected from the mid-crown of representative balsam fir trees. Sample sizes were 3-5 (1992) and 10 (1993) branch tips per site per sample date. Half-branch sections of these samples were examined for living spruce budworm larvae and pupae as well as empty pupal cases. Larval instars were determined from head-capsule width measurements made under a microscope with a graduated ocular. An index of development, *a* (average instar) was calculated from the frequencies of the various budworm life stages f_i , i = 2, 3, 4, 5, 6, 7 (pupae) and 8 (pupal cases) in the samples using:

$$a_t = \frac{\sum_{i=2}^{8} i\, f_{i,t}}{\sum_{i=2}^{8} f_{i,t}} \qquad [1]$$

Dates of peak larval indices (*a* = 3.0, 4.0, 5.0 and 6.0) for each sample site in 1992 and 1993 were estimated graphically, to the nearest day, from running average curves of *a versus* sample date. The running average $\hat{a}$ was calculated using data from successive samples with the equation:

$$\hat{a}_t = \begin{cases} 0.75\ a_t + 0.25\ a_{t+1} & for\ t=1 \\ 0.25\ a_{t-1} + 0.50\ a_t + 0.25\ a_{t+1} & for\ 1 < t < n \\ 0.25a_{t-1} + 0.75\ a_t & for\ t=n \end{cases} \qquad [2]$$

where t is an index of date, and n is the total number of sample dates in a series. This procedure reduced the influence of sampling error on the estimates of the dates of peak larval instar.

Simulation models

Both the Régnière and Lysyk models output the frequencies of the various life stages present in the simulated population on any given day. They were programmed to compute average instar using equation [1]. In addition, both models were modified to accept calibration information in the form of an observed larval index value and date of the observation. Each model used this information to adjust the physiological age of the simulated population to match the observation as closely as possible. This was done differently by the two models because of their vastly different nature. Régnière's model simulates the development of several subpopulations partitioned according to phenotypic (*i*), sex (*j*) and microclimatic (*k*) criteria; physiological age (from early post-diapause to moth emergence: $1 \leq D_{ijk} \leq 8$) is accumulated separately for each subpopulation (Régnière 1982). On the calibration date, the difference between observed and simulated larval indices (a_o - a_s) was simply added to the physiological age of each subpopulation to yield the adjusted age (D'_{jk}):

$$D'_{ijk} = D_{ijk} + a_o - a_s \qquad [3]$$

The Lysyk model is a series of nonlinear functions of accumulated degree-days above 8°C (DD_8). The value of DD_8 on the calibration date was set to the accumulated degree-days that predicted the observed larval index, as determined iteratively.

None of the real-time temperature data sets available in 1992 and 1993 covered the entire period for which these models require air-temperature data (from March 1 to mid-July). In particular, real-time temperature data were not available for March. Therefore, all input temperature regimes in this study contained a certain amount of temperature information generated from normals. For this reason, all simulations were replicated 10 times, and BioSIM was used to compute average output.

Mean dates of peak average instar (defined as the last day on which $a < 3.0$, 4.0, 5.0 or 6.0) were computed by BioSIM. Prediction bias was computed by averaging the deviations between observed and simulated dates of peak average instars (over sites and stages, 6 x 4 in 1992 and 5 x 4 in 1993). Similarly, model precision was calculated by averaging the absolute difference between observed and simulated peak dates.

Tests of system performance

Measurement of α and β error

On-site air temperature recorded in the 1993 sample sites provided input data to estimate α error from the simulation models. The accuracy of model predictions using projected temperature data as input was tested for the 1992 and 1993 sample sites. Average model output over 10 replicates for each location and year was compared graphically with observations. Bias was tested for significance using t-tests. Differences in bias and precision between models were tested with analysis of variance.

Relationships between elevation, air temperature and spruce budworm development

To gain further insight and confidence in BioSIM's temperature-projection algorithm, relationships between elevation and mean daily air temperature (from April 1 to July 10) were derived for on-site (1993) as well as projected (1992, 1993) temperature regimes. Similar relationships were obtained from all the weather stations available in the real-time database for either 1992 or 1993 within the area defined by 46°-48°N and 65°-67°W. Slopes and intercepts were compared by analysis of variance-covariance within years.

Relationships between elevation and observed or simulated dates of peak larval indices ($a = 3.0$, 4.0, 5.0 and 6.0) using on-site (1993) and projected (1992) temperature data were determined and compared by analysis of variance-covariance.

Weather-station selection criteria

BioSIM uses two criteria other than cartesian distance in the selection of temperature data sources for a simulation: elevation-difference tolerance and climatic zones. The influence of these criteria on prediction accuracy was tested by relaxing each one separately or both simultaneously. Relaxing these criteria led to the selection of different sources of real-time or normal temperature data for only a portion of the sample sites. This depended on the location and elevation of the sites in relation to climatic zone boundaries and the spatial distribution of the weather stations in either database. A simulation was conducted (10 replicates) for each sample site where changing the selection criteria made a difference in the weather stations selected. When the station type affected was real-time, the simulations were based on available real-time temperature data. When the difference was in the source of normals, only normals were used to generate input temperature information. Average differences in larval indices predicted from the standard and from the alternative weather stations were computed and tested using t-tests (H_0: $\mu = 0$, H_1: $\mu \neq 0$).

Usefulness of model calibration

A series of simulations using projected temperature regimes from stations selected with default selection criteria (maximum elevation-difference at 250 m and using climatic zones) was run with calibration information corresponding to the observed dates of peak 3rd instar ($\hat{a} = 3.0$) for each 1992 and 1993 sample site. Comparisons were made between observed larval indices and those predicted by either the Régnière or the Lysyk model, with and without calibration. Bias, over all sites and years as well as on a site-by-site basis, was tested for significance using t-tests (H_0: $\mu = 0$, H_1: $\mu \neq 0$). Average bias with and without calibration was compared within sites and years, as well as overall, using analysis of variance. The influence of calibration on model precision, averaged over all sites and years, was also tested by analysis of variance.

Forecasting error, δ

The overall patterns of forecasting error (δ) associated with the four target larval indices ($a = 3.0$, 4.0, 5.0 and 6.0) were determined for 1992 and 1993. BioSIM's temperature-regime assembly algorithm accepts as a parameter the latest day (λ) on which real-time temperature data, if available, should be incorporated in a composite temperature regime. Thus, the length of the forecast period can be varied systematically by incrementing λ to simulate the accumulation of real-time temperature data as a season progresses. In the present analysis, λ was incremented from 121 (May 1) to 190 (July 8) in steps of two days. This was done for both models, for all 1992 and 1993 sites, using the default weather-station selection criteria outlined above. In addition, models were run with and without calibration with the "latest" (most recent sample date $\leq \lambda$) phenology information (larval index) from each site. To reduce the importance of the stochastic component of forecasting error (ε), all simulations were replicated 10 times and the two models were run simultaneously using the same input temperature regimes (this task represented a total of 7,700 simulations, requiring 32 CPU hours on a 486/50 computer). The differences between observed and predicted dates of occurrence of the peak larval indices as a function of length of the forecast period were computed for all sites and years, for each model, and for simulations conducted with or without calibration information.

RESULTS

Tests of system performance

Measurement of α error

Simulations using as input the five on-site temperature data sets available from the 1993 sample sites required recourse to BioSIM only to supply March temperature data from the nearest normal-generating weather station. Observed and average simulated larval index curves for the five sites are presented in Fig. 4. Dates of observed and predicted peak larval indices (a = 3.0, 4.0, 5.0 and 6.0) are listed in Table 1.

Both simulation models predicted very closely the early development observed in sites 1993-1, 2, 4 and 5 (Fig. 4). In site 1993-3, the predictions of both models were 5-10 days earlier than observed development in instars 2-4, but agreement was good in instars 4-6. This discrepancy between predicted and observed phenology in site 1993-3 resulted from a combination of circumstances. First, both models predicted molt from 2nd to 3rd instar 2-5 days earlier than observed (this was not the case in other sites). The simulated populations proceeded into the 3rd instar and had reached a point where about 50% of the individuals had molted to the 4th instar by the time of a 5-day cold period between May 29 and June 2 (Fig. 5). While this cold period occurred in all five sites, only in site 1993-3 had the simulated population started molting to the 4th instar before its occurrence. These circumstances exaggerated the lack of fit of both models in this site. The daily range of temperatures recorded in site 1993-3 over the period from April 1 to July 10 averaged 16.24°C, almost 3°C higher than the average over the four other sites (13.26°C; $F = 6.08$, df = 4,520, $P < 0.001$). Daily air temperature ranges in nearby sites 1993-2 and 3 are illustrated in Fig. 5. The cause of this difference is not known, but may be related to the fact that there was relatively little regrowth surrounding the temperature-recording equipment in the clearcut area associated with site 1993-3. An exaggerated range of daily temperatures can have an accelerating effect on phenology models, particularly during the spring (Régnière and Bolstad 1994).

Model predictions and observations were in considerable disagreement during and after the 6th instar, in all sites except 1993-4 (Fig. 4). This discrepancy was most pronounced in sites 1993-2 and 3. The considerable delay in observed development, particularly in these two sites, is typical of collapsing epidemic populations (unpublished data). In such populations, very high mortality rates prevail due to diseases, parasitoids and predators exploiting the late larval and pupal stages. In the first years of outbreak decline, spruce budworm populations often exhibit high parasitism rates by *Meteorus trachynotus* Vier., a braconid wasp that delays development of its 6th-instar hosts. A live 6th instar larva is left behind by the parasitoid when it exits to pupate. These moribund insects can survive several days, even weeks, and are over-represented in samples (Maltais et al. 1989). Although this phenomenon may explain the disagreement in late development in sites 1993-2, 3 and 5, and to a lesser extent in sites 1993-1 and 4, no information on parasitism rates was collected in any of the sites.

Lysyk's model tended to predict slightly earlier than Régnière's, especially in the 5th instar. However, both models predicted the dates of peak larval indices from on-site temperature data in 1993 without significant bias (Fig. 6). Deviations between observed and predicted dates of peak larval indices were not significantly different from 0 (Régnière: 0.4 days, $t = 0.53$, $n = 20$, $P > 0.60$; Lysyk: 1.7 days, $t = 2.04$, $n = 20$, $P > 0.06$) and were not significantly different between models ($F = 1.31$, df = 1,38, $P > 0.26$; Fig. 6A). Similarly, precision (average absolute deviations) was not significantly different between models (Régnière: ± 2.3 days; Lysyk: ± 2.9 days; $F = 0.51$, df = 1,38, $P > 0.48$; Fig. 6B).

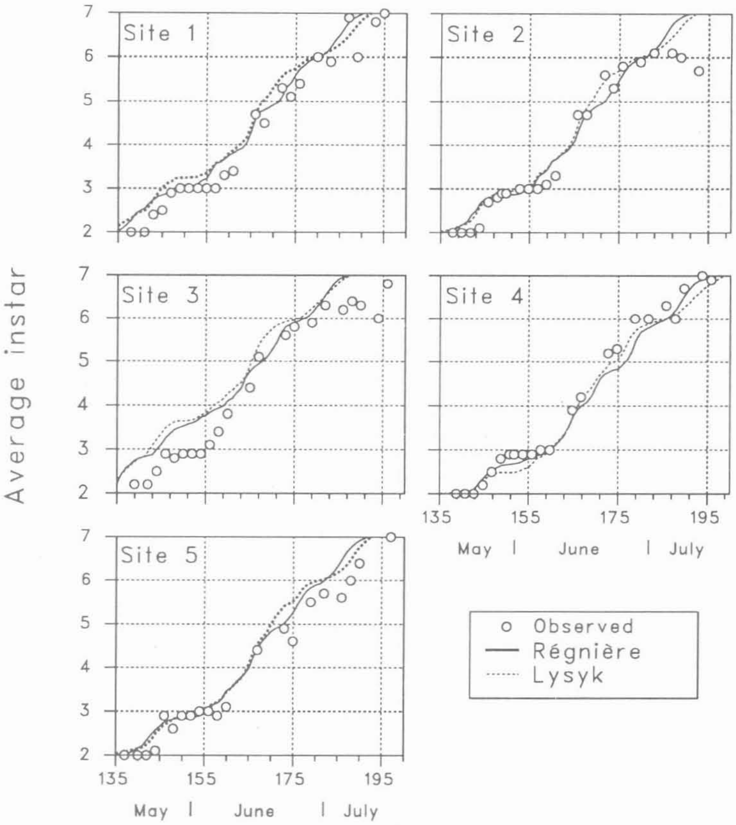

Figure 4.
Observed larval index trends in the five sample sites in 1993 compared with simulations based on on-site temperature records with the phenology models of Régnière and of Lysyk.

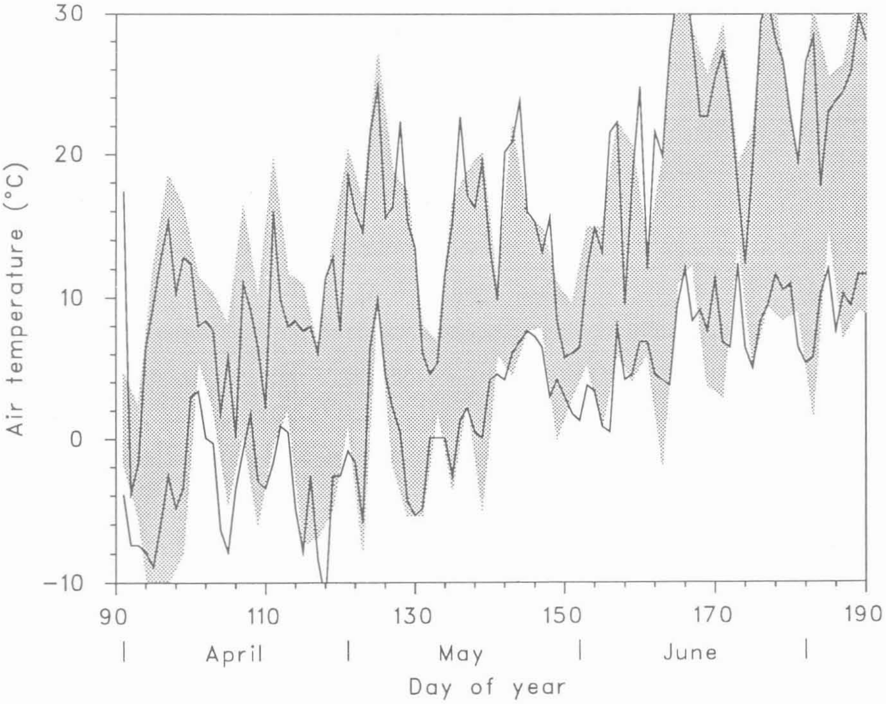

Figure 5.
Daily minimum and maximum air temperatures observed in sites 1993-2 (solid lines) and 1993-3 (shaded area). Note the cold period between days 149 and 152. A similar cold period in early May (days 130-134) did not produce a noticeable problem with simulations because simulated insect populations were still in overwintering. Note also the slightly exaggerated range of temperatures recorded in site 1993-3.

Table 1. Summary of observed and predicted peak larval index target dates (Julian days) for 1992 and 1993 sites

Larval Index	Site	1992			1993				
		Observed	Régnière	Lysyk	Observed	Régnière		Lysyk	
						On site	Projected*	On Site	Projected*
3	1	146	142.6	142.6	150	149.7	155.1	145.5	152.6
	2	146	149.9	146.6	154	155.0	154.8	154.4	154.1
	3	147	151.3	146.7	155	144.2	151.4	142.6	147.0
	4	146	142.0	148.8	157	160.4	161.0	160.0	160.9
	5	146	147.1	143.3	156	156.1	152.4	156.0	146.8
	6	147	149.0	144.2					
4	1	154	151.5	150.4	164	163.8	164.8	163.0	164.7
	2	154	159.1	155.6	164	164.6	164.7	164.4	164.3
	3	155	159.8	158.1	161	158.6	163.0	157.0	162.0
	4	153	150.9	156.8	166	167.4	168.2	166.9	166.7
	5	156	156.8	152.1	166	165.6	164.1	165.0	163.6
	6	155	158.3	154.8					
5	1	164	160.0	158.5	172	170.9	173.4	168.0	170.9
	2	164	171.7	166.5	169	171.6	173.7	169.3	171.9
	3	164	171.5	166.9	167	167.5	169.2	165.7	167.7
	4	160	159.0	164.1	173	176.7	177.9	174.8	176.0
	5	162	166.3	160.1	175	172.8	172.2	171.0	170.4
	6	167	168.0	163.5					
6	1	175	171.0	171.3	182	180.4	181.7	179.0	183.7
	2	175	180.7	177.8	182	180.7	182.7	180.0	185.0
	3	177	181.9	179.8	179	177.1	177.5	176.2	177.7
	4	178	170.0	174.6	181	186.3	187.8	186.0	188.0
	5	173	174.4	172.5	187	182.6	181.3	181.6	183.6
	6	179	175.9	174.9					

* Temperature data from the nearest real-time weather station, adjusted for differences in elevation and latitude. All 1992 predictions are based on projected weather data.

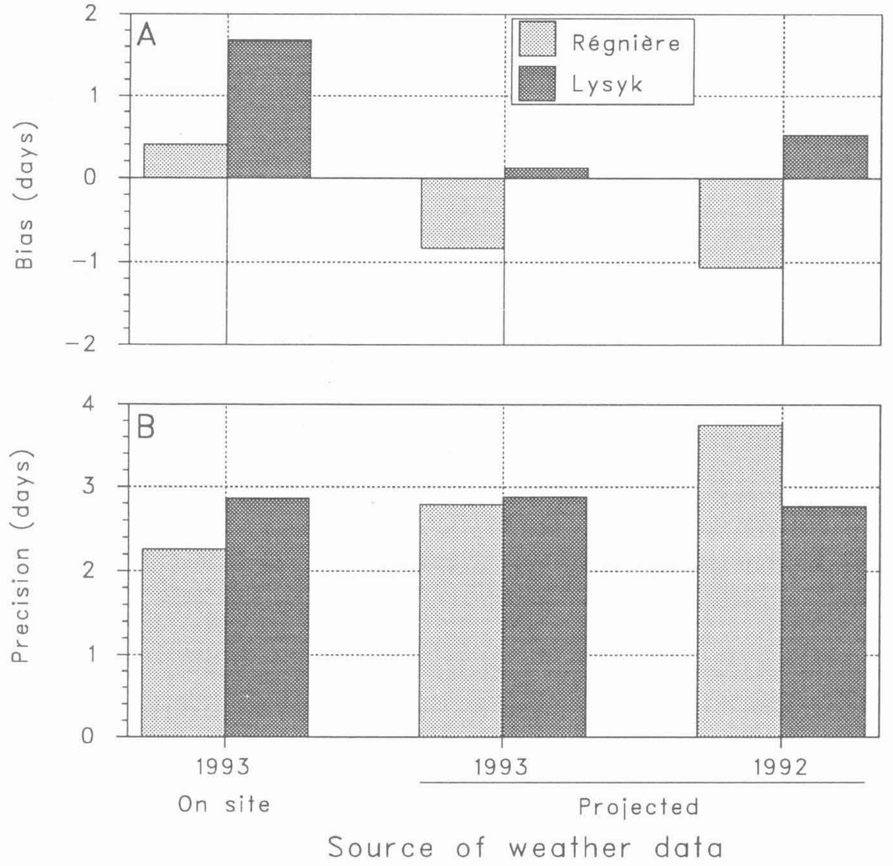

Figure 6. Comparison of deviations between observed and simulated dates of peak larval indices in the sample sites in 1993 (using on-site or projected temperature data) and 1992 (projected temperature data only): (A) bias (average deviations); (B) precision (average absolute deviations).

Measurement of β error

In these simulations, on-site temperature data for 1993 were not used. The weather stations selected by BioSIM (with standard station-selection criteria) for each sample site are listed in Table 2. Sites 1992-1, 1992-4, 1993-3 were located in the East Shore climatic zone (Fig. 3). They were matched with the Bathurst, Chatham and Nepisiguit Falls normals stations, respectively. Real-time sources of temperature data associated by BioSIM with these sites were Bathurst (1992-1 and 1992-4) and Chatham (1993-3). All other sites were located in the Inland climatic zone. Normals stations selected in that zone were Little River Mine (sites 1992-2, 1992-3, 1992-5, 1993-1, 1993-2 and 1993-4), McGraw Brook (site 1992-5) and McGivney (site 1993-5). Real-time weather stations selected were Mannm (site 1992-1), Nictau (sites 1992-3, 1992-5, 1992-6, 1993-2 and 1993-5) and Kedgwick (site 1993-4). Kedgwick (274 m elevation) is at least 92 km northwest of site 1993-4 (425 m), but was the closest source of real-time data within the 250 m maximum elevational difference used as a criterion in BioSIM's selection algorithm.

Table 2. Coordinates of the 1992 and 1993 sample site locations, with the normals and real-time weather stations matched to them by BioSIM

Sample sites	Normals weather stations	Real-time weather stations
1992-1, 47°36’ N, 65°35’ W, 30 m[E]	Bathurst, 47°37’ N, 65°39’ W, 12 m	Bathurst A, 47°38’ N, 65°45’ W, 57 m
1992-2, 47°23’ N, 65°58’ W, 259 m	Little River Mine, 47°17’ N, 66°4’ W, 341 m	Mannm, 47°56’ N, 66°57’ W, 91 m
1992-3, 47°23’ N, 66°21’ W, 366 m	Little River Mine, 47°17’ N, 66°4’ W, 341 m	Nictau, 47°11’ N, 67°12’ W, 171 m
1992-4, 47°02’ N, 65°52’ W, 46 m[E]	Chatham, 47°1’ N, 65°27’ W, 34 m	Bathurst A, 47°38’ N, 65°45’ W, 57 m
1992-5, 47°00’ N, 66°07’ W, 226 m	McGraw Brook, 46°49’ N, 66°07’ W, 53 m	Nictau, 47°11’ N, 66°52’ W, 171 m
1992-6, 47°11’ N, 66°10’ W, 305 m	Little River Mine, 47°17’ N, 66°4’ W, 341 m	Nictau, 47°11’ N, 66°52’ W, 171 m
1993-1, 47°23’ N, 66°22’ W, 300 m	Little River Mine, 47°17’ N, 66°4’ W, 341 m	Upsalquitch, 47°49’ N, 66°52’ W, 91 m
1993-2, 47°18’ N, 66°5’ W, 360 m	Little River Mine, 47°17’ N, 66°4’ W, 341 m	Nictau, 47°11’ N, 67°12’ W, 171 m
1993-3, 47°11’ N, 65°51’ W, 61 m[E]	Nepisiguit Falls, 47°24’ N, 65°47’ W, 106 m	Chatham, 47°1’ N, 65°28’ W, 34 m
1993-4, 47°13’ N, 66°14’ W, 425 m	Little River Mine, 47°17’ N, 66°4’ W, 341 m	Kedgwick, 47°38’ N, 67°19’ W, 274 m
1993-5, 46°47’ N, 66°30’ W, 370 m	McGivney, 46°22’ N, 66°34’ W, 177 m	Nictau, 47°11’ N, 66°52’ W, 171 m

[E] East Shore climatic zone.

The comparison between observed and simulated spruce budworm development, using 1992 and 1993 projected temperature regimes with both phenology models, are presented in Fig. 7. Model bias and precision are illustrated in Fig. 6. In 1993, the predicted phenology using projected temperature data was in slightly closer agreement with observations than predictions based on on-site temperature records. The improvement in accuracy was particularly dramatic in site 1993-3, a fact supporting the hypothesis that temperature records taken in that site were somehow defective. There was no significant bias in the output of either model (Fig. 6), as the average deviations between observed and predicted dates of peak larval indices were not significantly different from 0 (Régnière: -0.8 day, t = -1.14, n = 20, P > 0.27; Lysyk: 0.1 day, t = 0.14, n = 20, P > 0.89). There was no significant difference between models either in bias (F = 0.7, df = 1,38, P > 0.41) or in precision (Régnière: ± 2.8 days; Lysyk: ± 2.9 days; F = 0.02, df = 1,38, P > 0.9; Fig. 6).

The 1992 simulations were also in generally good agreement with observations, although the fit was somewhat less satisfactory than in 1993 (Fig. 7). In all cases, Lysyk's model predicted earlier than Régnière's (3.8 days on average). In the two maritime sites (1992-1 and 4), Régnière's model predicted development more accurately than Lysyk's. In sites 1992-2 and 3, the reverse was true. In sites 1995-5 and 6, the two models performed equally well. Once again, no significant bias was found in the output of either model (Régnière: -1.1 days, t = -1.24, n = 24, P > 0.23; Lysyk: 0.5 day, t = 0.83, n = 24, P > 0.42; Fig. 6) and there was no difference between models in either bias (F = 2.22, df = 1,46, P > 0.14) or precision (Régnière: ± 3.8 days; Lysyk: ± 2.8 days; F = 3.69, df = 1,46, P > 0.06).

Relationships between elevation, air temperature and spruce budworm development

Sample sites ranged in elevation from 30 m (site 1992-1) to 425 m (1993-4). The normals and real-time weather stations linked by BioSIM to these sites covered the ranges 12 to 341 m and 57 to 274 m.

There was a significant relationship between average April-July temperature and elevation in the 1993 data sets (F = 4.52, df = 1,1046, P < 0.034; Fig. 8A). This relationship did not differ significantly between on-site and projected temperature regimes (difference in intercept: F = 0.01, df = 1,1046, P > 0.976; difference in slope: F = 0.05, df = 1,1046, P > 0.816). The pooled slope was -0.32°C per 100 m. The vertical lapse rate calculated for the same period from the 12 real-time weather stations located within the area defined by 46°-48°N, 65°-67°W was not significantly different from that calculated for the sample locations (difference in intercept: F = 1.26, df = 1,2306, P > 0.262; difference in slope: F = 0.03, df = 1,2306, P > 0.857; Fig. 8A).

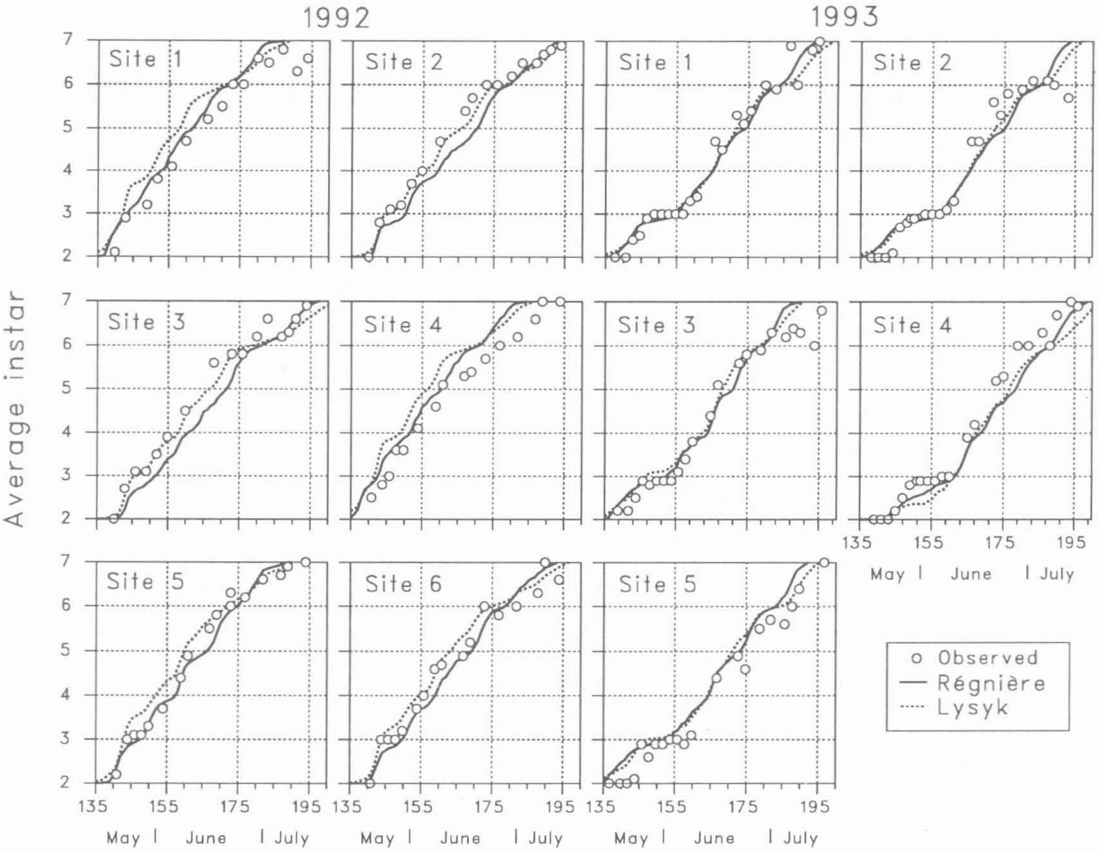

Figure 7. Observed and predicted larval index trends in all sample sites in 1992 and 1993, based on projected temperature data.

No on-site temperature data were available in 1992. Among the six projected 1992 temperature regimes, there was a significant relationship between average April-July temperature and elevation (regression F = 11.29, df = 1,628, P < 0.001; Fig. 8B). The slope of this relationship was -0.75°C per 100 m (Fig. 8B), more than twice that recorded in 1993. The vertical lapse rate calculated for the same period among the 11 real-time weather stations within 46°-48°N, 65°-67°W was not significantly different (difference in intercept: F = 0.14, df = 1,1991, P > 0.710; difference in slope: F = 1.45, df = 1,1991, P > 0.229; Fig. 8B).

The relationships between elevation and observed or predicted dates of peak larval indices in 1992 and 1993 are shown in Fig. 9. In both years, these relationships were highly significant (Table 3). As could be expected, the intercept (mean dates) varied significantly between instars and years, but the slopes of the relationships with elevation were not significantly different between instars. In 1992, this slope was significantly lower for observed (0.48 ± 0.2 days per 100 m) than for predicted (1.79 ± 0.2 days per 100 m) development (Fig. 9). Predicted development was earlier than observed in low-elevation maritime sites 1992-1 and 4, and later than observed in the higher elevation inland sites, particularly 1992-2, 3 and 6. The reason for this difference is not clear. It does not seem likely that it resulted from vertical lapse-rate over-compensation by BioSIM, judging from the lapse rates illustrated in Fig. 8. In 1993, there was no significant difference in slope between observed and simulated development (pooled slope: 1.38 ± 0.3 days per 100 m).

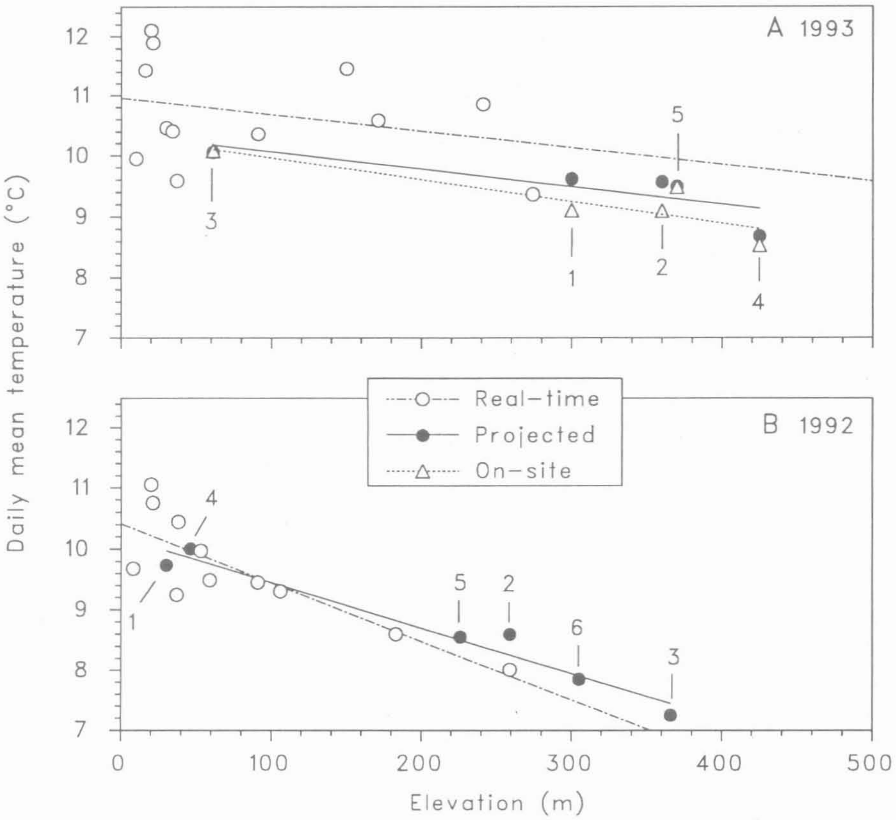

Figure 8.
Relationships between elevation and average air temperature between April 1 and July 10 in northern New Brunswick among on-site (1993 only) and projected temperature data sets, as well as data from all real-time weather stations within the area defined by 46°-48°N and 65°-67°W. (A) 1993; (B) 1992.

Table 3. Analysis of variance tables, influence of elevation on observed and predicted dates of peak larval indices, 1992 and 1993

Source	df	F	P
1992			
Elevation	1, 32	78.71	0.000
Instar	3, 32	160.77	0.000
Observed/Predicted	1, 32	19.71	0.000
Instar * Elevation	3, 32	0.87	0.467
Observed/Predicted * Elevation	1, 32	42.29	0.000
Instar * Observed/Predicted	3, 32	0.68	0.569
Instar * Observed/Predicted * Elevation	3, 32	0.14	0.936
1993			
Elevation	1, 24	22.71	0.000
Instar	3, 24	30.09	0.000
Observed/Predicted	1, 24	0.20	0.659
Instar * Elevation	3, 24	0.37	0.777
Observed/Predicted * Elevation	1, 24	0.91	0.349
Instar * Observed/Predicted	3, 24	0.59	0.627
Instar * Observed/Predicted * Elevation	3, 24	0.46	0.710

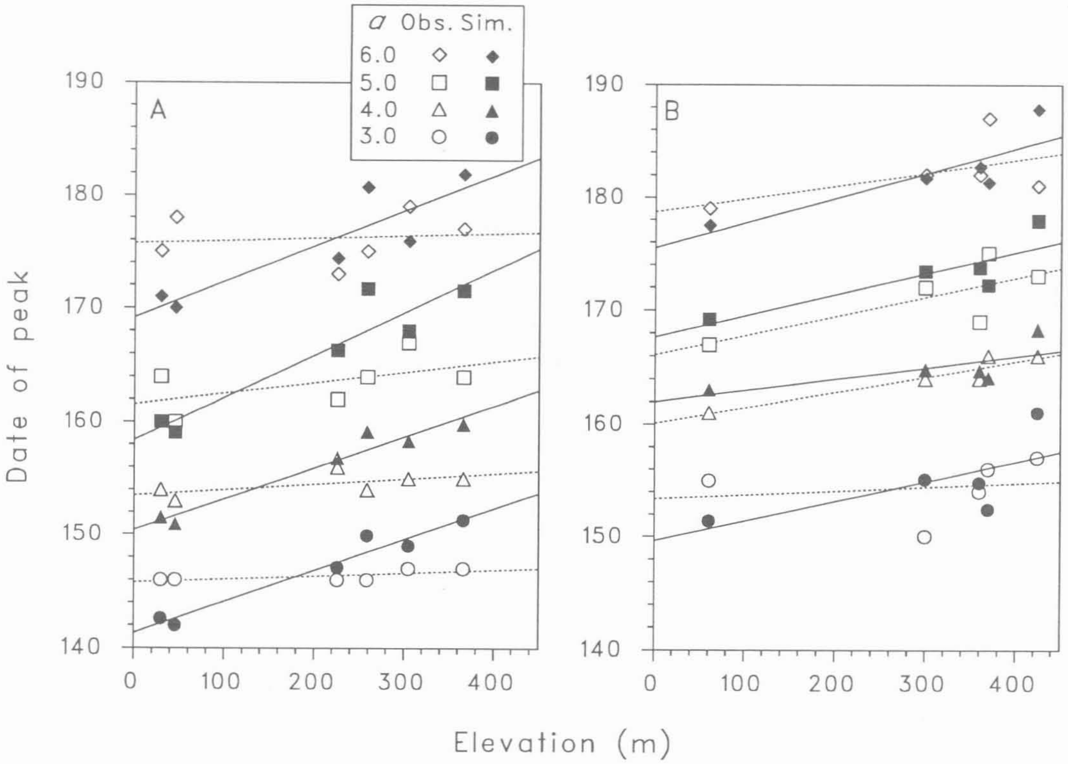

Figure 9. Relationship between elevation and observed or simulated dates of peak larval indices among sample sites in (A) 1992 and (B) 1993.

Weather-station selection criteria

Relaxing the elevation-difference tolerance or the climatic-zone criteria singly or simultaneously led to the selection of alternate real-time and normal weather stations in several cases in 1992 and 1993 (Table 4). Mean differences between larval indices predicted with the standard set of weather data sources (Table 2) and those predicted with data from the alternative sources were often quite large (Table 4). For example, when both criteria were omitted in the selection of a source of real-time temperature data for site 1993-2 (Table 4), model predictions were nearly a whole instar late compared with predictions made from more adequate sources of temperature data.

There was no significant difference between the two models with respect to the effect of relaxing these criteria on model predictions ($F = 0.10$, df = 1,11, $P > 0.757$), regardless of year (interaction $P > 0.82$), selection criterion (interaction $P > 0.804$) or weather-data type (normals or real-time; interaction $P > 0.72$). Deviations in predictions made by the models using the alternate temperature-data sources were significantly different between years (0.01 and 0.55 instar in 1992 and 1993; $F = 59.74$, df = 1,11, $P < 0.001$). Relaxing the elevation-difference criterion alone had a negligible overall effect on model deviations (0.03 instar), but disregarding climatic zones alone or in combination with elevation introduced considerable error in model predictions (0.43 and 0.38 instar; $F = 21.96$, df = 2,11, $P < 0.001$). The influence of climatic zones was most consistent when simulations were based on normals (interaction $F = 7.99$, df = 2,11, $P < 0.007$). When using real-time temperature data, the precise influence of relaxing the station selection criteria depended on each year's specific temperature patterns.

Table 4. Effect of relaxing the elevation-difference and climatic zone criteria for matching weather stations with sample sites on simulated development.

Site	Weather-station type	Matched weather-data source	Régnière		Lysyk	
			$\bar{X} \pm S_{\bar{X}}$	$P(\bar{X} \neq 0)$	$\bar{X} \pm S_{\bar{X}}$	$P(\bar{X} \neq 0)$
		Elevation-difference criterion				
1993-2	Real-time	Upsalquitch Lake, 47°49' N, 66°52' W, 91 m	-0.2324 ± 0.0154	< 0.001	-0.1233 ± 0.0073	< 0.001
1993-4	Real-time	Nictau, 47°11' N, 67°12' W, 171 m	0.0574 ± 0.0073	< 0.001	0.1617 ± 0.0119	< 0.001
1992-3	Normals	Upsalquitch Lake, 47°27' N, 66°25' W, 625 m	0.0712 ± 0.0293	< 0.017	-0.0239 ± 0.0466	> 0.610
1993-5	Normals	McGraw Brook, 46°49' N, 66°7' W, 53 m	-0.4782 ± 0.0280	< 0.001	-0.4336 ± 0.0236	< 0.001
		Climatic zones				
1992-2	Real-time	Mannm, 47°56' N, 66°57' W, 91 m	0.0764 ± 0.0191	< 0.001	-0.0211 ± 0.0159	> 0.190
1992-5	Real-time	Nictau, 47°11' N, 67°12' W, 171 m	-0.0872 ± 0.0241	< 0.001	-0.1482 ± 0.0236	< 0.001
1992-6	Real-time	Nictau, 47°11' N, 67°12' W, 171 m	0.0076 ± 0.0239	> 0.750	-0.1437 ± 0.0172	< 0.001
1992-4	Normals	Renous, 46°48' N, 65°48' W, 46 m	-0.2392 ± 0.0308	< 0.001	-0.2392 ± 0.0386	< 0.001
		Both criteria				
1992-3	Real-time	Bathurst, 47°37' N, 65°39' W, 10 m	0.0493 ± 0.0253	> 0.057	-0.0707 ± 0.0174	< 0.001
1993-2	Real-time	Bathurst, 47°37' N, 65°39' W, 10 m	-0.8566 ± 0.0271	< 0.001	-0.8958 ± 0.0174	< 0.001
1993-4	Real-time	Bathurst, 47°37' N, 65°39' W, 10 m	-0.5244 ± 0.0354	< 0.001	-0.6284 ± 0.0493	< 0.001
1993-3	Normals	Little River Mine, 47°17' N, 66°4' W, 341 m	0.5573 ± 0.0439	< 0.001	0.5917 ± 0.0447	< 0.001

Usefulness of model calibration

Over all sites and years, there was no significant bias (average deviation between observed development and model predictions) in the output of either Régnière's or Lysyk's model, whether or not they were calibrated with the date of observed peak 3rd instar (Table 5). However, on a site-by-site basis, bias was significantly reduced by calibration in 4 of the 11 sites (Table 5). Without calibration, significant bias (either positive or negative) in model output was found in the majority of the 11 sites. Calibration reduced considerably the number of occurrences of significant bias, particularly with Régnière's model. With Lysyk's model, several highly significant biases ($P < 0.001$) became only slightly significant ($P < 0.01$ or 0.05). Over all sites, the average amplitude (absolute values) of biases was significantly smaller with calibration (0.10 instar) than without (0.25 instar).

Table 5. Comparison of average deviations (bias) between observed development and development predicted with and without an observation fix at peak 3rd instar (average instar = 3). Simulations based on projected real-time temperature data

Site	Régnière			Lysyk		
	Fix		**No fix**	**Fix**		**No fix**
1992-1	-0.15	⟸⟹	-0.37***	-0.18*		-0.46***
1992-2	0.06		0.23**	0.07	⟸⟹	0.08*
1992-3	0.06		0.31***	0.11*	⟸⟹	0.12*
1992-4	-0.15		-0.44***	-0.17*		-0.56***
1992-5	0.06	⟸⟹	0.04	-0.01		-0.22***
1992-6	-0.04	⟸⟹	0.08	-0.10	⟸⟹	-0.18**
1993-1	-0.01	⟸⟹	-0.01	-0.04	⟸⟹	-0.02
1993-2	-0.02	⟸⟹	-0.00	-0.03	⟸⟹	-0.05
1993-3	-0.15	⟸⟹	-0.26**	-0.23**	⟸⟹	-0.27***
1993-4	0.16***	⟸⟹	0.26***	0.18**		0.33***
1993-5	-0.13*		-0.32***	-0.20**	⟸⟹	-0.26***
Bias	-0.03 ± 0.03	⟸⟹	-0.04 ± 0.08	-0.05 ± 0.04	⟸⟹	-0.14 ± 0.09
Precision	0.09 ± 0.02		0.21 ± 0.05	0.12 ± 0.02		0.30 ± 0.05

Values significantly different from 0 (t-test) indicated by *, ** or *** ($P < 0.05$, 0.01 or 0.001).

⟸⟹ indicates neighbouring values are not significantly different (ANOVA, $P > 0.05$).

Forecasting error, δ

There was a clear relationship between the length of the forecast period (time remaining to the date of the target event) and the accuracy of model predictions, in both years, and for the peaks of the 3rd, 4th, 5th and 6th instars predicted by both models (Figs. 10 and 11). In 1992, model predictions were later than actual events, because spring and early summer temperatures were warmer than normals. In early spring, forecasts were on average 5-10 days late. In 1993, temperatures were colder than normal in May. Model predictions based on normals were correspondingly early (3-5 days on average). There was little improvement in the forecast accuracy of peak 3rd instar until the forecast period dropped to within 10 days of the actual event (Figs. 10, 11). Peak 4th instar prediction accuracy did not improve until about 15 days from the actual event (Figs. 10, 11). The dates of peak 5th and 6th instars became increasingly easier to predict as the forecast period dropped below 20 (Figs. 10, 11), or even 40 days (Fig. 10).

The use of phenology information to calibrate model predictions did little to improve the predictability of target events (Figs. 10, 11). In this context, predictability is the length of the forecast period over which the predicted target event converges to the observed event. This is not a surprising result given the high degree of accuracy achieved by these models in simulating spruce budworm phenology when provided with adequate (i.e. properly matched) temperature data. Deviations between observed dates of peak larval instars and dates forecasted by the Régnière and the Lysyk models, as well as by the Régnière model using the most recent phenology data, are illustrated on a site-by-site basis in the appendix (Figs. A1-A11).

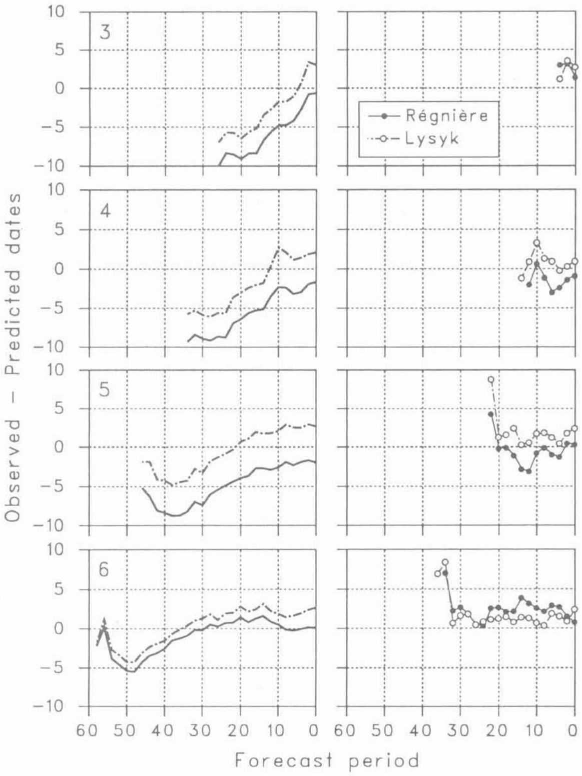

Figure 10.
Deviations between observed and predicted dates of peak larval indices, averaged over the 1992 sample sites, as functions of forecast period (the number of days over which forecast temperatures generated from normals are used as model input). First column: uncalibrated model; second column: models calibrated with "most recent" observed larval indices.

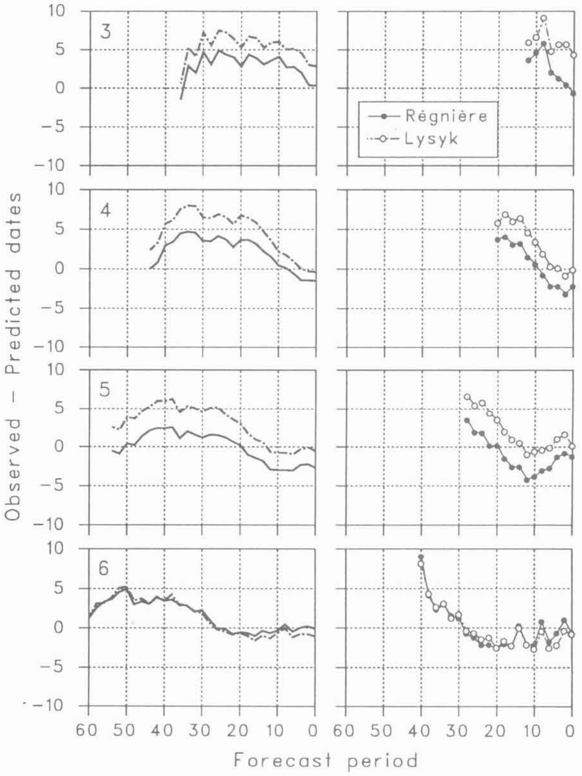

Figure 11.
Deviations between observed and predicted dates of peak larval indices, averaged over the 1993 sample sites, as functions of forecast period (the number of days over which forecast temperatures generated from normals are used as model input). First column: uncalibrated model; second column: models calibrated with "most recent" observed larval indices.

DISCUSSION

The phenology models (Régnière's and Lysyk's) are very consistent with each other and seem quite satisfactory. They show no systematic bias, although on a site-by-site basis they can be consistently off by a fraction of an instar. Their precision (± 3 days) is well within the requirements of operational programs for monitoring and control interventions. However, there is room for improvement in the area of late-larval development. This could most realistically be achieved with Régnière's model, which is process-oriented and therefore readily lends itself to this type of modification (e.g. consideration of natural enemy impact). For example, a model of *Meteorus trachynotus* interaction with spruce budworm already exists (Thireau and Régnière 1995).

BioSIM's temperature-regime assembly algorithm produces quite adequate air temperature series for input into the simulation models. However, three problems have been identified. The first is the necessity of adequately defined climatic zones to accommodate geographical sources of variation not accounted for by the system. In particular for New Brunswick, climatic zones must be used to circumvent the maritime influence. Model predictions for inland sites, if based on data from coastal weather stations, can be off by as much as a whole larval instar. There is a need for a detailed analysis of the maritime effect for incorporation into BioSIM. However, given adequate use of climatic zones, we feel the system can be used as it is. The second issue concerns the scarcity of real-time weather stations in the inland, forested portion of the province. When sufficiently close stations are lacking, BioSIM may be forced to use data from stations that are very far away to respect elevation-tolerance and climatic-zone selection criteria. This was the case, for example, with site 1993-4, which was linked to real-time temperature data from distant Kedgwick. The influence of this problem on model output may not be critical. Finally, automatic weather stations deployed to provide real-time temperature information for BioSIM should be installed and operated according to established meteorological standards. For example, there is some question about the validity of data provided by the weather station installed in site 1993-3 because of the atypically large range of temperatures recorded. In addition, it is important to realize that an unknown and sometimes significant amount of insect development can occur in late March and April at the latitudes and elevations represented in New Brunswick. Thus, the accuracy of model predictions will necessarily be reduced, sometimes quite dramatically, if real-time temperature data are not collected until the beginning of May, as is commonly done with the current weather-station network used in forest fire management in New Brunswick.

BioSIM's air-temperature projection algorithm makes adjustments for elevation and latitude. These adjustments produced relationships between elevation and mean temperature that were realistic and indistinguishable from observations. Interestingly, these relationships varied significantly between years. When using BioSIM in forecasting mode (normals only), however, this relationship would be constant and determined only by the weather stations selected to generate it. The influence of elevation on spruce budworm development seems somewhat lower than in other species. For example, slopes of 1.4 and 3.0 days per 100 m were reported by Russo et al. (1993) and Schaub et al. (1995) for gypsy moth egg hatch. However, low-elevation sites in the present study were located in an area subject to pronounced maritime influence. This influence reduces both average and daily range of spring and summer temperatures, both leading to slower insect development and thereby reducing the developmental gradient assigned to elevation. Given the relatively good general agreement in relationships with elevation between observed and simulated spruce budworm development, topographical projections of spruce budworm phenology can be accurately simulated using BioSIM. Thus, so-called t-functions derived with BioSIM from series of simulations could be used to transform algebraically digital terrain models into digital phenology models for use in the development of pest management plans. To further refine the precision of such topographical projections, it may be desirable to investigate the influence of other terrain-related factors, such as cold-air drainage and exposure (slope, aspect) on local or microhabitat temperatures.

The use of model calibration (most recent local phenology information, or regional adjustments) can significantly enhance the accuracy of model predictions, particularly in terms of increased site-by-site precision. Thus, in an operational context, it would be beneficial to maintain a limited number of strategically located sample sites for model calibration. It is important to emphasize that the models tested here were highly accurate and that the data provided for calibration must be rather precise themselves to avoid degrading model performance. Such a regional approach to model calibration would require minor modifications to BioSIM to accept a relative calibration instruction (Δa rather than a itself).

The accuracy of phenology forecasts based on normals depends on two main factors: the length of the forecast period (the farther in the future the target is, the less accurate the forecast), and the deviation of the actual season's temperature from normals (i.e. "warm" or "cold" weeks or months). However, this study indicated that the predictability of a target event also depends to a large extent on the amount of development that needs to accumulate before its occurrence. Thus, early-occurring events (e.g. peak 3rd instar of spruce budworm) are difficult to predict far in advance simply because most of the development involved takes place in the few days or weeks immediately preceding their occurrence. This unavoidable situation directly affects the reliability of phenology forecasts relating to operational timing of treatments having early phenology targets. It is in this context that accurate 5-day temperature forecasts would be the most valuable. In the case of spruce budworm peak 3rd instar, such a 5-day increase in the forecast period may provide a 30-50% improvement in predictability. Later-occurring events, such as 5th or 6th instars, require a much longer development period and are easier to predict quite some time in advance. Under these conditions, there would be less advantage to using 5-day temperature forecasts.

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APPENDIX

Figures A1 to A11 depict the seasonal progression of BioSIM forecasts of the dates of peak larval stages as real-time temperature data became available for the six sites in 1992 and five sites in 1993. The sequence of events are peak 3rd, 4th, 5th and 6th instars (Larval indices = 3.0, 4.0., 5.0 and 6.0). Horizontal lines: observed dates. Solid lines: Régnière's model predictions. Dotted lines with open circles: Régnière's model using most recent phenology data from the site as calibration. Dot-dashed lines: Lysyk's model predictions (without calibration).

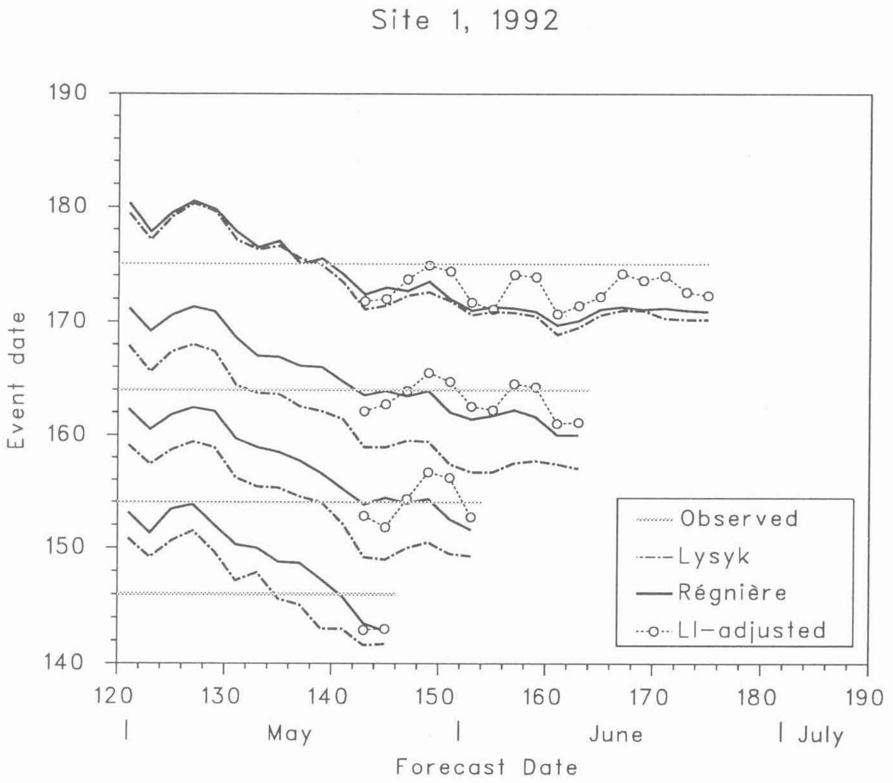
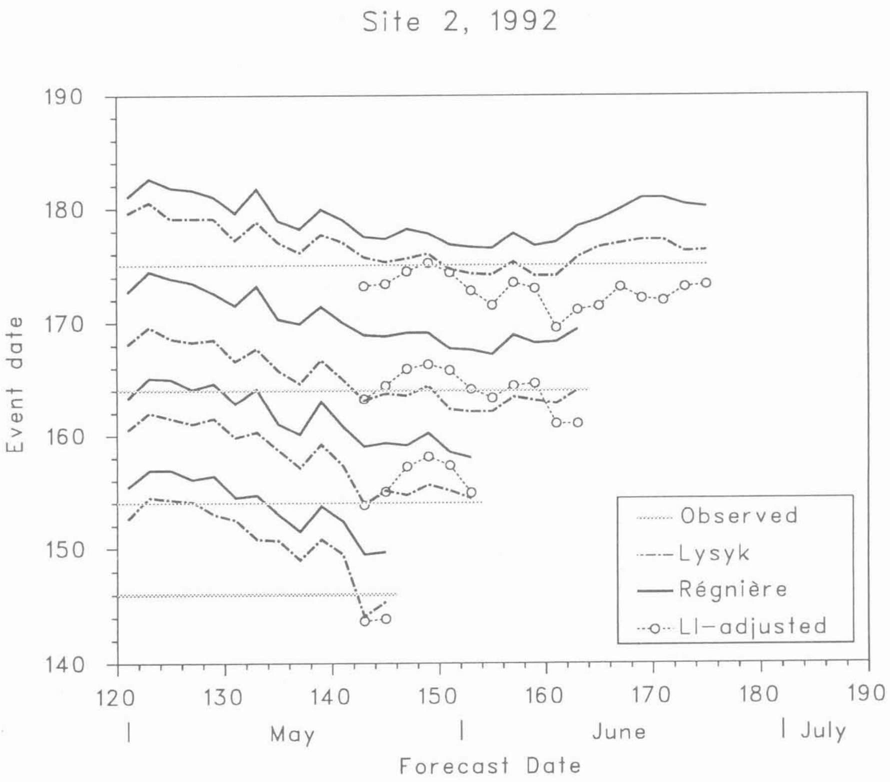


Figure A1



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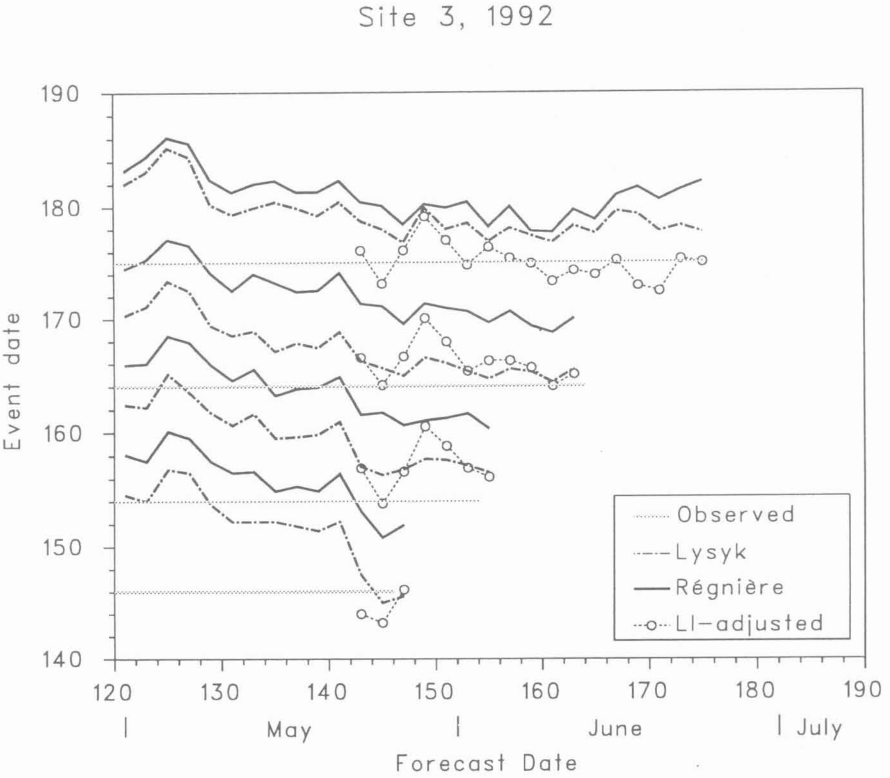

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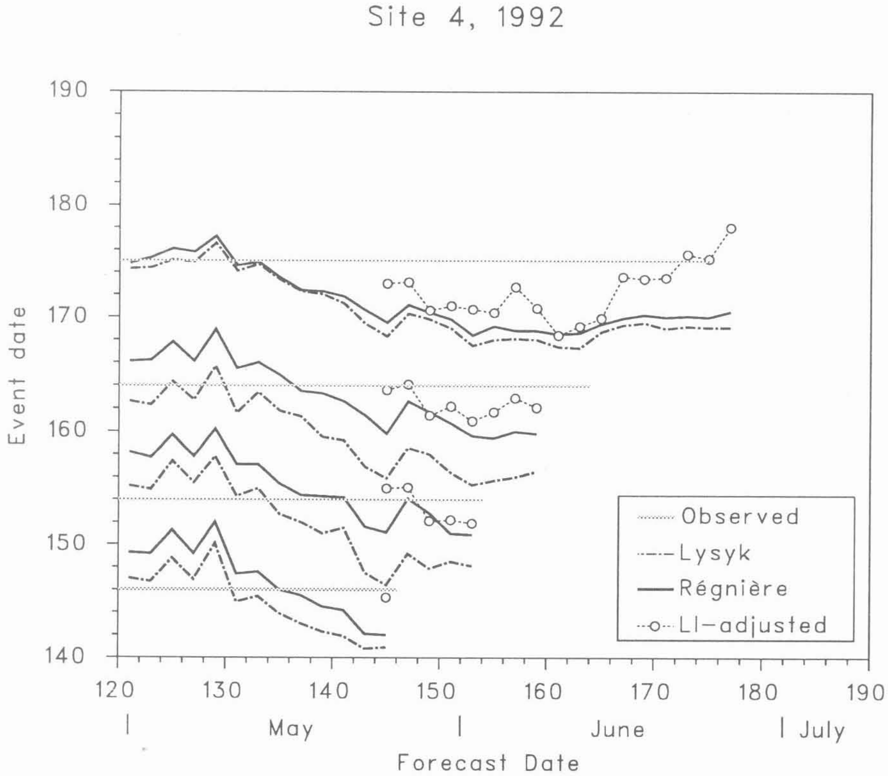

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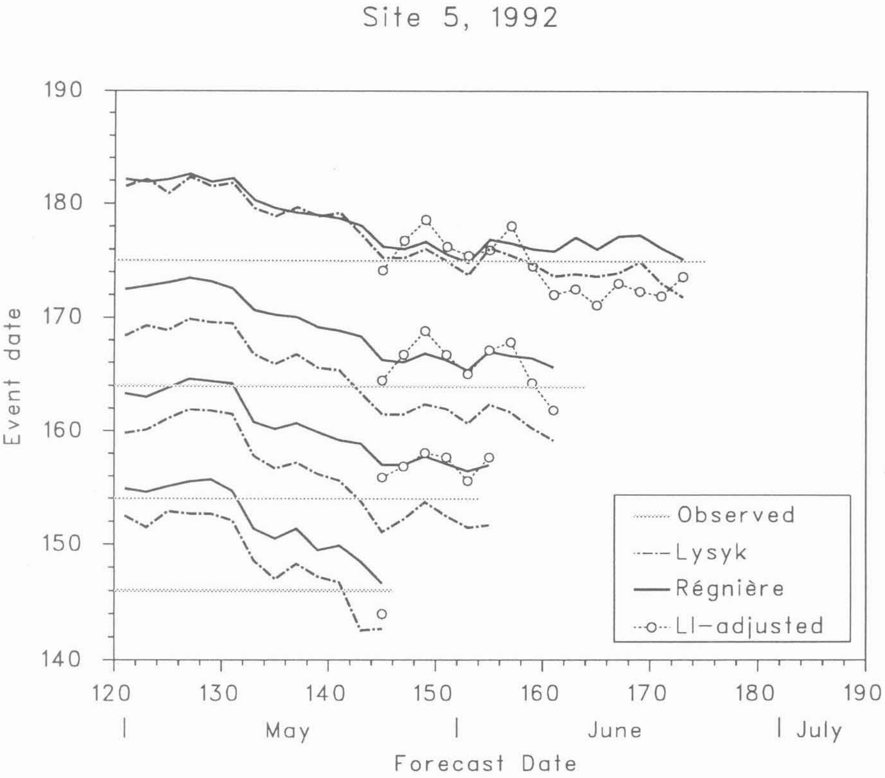

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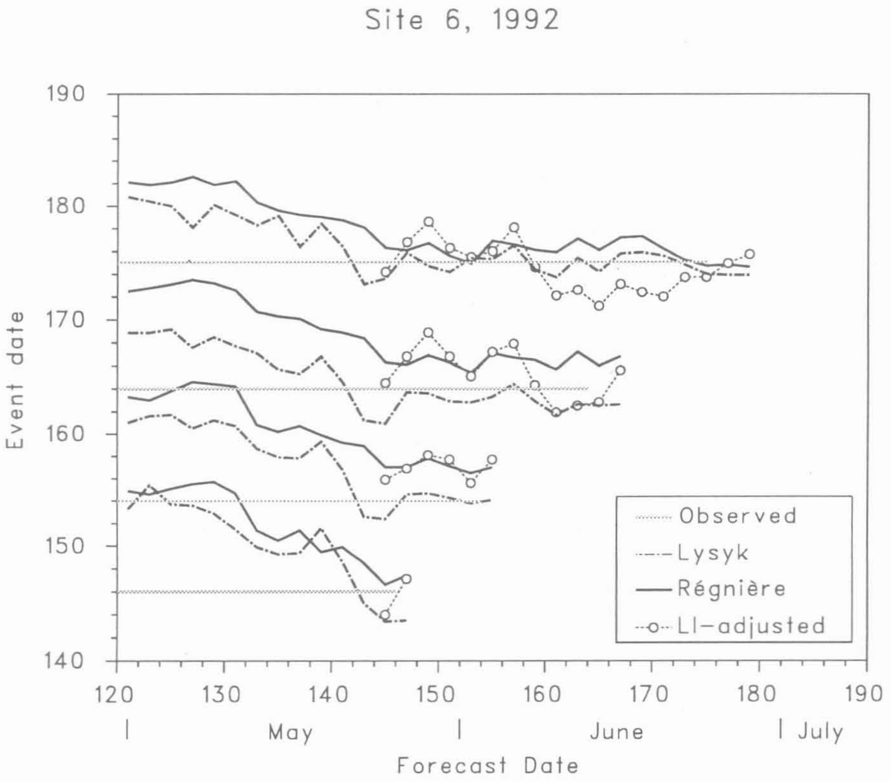

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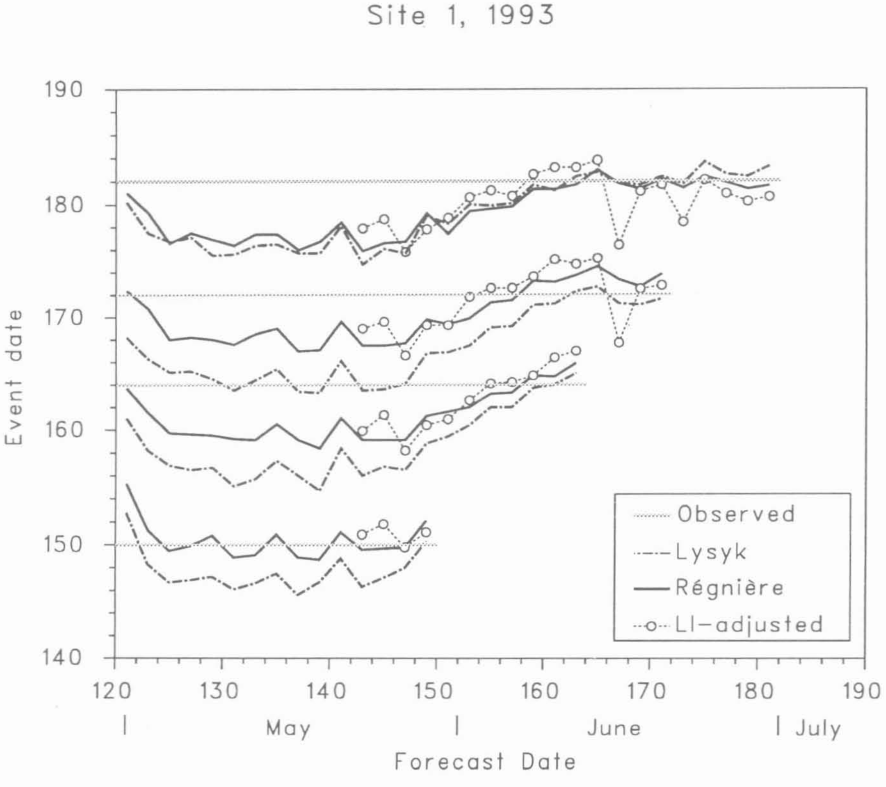

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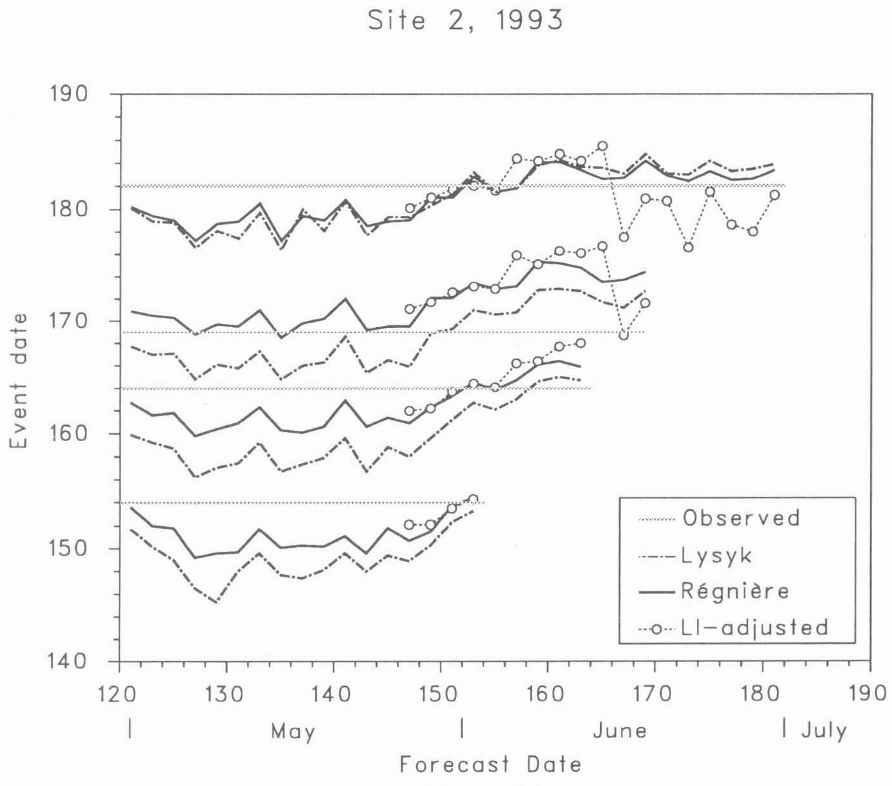

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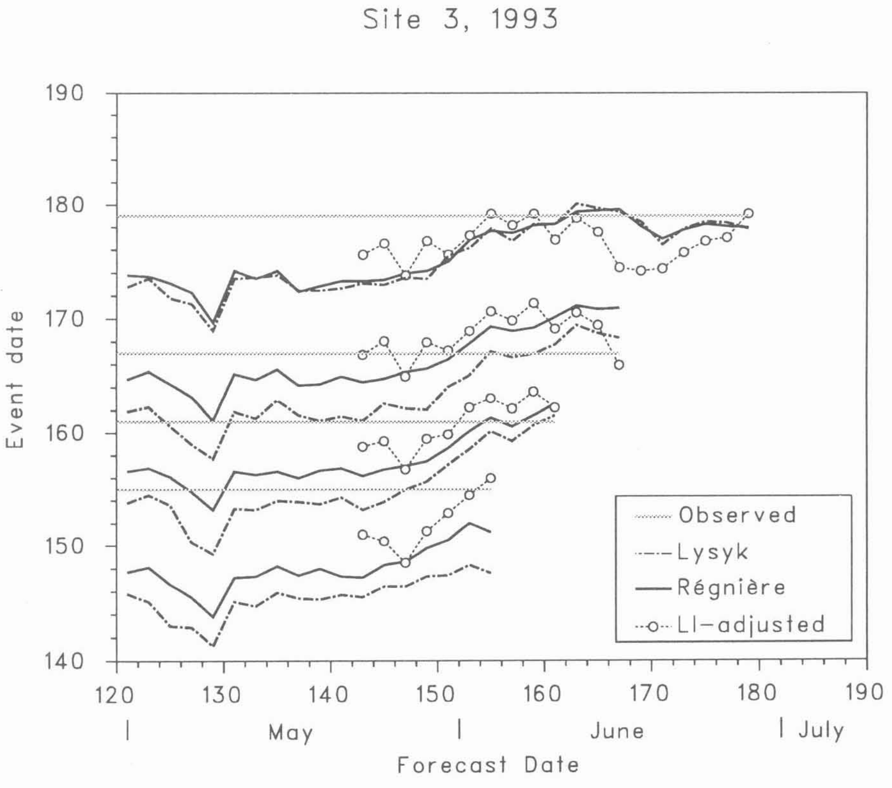

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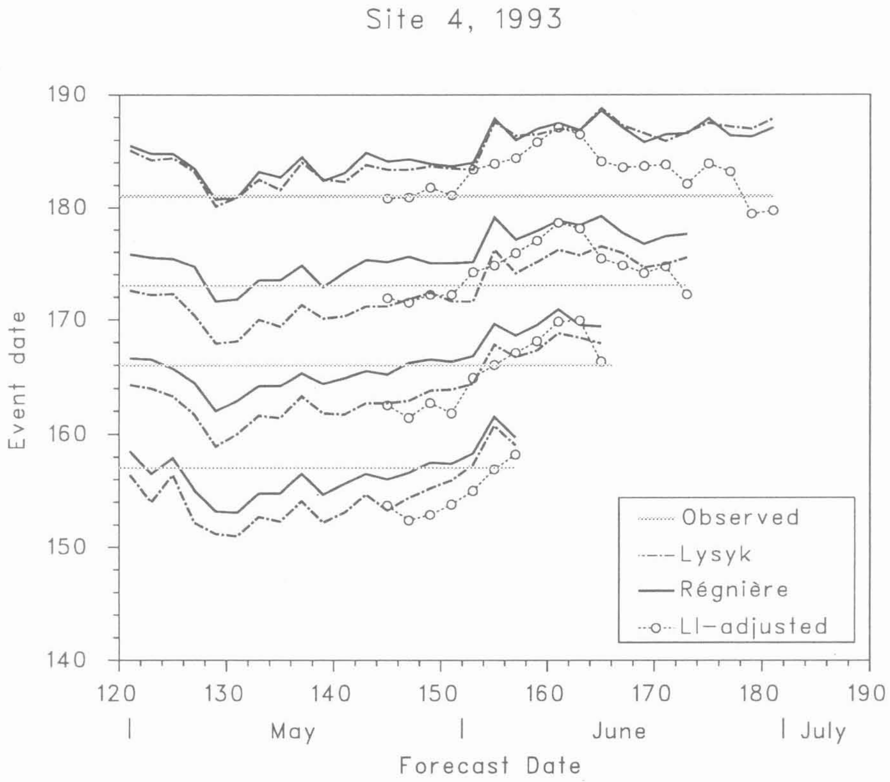

Figure A10

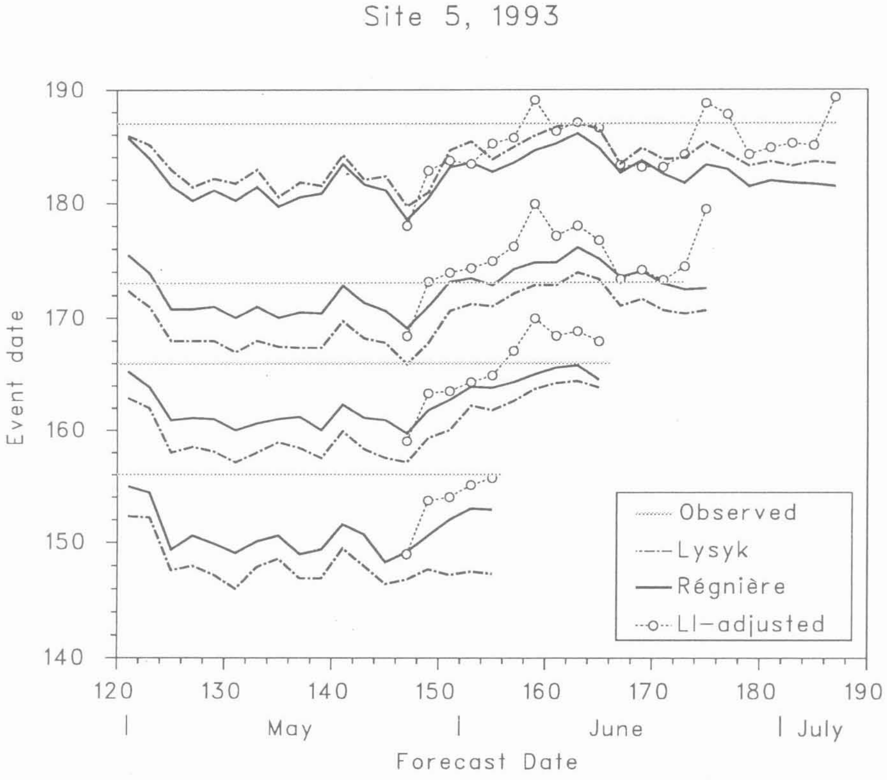

Figure A11