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Using Geographically Robust Models of Insect Phenology in Forestry

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1. Introduction

The history of observations of phenology dates to at least the 11th C BCE (Chen, 2003) when phenological events (commonly the flowering of woody plants) were recorded together with descriptions of weather and farming events. The principle objective of these early unsystematic observations was to improve agriculture. This general objective continued into the 13th C when it became accepted that repeated observations could provide insight into natural processes (Demarée & Rutishauser, 2011). In the 18th C Carl Linnaeus made special note of anomalous phenological events and inter-species synchrony. The principle objective remained the improvement of agriculture, and phenological calendars were compiled for individual regions in recognition that phenology varied geographically. Phenological calendars of the modern era include attempts to predict phenology based on longitude, latitude and elevation (Chen, 2003). Hopkins "Bioclimatic Law" (Hopkins, 1938) predicts the progression of spring phenological events based on these three geographic coordinates.

Despite the long history of phenological observations, it was not until 1849 that the term "phenology" first appeared in print (Demarée & Rutishauser, 2011) in an article by Charles-François-Antoine Morren (1807–1858). In 1735 Réne Antoine Ferchault Réaumur suggested that differences between locations in phenological events could be explained by differences in daily temperatures summed from some arbitrary date to the date of interest (Réaumur, 1735). Réaumur is now commonly credited with the concept of the degree-day sum model that continues to be widely used today.

Integrated pest management (IPM) has been one of the strategies to improve agricultural (including forestry) productivity. The prediction of pest phenology is a critical component of an IPM strategy (Damos & Savopoulou-Soultani, 2010) whether it is for the efficacious application of pesticides or for optimizing biological control tactics (Moerkens et al., 2011). Insect phenology models have been developed in response to this need, particularly within the agricultural industry. Insect phenology models are less common within forestry probably because there are fewer insect pest species and options for pest control are more limited so a model is not needed. Insect phenology models may be less common in forestry also because major insect pest species occur over a larger spatial scale in forestry than in agricultural, the accompanying topographic and climatic complexity is therefore greater, and the ability to accurately predict phenological events has been more difficult (Schaub et al., 1995).

The ability of a phenology model to perform satisfactorily over a broad, and climatically variable geographic range has been termed geographic robustness (Gray, 2004). This chapter examines the development of two geographically robust models of insect phenology in forestry, and the emerging application of geographically robust phenology models to investigate basic ecological questions such as population establishment and stability under changing climatic conditions, and risk assessment of alien pest introduction.

2. Insect developmental rates and temperature

Among the requisites of every insect is the availability of food during its feeding stage[s] and suitable temperatures to complete its life cycle. These needs can be summarized as a requisite seasonality. Seasonality is the predictable "occurrence of [a life stage event] within a definite limited period or periods of the astronomic (solar, calendar) year" (Lieth, 1974: 5). Implicit in this definition for temperate forest insects is the attainment of a cold-hardy stage before the onset of cold winter temperatures, that the emergence of the post-winter feeding stage will coincide with the availability of suitable food (which is often newly emerged foliage, hence the requisite of phenological synchrony between host trees and its insect herbivores), and that these events will coincide sufficiently each year for the continual survival of the population. Temperature, photoperiod, moisture and nutrition all influence insect phenology. Of these factors, temperature is the most spatially and temporally variable, is the strongest determinant of poikilotherm phenology, and is perhaps the best understood.

Insects progress through a life stage at a rate (R) that is dependent on the temperature (T) of that time (t):

$$R(t) = f\left(T\left[t\right]\right) \tag{1}$$

The developmental rate at a constant temperature T is calculated as the inverse of the time (d) needed to complete the life stage ($1/d$). The physiological age (A) of an individual at time t is given by the integral of the function

$$A(t) = \int_0^t f\left(T\left[t\right]\right) dt \tag{2}$$

and physiological age can be thought of as the state of the individual (i.e., the proportion of the life stage completed). The life stage is completed (and the subsequent life stage is begun) when physiological age reaches 1. In a computational environment (i.e., a simulation of insect phenology) developmental rates are calculated for each small time step Δt, and the stage is completed at $t = t_c$ when

$$\sum_{t=0}^{t=t_c} f\left(T\left[t\right]\right) = 1 \tag{3}$$

This generalized construct assumes that the response to a given temperature (T) is uniform for the duration of the life stage (i.e., $A = 0$ to 1). As we shall see (below), this assumption is infrequently tested, and at least in some cases where tested has been shown to be invalid, and developmental rate (R) is temperature and age dependent :

$$R(T[t]) = f\left(T[t], A[t]\right) \tag{4}$$

The earliest numerical relationship between developmental rate of insects and temperature used the linear heat summation model of Réaumur (1735). The general form of the model is

$$d = DD/\left(T - T_{\min}\right) \tag{5}$$

where d is the duration of the phenophase at temperature T, $T_{\min}$ is the temperature below which no development occurs, and DD is the thermal constant (i.e., the number of degree-days above $T_{\min}$ during the phenophase). Estimates of the thermal constant (DD) of a species can be obtained in the laboratory under a range of constant temperature regimes by conducting a simple linear regression between temperature (T) and the inverse of the duration of the life stage at constant T:

$$\frac{1}{d} = \frac{1}{DD}T + m \tag{6}$$

A minimum temperature threshold ($T_{\min}$) for development is the x-intercept of regression equation (6), and is equal to

$$T_{\min} = -m \times DD \tag{7}$$

Field estimates of DD are obtained by assuming a reasonable $T_{\min}$ and summing the number of degrees by which the daily mean temperature exceeds $T_{\min}$ until the phenophase is completed. The ease with which parameters can be estimated, and more importantly, the ease with which phenological predictions can be made, have made linear heat summation (i.e., degree-day) models very popular.

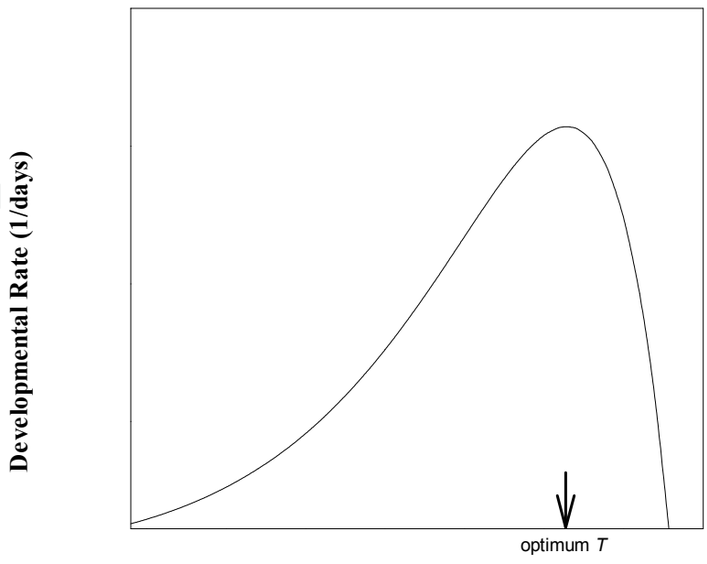


Fig. 1. Generalized developmental rate curve.

As early as 1932, the non-linear nature of the developmental rate function in insects was observed (Janisch, 1932) and various non-linear functions have been proposed and adopted (see (Wagner et al., 1984) for an early review). It is now widely accepted that developmental rates increase, with a positive first derivative, at low temperatures and decrease abruptly above some optimum temperature (Fig. 1). Logan et al. (Logan et al., 1976) used the technique of matched asymptotic expansion to capture this dual and asymmetric nature of the developmental rate function; their two formulas (with an exponential or a sigmoidal behavior for the low temperature segment) are now widely used. But non-linear models of phenological development did not become common until parameter estimation and summation of non-linear functions were simplified by the ready availability of digital computers.

3. Variability in developmental rate response

Part of the inherent variability within a population of insects includes developmental responses to temperature. Estimating this variability, and including it, in phenology models is important: pest management decisions are often made on the basis of the timing of early emerging insects (i.e., those with faster than average developmental responses); estimates of population stability depend more on the responses of the population as a whole than the response of just the average (or median) individual in the population (see below for a discussion of estimating population stability from phenological predictions). Population variability has been included in phenology models most often by one of three methodologies. The first is by using distributed delays (Manetsch, 1976) wherein individuals pass through a number of discrete "boxes" within each life stage in such a way that output from the life stage (and progression to the next life stage) depends on the number of boxes and transition rates between boxes. The second, and admittedly less abstract method, is to partition the population into subsets that each display a different developmental response (Stinner et al., 1975); the combination of the subsets reflects the population variability. This can be termed the "same-post" construct, in that all individuals develop to the same end post, but at different rates. The third methodology involves calculating normalized developmental times (τ) from a set of constant temperature observations:

$$\tau = \frac{time@T}{\text{median } time@T} \tag{8}$$

and describing the cumulative probability distribution of normalized times with an appropriate function (Sharpe & Demichele, 1977; Sharpe et al., 1977). This method is the most computationally efficient because the entire population is simulated using only the median developmental rates ($\tilde{R}(T)$ with the result that the proportion of the population (p) that has completed the life stage at time t is equal to the value of the cumulative probability distribution function for the summed developmental rates at time t

$$p(t) = \int_0^t \tilde{R}(T)\, dt \tag{9}$$

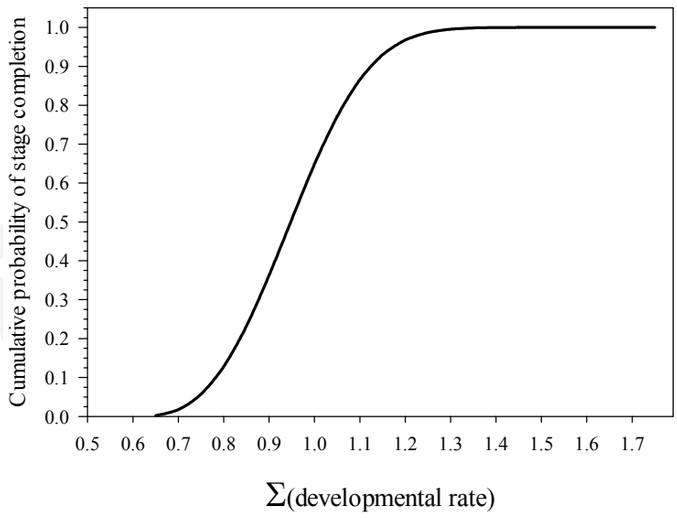


Fig. 2. Probability of stage completion with same-rate construct.

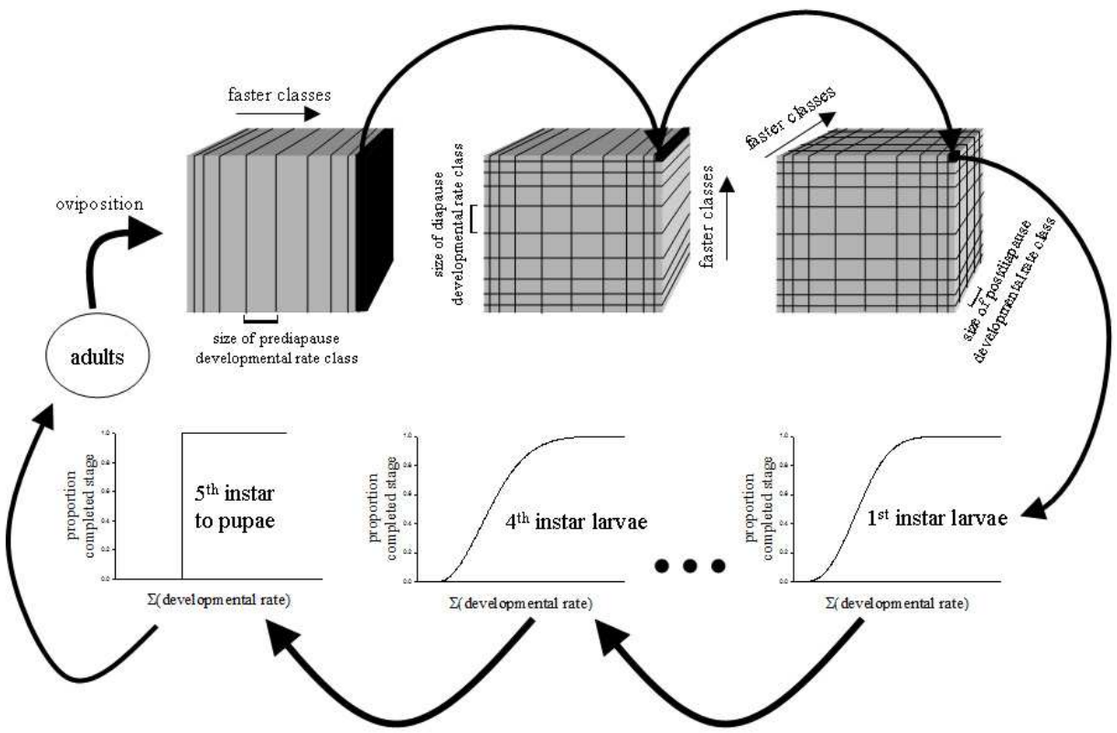


Fig. 3. A mixture of same-post and same-rate construction.

(Fig. 2). This can be termed the "same-rate" construct, in that all individuals develop at the same rate, but to different end posts. It has the obvious drawback that the whole population is assumed to respond according to the same developmental rate function; and therefore, the whole population fails to age when temperature (T_i) is below the developmental threshold, whereas it would be more accurate to age the portion of the population whose developmental threshold is lower than T_i. Gilbert et al. (2004) expanded an age-structured partial differential

model to account for variability over the full range of the rate curve. Gray (2004) used a combination of the same-post and the same-rate methods (Fig. 3) to model gypsy moth (*Lymantria dispar* (L.)) egg development after showing that developmental responses during diapause (Gray et al., 2001) and postdiapause (Gray et al., 1995; Gray, 2009) are dependent on physiological age and temperature—this violation of independence on physiological age meant that age variability had to be specifically modeled in the population.

4. Geographic robustness of phenology models

High populations of forest insects often exist over very large geographic areas: during periods of outbreaks the spruce budworm (*Choristoneura fumiferana* Clem.) can occur in great abundance over an area of several hundreds of thousand km² (Hardy et al., 1986); a recent outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) occurred in over 90 ×10³ km² (Aukema et al., 2008) of topographically diverse western Canada; the range of gypsy moth (*Lymantria dispar* L.) in North America extends from the Atlantic coast to the western Great Lakes, south to North Carolina and north into New Brunswick, and isolated populations have been detected in British Columbia, California, Utah, and many other

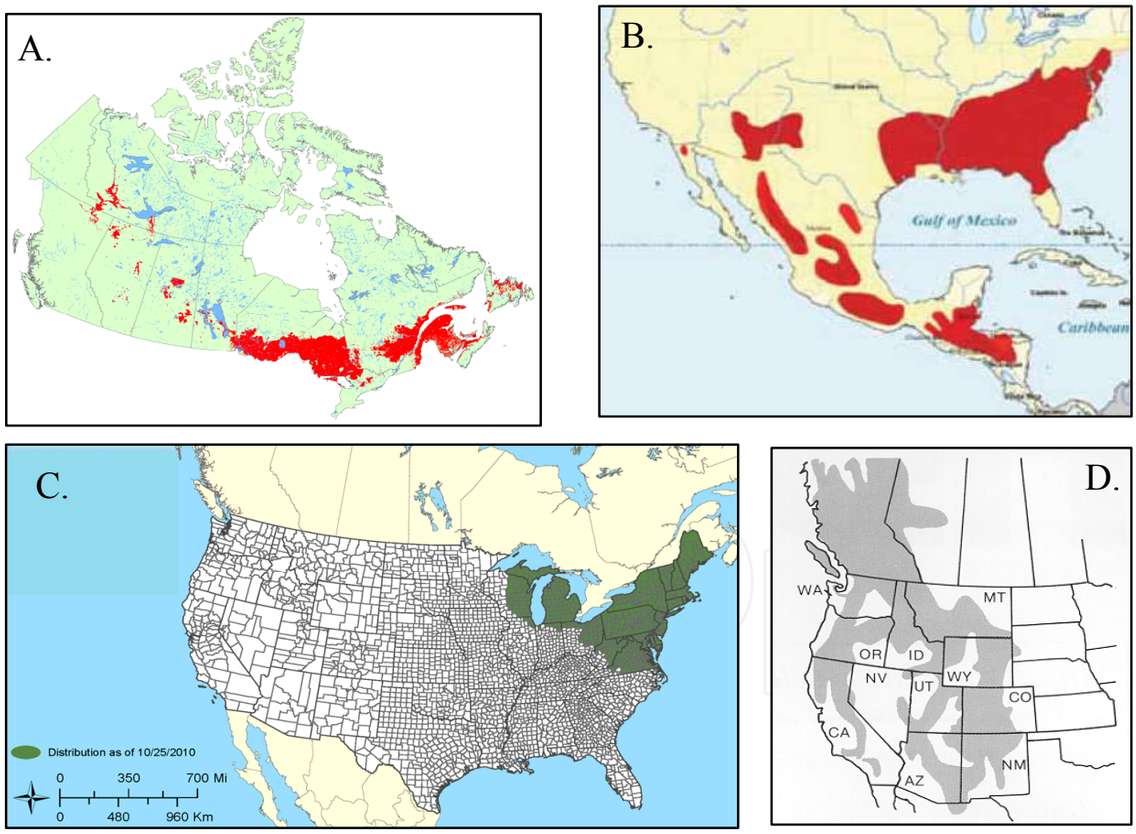


Fig. 4. Outbreak ranges of four dominant forest insect pests in North America
A) spruce budworm (Gray, unpublished; USA range not shown);
B) southern pine beetle (Salinas-Moreno et al., 2004);
C) gypsy moth (Canadian range not shown) (USDA: http://nrs.fs.fed.us/tools/afpe/?src=);
D) mountain pine beetle (Amman et al., 1990 (reprinted)).

locales; the range of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) extends from Pennsylvania to Nicaragua (Fig. 4). Temperatures vary greatly over such large areas, and, therefore, insect development will vary also. The expected accuracy of a phenology model, measured on a large landscape scale is a function of the geographic robustness of the model—the ability to perform satisfactorily over a broad, and climatically variable geographic range (Gray, 2004). That few phenology models exhibit satisfactory geographic robustness can probably be attributed to at least one factor, and the implications that arise from that factor: an accurate description of the relationship between temperature and insect development has been elusive for the diapause developmental phase that is common among temperate insects.

The circular nature of insect life-cycles means that there is no default life stage at which to initiate a phenology model; instead an arbitrary "biofix" is chosen at which all individuals begin development (Logan & Bentz, 1999). The combination of the difficulty in modelling diapause development, and the greater interest in the feeding life stages (i.e., the larvae) has resulted in the construction of many phenology models that use diapause completion as the biofix (see as examples Moerkens et (2011) and many others). Here, I will describe early models of gypsy moth egg phenology to illustrate the likely reason for a lack of geographic robustness. The larvae within newly oviposited eggs begin development in a prediapause phase that is characterized by abundant morphological development (Leonard, 1968) and developmental rates that are favored by high temperatures (Gray et al., 1991). After spending 25 days in prediapause (assuming a constant temperature regime of 20°C), the gypsy moth enters the diapause phase, which is characterized by a virtual absence of morphological development and developmental rates that are favored by low temperatures (Gray et al., 2001). During the postdiapause phase, developmental rate is again favored by high temperatures (Gray et al., 1995). Eggs hatch upon completion of the postdiapause phase. Due largely to the difficulty in observing, either directly or indirectly, the transition between successive phases, model developers have modeled only the postdiapause phase after assuming that diapause is completed by the arbitrary biofix (Johnson et al., 1983; Waggoner, 1984; Lyons & Lysyk, 1989; Hunter, 1993). However, any error in choosing the date of diapause completion/postdiapause initiation (the biofix) results in an error in the amount of phenological development still to be completed for egg hatch, and a concomitant error in the estimate of developmental rate response to temperature. A date that precedes the true date of diapause completion will underestimate postdiapause developmental rates because d, the number of days to complete postdiapause was inflated by the portion of diapause not yet completed. A date that succeeds the true date of diapause completion will overestimate postdiapause developmental rates because d was deflated by the portion of postdiapause already completed. When such a model is run only in the locale where it was developed, the error in the date of diapause completion will tend to be compensated for by the error in developmental rates because the climatic regime within the locale tends to be consistent from year to year. However, when such a model is run in a locale with a markedly different climatic regime, the errors will lead to a bias in egg hatch prediction. Phenology models of larval development (Logan et al., 1991) will then commence with biased predictions of egg hatch. In two examinations of gypsy moth egg phenology models (Nealis et al., 1999; Régnière & Nealis, 2002), models that had been developed in NE United States (Johnson et al., 1983) and central Canada (Lyons & Lysyk, 1989) performed very

poorly when tested against observed egg hatch in western Canada (Victoria, British Columbia)—they lacked geographic robustness. The model of Sawyer et al. (1993) includes the diapause phase and was developed using a combination of geographically diverse laboratory and field observations of egg hatch. It performed better than the former two models in the Victoria test; however, it performed poorly against a small subset of the same observations used in model construction.

The gypsy moth egg phenology model of Gray includes the prediapause (Gray et al., 1991), diapause (Gray et al., 2001), and postdiapause phases (Gray et al., 1995) of egg development. They used detailed measurements of the respiration rates of individual eggs to monitor phase transition (and therefore phase duration) under controlled temperatures. Their observations of postdiapause development demonstrated that the classic assumption that developmental response to a given temperature is uniform for the duration of the life stage (or phase, in this case) is invalid (Gray et al., 1995). They estimated "instantaneous" developmental rates at five temperatures and constructed an age- and temperature-dependent response curve for the postdiapause phase (Fig. 5). Estimates of "instantaneous" developmental rates during the diapause phase could only be modeled assuming control by two simultaneous temperature-dependent processes: (1) a typical developmental response to temperature that is inhibited by a temperature-activated biochemical agent; and (2) the temperature-dependent removal of the inhibiting agent (Fig. 6). Diapause is a critical developmental phase in maintaining seasonal development within a locale; and an accurate estimation of the day of diapause termination is a critical component of a geographically robust phenology model. The egg hatch model of Gray showed the highest level of geographic robustness in the Victoria test (Nealis et al., 1999; Régnière & Nealis, 2002); its geographic robustness has been improved more recently by a newer postdiapause submodel (Gray, 2009).

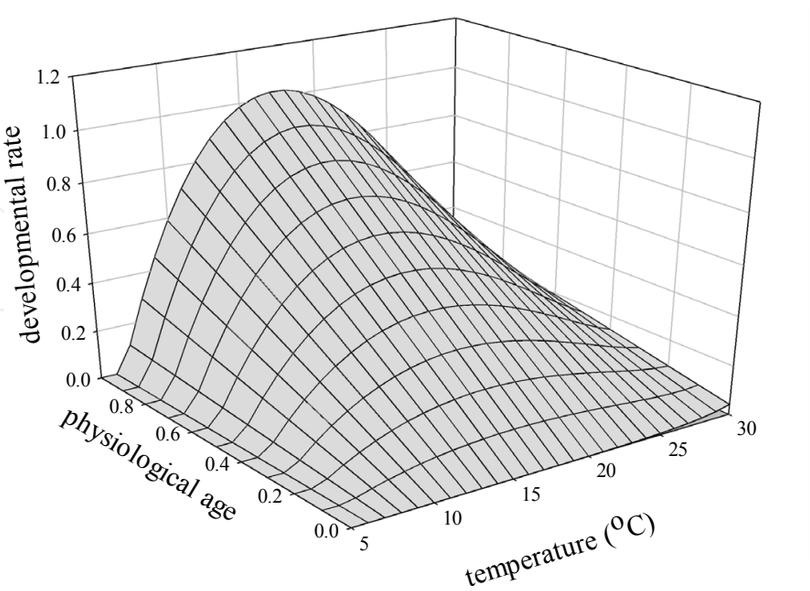


Fig. 5. Postdiapause developmental rates of gypsy moth are dependent on temperature and physiological age.

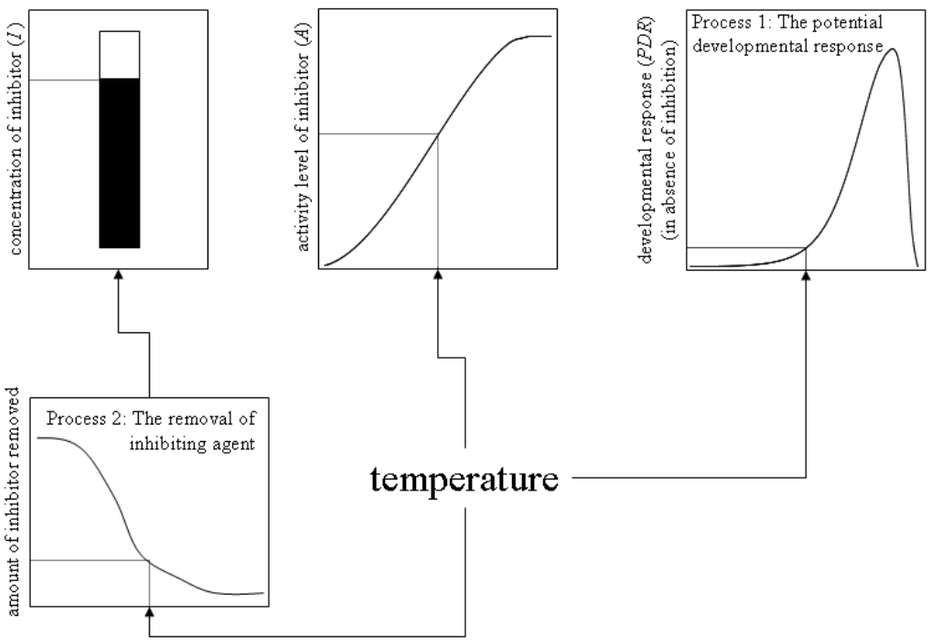


Fig. 6. Schematic representation of the dual-process diapause model. In the absence of an inhibiting agent, exposure to a given temperature (*T*) results in a developmental response (*PDR*) in the first process. However, the developmental response is inhibited at the onset of diapause by the presence of an inhibiting agent. In the second process a portion of the inhibiting agent is removed by exposure to *T*. Temperature also determines the level of activity (*A*(*T*)) of the remaining inhibitor (*I*).

Armed with a geographically robust model of egg hatch, a life-cycle phenology model was constructed by submitting a cohort of first instar larvae on each day that egg hatch occurred to the larval model of Logan et al. (1991). The size of each first-instar cohort is equal to the number of eggs that hatch on that day. Each day, the individuals that complete a larval life stage constitute a new cohort in the subsequent life stage. Individuals completing the final larval life stage constitute a new cohort in the pupal/adult model described by Sheehan (1992). Oviposited eggs constitute new egg cohorts of the next generation (Fig. 3). This composite, multi-generational phenology model was named the *GLS* model (=Gray/Logan/Sheehan, or Gypsy moth Life Stage model) (Gray, 2004).

5. Using phenology models to estimate population establishment and stability

Waggoner (1974) listed four requisites for the practical use of models of seasonality:

i. Considerable importance to mankind (usually, but not restricted to, economic importance).
ii. Variability in the phenophase—if inter-annual variation in the phenophase is relatively minor, the information probably already exists.
iii. Accuracy.
iv. Possibility of action; this may not be an absolute requisite, but it "certainly helps."

Forestry is not a classic example of crop production; the combination of the need for accuracy over extremely large, topographically complicated landscapes (Fig. 4) and the limited options for actions that depend on a phenological prediction may largely explain why insect phenology models are far fewer in forestry than in agriculture. However, climate has been linked to shifts in spring phenological events (Bradley et al., 1999), and one of the natural effects of climate change is to alter the spatial distribution of insect species (i.e., their natural range). Numerous examples already exist of a climate-mediated modification, in latitude and elevation, of historical ranges of insects (Parmesan & Yohe, 2003; Crozier, 2004). Perhaps the most interesting recent applications of phenology models within forestry have been to address the question of potential shifts in, or expansions of, the range of forest pest insects. Two prime examples are now discussed.

Given the existence of suitable host species, the ability to maintain seasonal development (defined above) is among the strongest determinant of the likelihood that an insect population can maintain seasonal development in a location (i.e., for that location to be part of the natural range of the insect). A geographically robust phenology model can estimate the probability of population establishment by quantifying the likelihood that temperature regimes in the location will consistently produce seasonal development (Gray, 2004). Gypsy moth and mountain pine beetle phenology modeling will illustrate this concept.

5.1 Mountain pine beetle

The mountain pine beetle is a native insect that constitutes a valuable link in the basic ecological cycle of western pine forests (Schmidt, 1988). Nonetheless, periodic, widespread, and severe outbreaks of mountain pine beetle pose a serious problem for the forest industry by killing trees, reducing wood supply, forcing changes to harvesting schedules, and increasing the fire hazard in areas of an outbreak. The most recent outbreak in the western province of British Columbia, which began in approx. 1994, eventually covered almost 14 million ha in 2008 (Safranyik et al., 2010). Previous outbreaks in British Columbia have normally collapsed following a severe, although not uncommon, cold weather event, and the Rocky Mountains have posed an impenetrable barrier to eastward expansion of outbreaks. However, the absence of a collapse-causing cold weather event, coupled with an abundance of highly suitable, even-aged host material, created an outbreak of historic proportions, and significant beetle populations appeared as far north in Alberta as Slave Lake (Safranyik et al., 2010), and as far east as the Alberta–Saskatchewan border, where the principle host, lodgepole pine (*Pinus. contorta* Dougl. *ex* Loud. var. *latifolia* Engelm. *ex* S. Watson), mixes with the closely related, potential host jack pine (*P. banksiana* Lamb.), which extends all the way to the Atlantic coast.

The mountain pine beetle phenology model (see Logan & Powell, 2001 for a description of rate curves), hereafter called the Logan et al. model, was used to evaluate mountain pine beetle seasonality in central Idaho under historic climate conditions and under a simulated climate regime with temperatures elevated by 2.5°C (Logan & Bentz, 1999) by testing for two requisite conditions of seasonality: (1) adult emergence from the host tree late enough to avoid lethal freezing temperatures but early enough to achieve full ovipositional potential before the onset of winter temperatures; and (2) synchronous adult emergence that leads to mass attack to overcome host defences. They demonstrated that historic temperatures satisfy the requisites of seasonality in central Idaho; that an increase in future temperatures

would cause previously inhospitable locations (higher elevation) to become hospitable; but that the same warming of temperatures can have deleterious effects on the necessary synchrony of adult emergence. Logan & Powell (2001) used the phenology model to demonstrate how synchronous adult emergence within narrow bands of climatic regime are separated by asynchronous emergence within warmer or cooler bands of climatic regimes. The results suggest that warmer than average temperatures during the 1930s may have, for a short period, made high-elevation white bark pine (*P. albicaulus* Engelmann) forests susceptible to mountain pine beetle, and that mortality during this period was, in fact, due to a self-sustaining mountain pine beetle outbreak.

The determination that the distribution and abundance of mountain pine beetle is highly sensitive to variation in mean annual temperature in climatically marginal habitats led to consideration of the potential shift or expansion of its range in Canada under simulated climate-change temperatures (Safranyik et al., 2010). The phenology model estimated regions of adaptive seasonality in the recent past that reached the Atlantic coast and that coincide very well with the current distribution of pine species. However, under their climate-warmed scenario, the regions east of the Rocky Mountains that will produce adaptive seasonality are predicted to shift northward and beyond the region with high-volume boreal pine forests.

5.2 Gypsy moth

Since the accidental escape of a purposeful introduction near Boston, Massachusetts in 1869 (Liebhold et al., 1989), gypsy moth populations have spread to the north, south, and west. Populations were first reported in the eastern province of New Brunswick in 1936. However, since that time, populations in New Brunswick have never reached the sustained level observed further south and frequently decline without intervention. Populations were detected in the province of Quebec in 1924, but northward expansion has not continued for much of the past 90 years. In the western province of British Columbia, there have been repeated introductions of gypsy moth since 1978. However, in the year following a detected introduction, intensive pheromone trapping programs have many times failed to capture a single moth (Humble & Stewart, 1994). Similarly, numerous introductions of gypsy moth occur in the western United States every year, and many fail to lead to established populations even without intervention (Logan et al., 2007). This apparent failure in New Brunswick, Quebec, and British Columbia and in the western United States for populations to either establish, expand, or grow to outbreak proportions, is likely linked to the climatic conditions in each locale.

The geographically robust *GLS* model has been used several times to assess the potential range of gypsy moth within North America (Gray, 2004; Régnière et al., 2009), or sections thereof (Régnière & Nealis, 2002; Logan et al., 2007), New Zealand (Pitt et al., 2007), and trans-nationally to estimate the risk of introduction via international trade routes (Gray, 2010) under current climate conditions and under projected climate conditions of the future. In addition, *GLS* is used in the large-scale multi-year effort to slow the spread of gypsy moth in the USA.[1] (Roberts & Ziegler, 2007). However, despite using the same basic phenology

[1] Slow the Spread of the Gypsy Moth Project; http://www.gmsts.org/operations/index.htm

model (*GLS*), certain variations exist among these investigations in how model outputs were managed and interpreted.

Four of the preceding six examples (Régnière & Nealis, 2002; Logan et al., 2007; Pitt et al., 2007; Régnière et al., 2009) chose to run *GLS* within the BioSIM© system (Régnière et al., 1995). BioSIM© is primarily a weather generator and can be used to generate daily temperatures for specific locales where temperature records do not exist or to generate a gridded network of weather traces (Régnière & St-Amant, 2007). Unfortunately, BioSIM© also imposes two limitations on *GLS* that weaken its geographic robustness and influence the estimates of climatic suitability. These impositions are discussed below.

5.2.1 An arbitrary and globally defined date before which a specific phenological milestone must be achieved for generation success

In brief, the central criterion in the four examples for generational success in a location is that a phenological event (e.g., oviposition) must be able to achieve a stable equilibrium (=same date in successive generations) under the climatic conditions of the location (Fig. 7). Régnière et al (2002) stipulate that generation success in the western province of British Columbia can occur only if oviposition occurs before 25 October each year. Logan et al. (2007) require median oviposition to occur by 2 October in Utah, USA. Pitt et al. (2007) require all immature life stages to be in the egg stage by 31 December in the eastern Canadian province of New Brunswick and by 30 June in New Zealand. Régnière et al. (2009) make the same stipulation as Pitt et al. (2007) in their Canada-wide estimation of where generation success will be climatically possible.

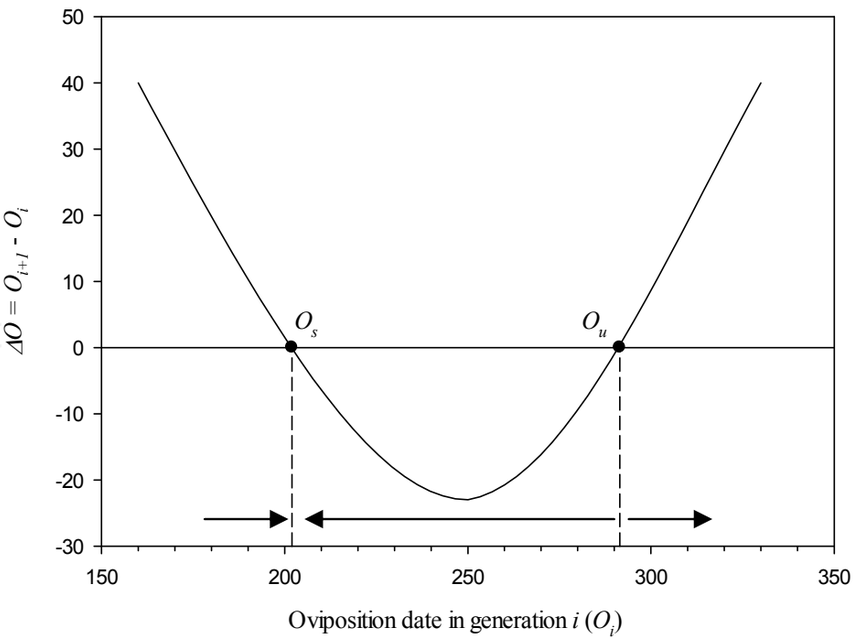


Fig. 7. Seasonal stability is possible in a location when the phenological event (e.g., oviposition) occurs earlier than O_u, an unstable equilibrium (identical dates in generation i and $i+1$). Oviposition later than O_u in generation i will result in ever-later oviposition dates. Oviposition dates earlier than O_u will result in a convergence to a stable equilibrium at O_s.

The rationale for the deadlines is that embryogenesis must reach the cold-hardy diapause phase (Leonard, 1968) before the onset of winter temperatures. However, these dates seem liberal (i.e., late), given that much of British Columbia and Utah will experience sub-zero temperatures by October, and sub-zero temperatures are extremely common throughout New Brunswick prior to 31 December. At the same time, daily maximum temperatures above the minimum prediapause developmental threshold 4°C (Gray et al., 1991) will still be common. Thus, these formulations of *GLS*, with arbitrary dates, allow the simulated population to escape cold-induced mortality while continuing prediapause development.

5.2.2 Removal of all population variability in oviposition date

In each location of interest, the authors (Régnière & Nealis, 2002; Logan et al., 2007; Pitt et al., 2007; Régnière et al., 2009) ran N independent simulations. Each simulation was initiated with a population oviposited on an arbitrary date; a stability flag (1 or 0) was assigned to the simulation based on the success or failure of the population to consistently achieve one or more specified phenological milestones by an arbitrary date during n generations under a climate regime typical of the location. All oviposition in generation $i+1$ occurred on the day of peak female abundance (or median female emergence) in generation i. The probability of stability was then calculated from the N stability flags.

Although the egg hatch model within *GLS* has been shown to be relatively insensitive to oviposition date, it is not entirely insensitive. Within the northern hemisphere, hatch success becomes strongly influenced by oviposition date in northern locations (Gray, 2004; Gray, 2010); presumably this is also the case in southern locations within the southern hemisphere, or at higher elevations regardless of the latitude.

Furthermore, initiating each generation with 100% of the oviposition on the single day of peak female abundance (or median female emergence) of the previous generation in essence "saves" a portion of the population whose true simulated oviposition dates were later than the peak (or median) date and, therefore, too late for survival of the oviposited eggs (Gray, 2004; Gray, 2010).

And finally, the combination of a binomial flag and the removal of population variability in oviposition date has the effect of estimating identical risk for locations where the real risk should be judged to be different. A location in which the median date of oviposition meets the arbitrary deadline in each of n generations—but 49% of oviposition each generation occurs too late—has an estimated p (viability: (Pitt et al., 2007), or probability of establishment (Régnière & Nealis, 2002; Logan et al., 2007; Régnière et al., 2009), equal to a location where 100% of the oviposition meets the deadline each generation. Conversely, a location in which the median date of oviposition fails to meet the deadline—but 49% of oviposition does meet the deadline—has a p equal to a location in which none of the oviposition meets the deadline.

Although it is correct that seasonal stability (Fig. 7) is a requisite for population establishment, it is not known what proportion of a population must survive each generation in order to maintain a population. Thus, it may be the case that less than 50% intergenerational survival is sufficient for gypsy moth establishment; or it may be the case that more than 50% is necessary. But until such a proportion is known, it is much preferable

to estimate probability of establishment (or viability) in a location by the intergenerational survival that a geographically robust model such as *GLS* permits. Contrary to the claim of Pitt et al. (Pitt et al., 2007), variability in oviposition dates within a population is a critical component in estimating the potential for seasonal development and establishment within a location. Within the broad geographic areas that are either highly climatically suitable or highly unsuitable, estimates of probability of establishment will be little affected (or unaffected) by the removal of oviposition variability. However, where climatic suitability is marginal, it is recommended that the risk of establishment be estimated from the intergenerational survival of a model that maintains population variability in all its life stages.

6. Conclusion

Although insect phenology models may be less common in forestry than in agricultural systems, at least two examples in forestry illustrate the potential of geographically robust phenology models to address questions of considerable ecological importance: the potential range of insect species under climate change scenarios.

There can be little doubt that establishment of a stable population of poikilothermic organisms can only occur where the climatic regime leads to adaptive seasonality. A stage-specific, geographically robust phenology model is ideally suited to determining where adaptive seasonality is possible, and therefore, the potential range of an insect species under current climatic regimes, and under the climate regimes that may exist in the future. However, it should be emphasized that imposing an arbitrary biofix on a geographically robustness model, and/or failing to maintain population variability in key phenological events (e.g., oviposition date) will negatively impact the accuracy of the predictions of even geographically robust models where climatic regimes are marginally suitable for adaptive seasonality. These marginal regions should be of greater interest, not less, than the broad regions where the climatic regime is highly suitable.

7. References

Amman, G.D., McGregor, M.D., & Dolph, R.E.J. (1990 (reprinted)). Mountain pine beetle. Forest Insect & Disease Leaflet 2. United States Department of Agriculture, Forest Service, Washington, DC, USA.

Aukema, B.H., Carroll, A.L., Zhen, Y., Zhu, J., Raffa, K.F., Moore, R.D., Stahl, K., & Taylor, S.W. (2008). Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography*, Vol. 31, pp. 348–358

Bradley, N.L., Leopold, A.C., Ross, J., & Huffaker, W. (1999). Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America*, Vol. 96, No. 17, pp. 9701–9704

Chen, X. (2003). Phenological data, networks, and research: East Asia. In: *Phenology: an integrative environmental science*. M.D. Schwartz. pp. 11–25, Kluwer Academic Publishers, ISBN 1-4020-1580-1, London, UK

Crozier, L. (2004). Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology*, Vol. 85, No. 1, pp. 231–241

Damos, P.T., & Savopoulou-Soultani, M. (2010). Development and statistical evaluation of models in forecasting moth phenology of major lepidopterous peach pest complex for Integrated Pest Management programs. *Crop Protection*, Vol. 29, No. 10, pp. 1190-1199

Demarée, G.R., & Rutishauser, T. (2011). From "Periodical Observations" to "Anthochronology" and "Phenology" - the scientific debate between Adolphe Quetelet and Charles Morren on the origin of the word "Phenology". *International Journal of Biometeorology*, Vol. pp. 1–9

Gilbert, E., Powell, J.A., Logan, J.A., & Bentz, B.J. (2004). Comparison of three models predicting developmental milestones given environmental and individual variation. *Bulletin of Mathematical Biology*, Vol. 66, No. 6, pp. 1821-1850

Gray, D.R., Logan, J.A., Ravlin, F.W., & Carlson, J.A. (1991). Toward a model of gypsy moth egg phenology: using respiration rates of individual eggs to determine temperature-time requirements of prediapause development. *Environmental Entomology*, Vol. 20, No. 6, pp. 1645–1652

Gray, D.R., Ravlin, F.W., Régnière, J., & Logan, J.A. (1995). Further advances toward a model of gypsy moth (*Lymantria dispar* (L.)) egg phenology: respiration rates and thermal responsiveness during diapause, and age-dependent developmental rates in postdiapause. *Journal of Insect Physiology*, Vol. 41, No. 3, pp. 247–256

Gray, D.R., Ravlin, F.W., & Braine, J.A. (2001). Diapause in the gypsy moth: a model of inhibition and development. *Journal of Insect Physiology*, Vol. 47, No. 2, pp. 173–184

Gray, D.R. (2004). The gypsy moth life stage model: landscape-wide estimates of gypsy moth establishment using a multi-generational phenology model. *Ecological Modelling*, Vol. 176, pp. 155–171

Gray, D.R. (2009). Age-dependent postdiapause development in the Gypsy Moth (Lepidoptera: Lymantriidae) Life Stage Model. *Environmental Entomology*, Vol. 38, No. 1, pp. 18–25

Gray, D.R. (2010). Hitchhikers on trade routes: a phenology model estimates the probabilities of gypsy moth introduction and establishment. *Ecological Applications*, Vol. 20, No. 8, pp. 2300–2309

Hardy, Y., Mainville, M., & Schmitt, D.M. (1986). An atlas of spruce budworm defoliation in eastern North America, 1938–1980. Miscellaneous Publication 1449. United States Department of Agriculture, United States Forest Service, Washington, DC, USA.

Hopkins, A.D. (1938). Bioclimatics—a science of life and climate relations. Miscellaneous Publication 280. United States Department of Agriculture, US Forest Service, Washington, DC, USA. p. 188.

Humble, L., & Stewart, A.J. (1994). Gypsy moth. Forest Pest Leaflet 75. Natural Resources Canada, Canadian Forest Service - Pacific Forestry Centre, Victoria, BC, Canada. p. 8.

Hunter, A.F. (1993). Gypsy moth population sizes and the window of opportunity in spring. *Oikos*, Vol. 68, No. x, pp. 531–538

Janisch, E. (1932). The influence of temperature on the life-history of insects. *Transactions of the Entomological Society of London*, Vol. 80, pp. 137–168

Johnson, P.C., Mason, D.P., Radke, S.L., & Tracewski, K.T. (1983). Gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), egg eclosion: degree-day accumulation. *Environmental Entomology*, Vol. 12, No. 3, pp. 929–932

Leonard, D.E. (1968). Diapause in the gypsy moth. *Journal of Economic Entomology*, Vol. 61, No. 3, pp. 596–598

Liebhold, A.M., Mastro, V.C., & Schaefer, P. (1989). Learning from the legacy of Leopold Trouvelot. *Bulletin of the Entomological Society of America*, Vol. 35, No. 2, pp. 20–22

Lieth, H. (1974). *Phenology and seasonality modeling*. Springer-Verlag, ISBN 0-387-06524-5, New York, New York, USA

Logan, J.A., Wollkind, D.J., Hoyt, S.C., & Tanigoshi, L.K. (1976). An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology*, Vol. 5, No. x, pp. 1133–1140

Logan, J.A., Casagrande, P.A., & Liebhold, A.M. (1991). Modeling environment for simulation of gypsy moth (Lepidoptera: Lymantriidae) larval phenology. *Environmental Entomology*, Vol. 20, No. 6, pp. 1516–1525

Logan, J.A., & Bentz, B.J. (1999). Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology*, Vol. 28, No. 6, pp. 924–934

Logan, J.A., & Powell, J.A. (2001). Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*, Vol. 47, No. 3, pp. 160–173

Logan, J.A., Régnière, J., Gray, D.R., & Munson, A.S. (2007). Risk assessment in face of a changing environment: gypsy moth and climate change in Utah. *Ecological Applications*, Vol. 17, No. 1, pp. 101–117

Lyons, D.B., & Lysyk, T.J. 1989. Development and phenology of eggs of gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae) in Ontario. *In* Proceedings, Lymantriidae: a comparison of features of new and old world tussock moths. USDA Gen. Tech. Rep. NE-123:351-365. *Edited by* W.E. Wallner, &K.A. McManus. United States Department of Agriculture, Forest Service, Radnor, PA, USA. pp. 351–365.

Manetsch, T.J. (1976). Time-varying distributed delays and their use in aggregative models of large systems. *IEEE Transactions on systems, and and cybernetics*, Vol. SMC-6, No. 8, pp. 547–553

Moerkens, R., Gobin, B., Peusens, G., Helsen, H., Hilton, R., Dib, H., Suckling, D.M., & Leirs, H. (2011). Optimizing biocontrol using phenological day degree models: The European earwig in pipfruit orchards. *Agricultural and Forest Entomology*, Vol. 13, pp. 301–312

Nealis, V., Régnière, J., & Gray, D. (1999). Modeling seasonal development of gypsy moth in a novel environment for decision-support of an eradication program. Gen. Tech. Report NE-277. *Edited by* A.M. Liebhold, M.L. McManus, I.S. Otvos, &S.L.C. Fosbroke. United States Department of Agriculture, Forest Service, Washington, DC, USA. pp. 124–132.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, Vol. 421, No. 6918, pp. 37–42

Pitt, J.P.W., Régnière, J., & Worner, S. (2007). Risk assessment of the gypsy moth, *Lymantria dispar* (L), in New Zealand based on phenology modellng. *International Journal of Biometeorology*, Vol. 51, pp. 295–305

Réaumur, R.A.F. (1735). *Obserations du thermomètre, faites à Paris pendant l'année 1735, comparées avec celles qui ont été faites sous la ligne, à l'isle de France, à Alger et quelques unes de nos isles de l'Amérique*. Académie Royale des Sciences, Paris, France

Régnière, J., Cooke, B.J., & Bergeron, V. (1995). BioSIM: a computer-based decision supprt tool for sseasonal planning of pest management activities. Information Report LAU-X-116. Natural Resources Canada, Canadian Forest Service - Laurentian Forestry Centre, Ste-Foy, QC, Canada. p. 35.

Régnière, J., & Nealis, V. (2002). Modelling seasonality of gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), to evaluate probability of its persistence in novel environments. *The Canadian Entomologist*, Vol. 134, No. 6, pp. 805–824

Régnière, J., & St-Amant, R. (2007). Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. *International Journal of Biometeorology*, Vol. 51, No. 5, pp. 415–430

Régnière, J., Nealis, V.G., & Porter, K.B. (2009). Climate suitability and management of the gypsy moth invasion into Canada. *Biological Invasions*, Vol. 11, pp. 135–148

Roberts, E.A., & Ziegler, A.H. (2007). Gypsy moth population monitoring and data collection. General Technical Report NRS-6. *Edited by* P.C. Tobin, &L.M. Blackburn. United States Department of Agriculture, Forest Service, Washington, DC. pp. 33–46.

Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., & Taylor, S.W. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist*, Vol. 142, No. 5, pp. 415–442

Salinas-Moreno, Y., Mendoza, M.G., Barrios, M.A., Cisneros, R., Macías-Sámano, J., & Zúñiga, G. (2004). Areography of the genus *Dendroctonus* (Coleoptera: Curculionidae: Scolytidae) in Mexico. *Journal of Biogeography*, Vol. 31, pp. 1163–1177

Sawyer, A.J., Tauber, M.J., Tauber, C.A., & Ruberson, J.R. (1993). Gypsy moth (Lepidoptera: Lymantriidae) egg development: a simulation analysis of laboratory and field data. *Ecological Modelling*, Vol. 66, No. x, pp. 121–155

Schaub, L.P., Ravlin, F.W., Gray, D.R., & Logan, J.A. (1995). Landscape framework to predict phenological events for gypsy moth (Lepidoptera: Lymantriidae) management programs. *Environmental Entomology*, Vol. 24, No. 1, pp. 10–18

Schmidt, W.C. (1988). Lodgepole pine: and ecological opportunist. GTR-INT-262. *Edited by* G.D. Amman. United States Dept. of Agriculture-Forest Service, Kalispell, MT, USA. pp. 14–20.

Sharpe, P.J.H., & Demichele, D.W. (1977). Reaction kinetics of poililotherm development. *Journal of Theoretical Biology*, Vol. 64, No. 4, pp. 649-670, 0022-5193

Sharpe, P.J.H., Curry, G.L., Demichele, D.W., & Cole, C.L. (1977). Distribution model of organism development times. *Journal of Theoretical Biology*, Vol. 66, No. 1, pp. 21–38, 0022-5193

Sheehan, K.A. (1992). User's guide for GMPHEN: gypsy moth phenology model. General Technical Report NE-158. United States Department of Agriculture, Forest Service, Washington, DC. p. 29.

Stinner, R.E., Butler, G.D., Jr., Bacheler, J.S., & Tuttle, C. (1975). Simulation of temperature-dependent development in population dynamcis models. *The Canadian Entomologist*, Vol. 107, pp. 1167–1174

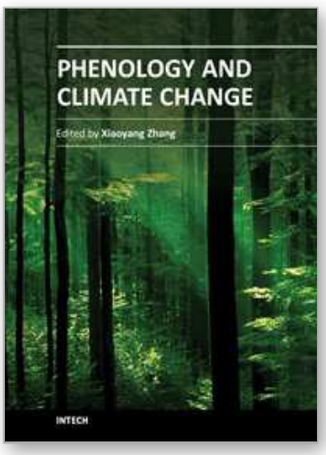
Waggoner, P.E. (1974). Using models of seasonality. In: *Phenology and seasonality modeling*. H. Lieth. pp. 401–405, Springer-Verlag, New York, NY, USA

Waggoner, P.E. (1984). The hatching of gypsy moth eggs, a phenological model. *Agricultural and Forest Meteorology*, Vol. 33, pp. 53–65

Wagner, T.L., Wu, H.-I., Sharpe, P.J.H., Schoofield, R.M., & Coulson, R.N. (1984). Modeling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America*, Vol. 77, pp. 208–225

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Phenology, a study of animal and plant life cycle, is one of the most obvious and direct phenomena on our planet. The timing of phenological events provides vital information for climate change investigation, natural resource management, carbon sequence analysis, and crop and forest growth monitoring. This book summarizes recent progresses in the understanding of seasonal variation in animals and plants and its correlations to climate variables. With the contributions of phenological scientists worldwide, this book is subdivided into sixteen chapters and sorted in four parts: animal life cycle, plant seasonality, phenology in fruit plants, and remote sensing phenology. The chapters of this book offer a broad overview of phenology observations and climate impacts. Hopefully this book will stimulate further developments in relation to phenology monitoring, modeling and predicting.

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