

Modelling Mountain Pine Beetle Phenological Response to Temperature

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Abstract

Maintaining an adaptive seasonality, with life cycle events occurring at appropriate times of year and in synchrony with ephemeral resources, is a basic ecological requisite. For poikilothermic organisms, phenology is largely determined through adaptive evolution with the prevailing climate, and in particular, annual temperature cycles. In addition to the direct effect of temperature, most temperate region insects have physiological mechanisms (e.g., diapause) that help to maintain an adaptive seasonality. The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), however, exhibits no obvious manifestations of diapause. This has led to the ecologically important question: How is an appropriate seasonality maintained in the mountain pine beetle without the synchronizing influence of diapause? In answer to this basic question, we briefly review the mathematical relationship between environmental temperatures and developmental timing and discuss the consequences of viewing these models as *circle maps* from the cycle of oviposition dates and temperatures of one year to oviposition dates for subsequent generations. Univoltinism, associated with reproductive success for the mountain pine beetle, is related to stable fixed points of the developmental circle map. Univoltine fixed points are stable and robust in broad temperature bands, but lose stability suddenly to maladaptive cycles at the edges of these bands. This leads to the obvious observation that temperatures (weather) can be too cold for the mountain pine beetle to thrive, as well as the less obvious implication that it can also be too warm.

These results are placed in an ecological and management context by relating adaptive seasonality to outbreak potential. The relationship between outbreak potential and temperature is further considered in view of climate change (i.e., global warming). We briefly note the potential for global warming to intensify outbreak characteristics in the current range of mountain pine beetle, as well as promote invasion into new habitats, such as the high elevation pines and northern range expansion into Canadian jack pine.

Introduction

Maintaining an adaptive seasonality is a basic ecological requirement for all organisms. Critical life history events must be keyed to appropriate seasonal cycles in order to avoid lethal temperatures or other environmental extremes, provide for coincident timing of reproductive cycles, avoid predation through simultaneous mass emergence, and a multitude of other requirements for maintaining ecological and biological viability. Seasonality and phenology are essentially synonymous terms that have been used to describe these seasonally predictable events, although seasonality is a more general term referring to both periodic changes in the physical environment and the biological response to these changes. Phenology is more specifically used to describe the seasonal progression of a series of biological stages or life history events. At any rate, phenology is central to seasonality and the response of organisms to the climate in which they are embedded.

Climate has long been recognized as an important constraint on mountain pine beetle (*Dendroctonus ponderosae* Hopkins) population dynamics, providing both the limitation on distribution and localized outbreak (including regional) potential (Amman 1973; Safranyik 1978). The aspects of mountain pine beetle biology and life history that are particularly important in view of adaptive seasonality are: (1) The mountain pine beetle is one of a handful of “aggressive” bark beetles that regularly reach outbreak conditions in which large numbers of apparently healthy trees are killed. In fact, successful reproduction by the beetle typically requires killing the host in order to overcome its substantial chemical defenses¹. (2) The beetle and the host have co-evolved, or at least adapted to one another, over countless millennia, each incorporating the other in their respective survival strategies (Roe and Amman 1970; Peterman 1978). In response to host tree defenses, the beetle has evolved a “mass attack” strategy that overwhelms tree defenses by sheer number of attacking beetles. (3) The mass attack strategy requires essentially simultaneous emergence of adult beetles to provide the large numbers required for a successful attack. (4) In spite of the strong selection pressure for simultaneous adult emergence, existence of diapause or any other physiological timing mechanism has not been observed for the mountain pine beetle. The synchronization of life-history events without a controlling physiological mechanism has been termed “direct” control of seasonality (Danks 1987).

The combination of these four key life-history traits has resulted in an interesting question: How can the prolonged ovipositional period, lasting several months, be focused into an essentially simultaneous emergence period? This question has been the focus for a sustained research effort dating back to the early 1980s (Logan and Amman 1986). Our past work (Bentz et al. 1991; Logan and Bentz 1999; Powell et al. 2000; Jenkins et al. 2001; Logan and Powell 2001) has demonstrated that quiescence and differing developmental thresholds are sufficient for synchronizing adult emergence. The mathematical tools we have developed to analyze phenology and predict seasonality in the mountain pine beetle provide a general framework for any plant or animal with phenology under direct temperature control. In this article, we explore the quantitative analysis of direct temperature control and how these models shed light on adaptive seasonality in the mountain pine beetle. We first set the mathematical framework for modelling seasonality; we then describe analytical tools that result from this framework; and finally, we examine the current unprecedented outbreaks of this insect in light of the quantitative framework for seasonality analysis.

¹ Host trees can be partially killed, or strip attacked with successful brood production in the killed tissue. This is more common in endemic or incipient populations. After an outbreak is initiated, there are generally enough beetles present that defenses of even healthy trees are overwhelmed.

Methods and Materials

Temperature dependent models

Relating temperature to the development of insects requires differentiating between *age* and *stage*. Although both are related to time, age is chronological in nature and may not be directly observable. Stage, on the other hand, is a developmental concept usually defined by distinct morphological characteristics and a moult for transition from one stage to the next. Another concept, *developmental rate*, is the speed of temporal progression through an instar or stage and is dependent on temperature in a predictable fashion. Assuming that it is the same function throughout a stage, the developmental rate, $r(T)$, at a constant temperature, T , is the inverse ($1/t$) of the time required to complete that life stage. The developmental index, a_j , (or physiological age) in stage j , is then the fraction of the j^{th} life stage completed at any particular time by the median individual in the population, and is not directly observable. It is related to the developmental rate by a differential equation:

$$\frac{d}{dt}a_j(t) = r_j[T(t)]; \quad a_j(t=t_{j-1})=0; \quad a_j(t)=\int_{t_{j-1}}^t r_j[T(t)]dt; \quad a_j(t=t_j)=1 \quad (1)$$

Life stage j begins at time t_{j-1} , which is the time of completion of the previous life stage (t_{j-1} , as indicated by the initial condition of the differential equation above), and finishes at time, t_j , at which $a_j=1$. What is observable are the developmental milestones, or the times at which one life stage terminates and another begins.

These relationships underlie almost all models of insect phenology (see Logan and Powell 2001). Once the mathematical relationship between temperature, time, and physiological age is defined, there remains the issue of finding an appropriate functional relationship between temperature, T , and the developmental rate, $r(T)$. The rate curves for the eight life-stages of the mountain pine beetle are shown in Figure 1.

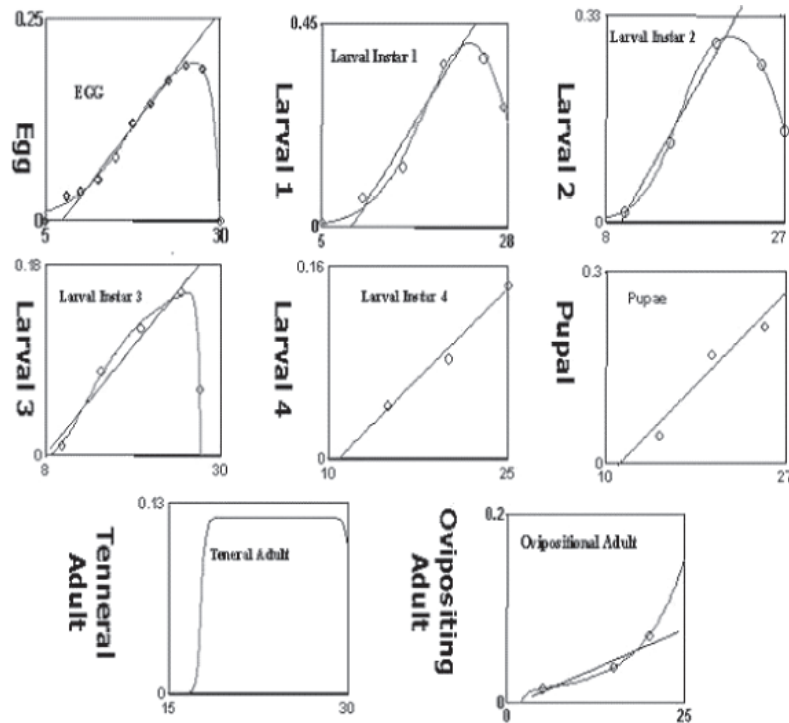


Figure 1. Rate curves for the mountain pine beetle. In all curves, the vertical axis is measured in development/day and the horizontal axis is temperature in centigrade. Data points determined by rearing at controlled temperatures are depicted as open circles.

Parameters for the functional relationships in Figure 1 can be found in Logan and Amman (1986), and Bentz et al. (1991), and a detailed description of the mountain pine beetle model in Logan et al. (1995).

Determining ovipositional dates from year to year

When developmental rate curves are determined for all stages of an insect's life cycle, the question becomes: How should they be used to make predictions regarding adaptive seasonality? Returning to equation [1], solutions can be written by direct integration:

$$a_j(t) = \int_{t_{j-1}}^t r_j(T(s)) ds.$$

Unlike traditional differential equations, where the aim is to investigate the structure of the solution, in this case we wish to determine when the solution reaches $a_j=1$, corresponding to the termination of the j^{th} life phase. This time, t_j , is defined implicitly using the solution to the differential equation [1] and the condition $a_j(t_j) = 1$,

$$1 = a_j(t_j) = \int_{t_{j-1}}^{t_j} r_j(T(s)) ds.$$

In general, it is not possible to calculate this integral analytically and even less possible to find an explicit expression for t_j , and we resort to numerical solution. The time at which the numerical integral exceeds one is the computational approximation to t_j .

Given a sufficiently long series of temperature measurements and a set of rate curves parameterized for all N stages of an organism, we have outlined a mathematical approach to calculating the sequence of times of developmental milestones, $t_0, t_1, t_2, \dots, t_N$; corresponding to the date of oviposition (t_0), hatching of the eggs (t_1), progression through larval instars and whatever other life history stages occur, culminating in the emergence of the reproductive adult and oviposition (t_N). The reproductive input from adults of one generation is the initial condition for the egg stage of development in the next generation; we therefore introduce the notation t_0^n to indicate the median date of oviposition in the n^{th} generation, and connect with the sequence of dates of developmental milestones,

$$t_0^n = t_0, t_1, t_2, \dots, t_{N-1}, t_N = t_0^{n+1}. \quad (2)$$

This sequencing mathematically captures the essential circularity of life history, in which egg begets egg through the intermediaries of adults and the other life stages, as shown in Figure 2.

Model iteration and bifurcation

An initial application of the modelling framework of Equations (1) and (2) can be found in Logan and Bentz (1999). They used observed annual phloem temperature from several ecologically interesting sites to investigate the dynamical properties of the model. The model was initialized for the broadest temporal ovipositional distribution possible, i.e., an egg initiated on each day of the year. Adult emergence dates from one generation was used as the ovipositional distribution for the next, and this procedure was followed for twenty generations using the identical annual temperature cycle. It was observed that the original distribution of 365 days converged to either a fixed point (the initial 365 day ovipositional distribution converged to a single emergence date) or a complex cycle of oviposition and subsequent emergence dates. A bifurcation analysis (in which the same iterative procedure is followed for an incremental sequence of annual temperature cycles, each of which is obtained by adding a small amount to the original 8760 hourly temperatures) further indicated that regimes of stable points were separated by regimes of complex cycles (Fig. 3).

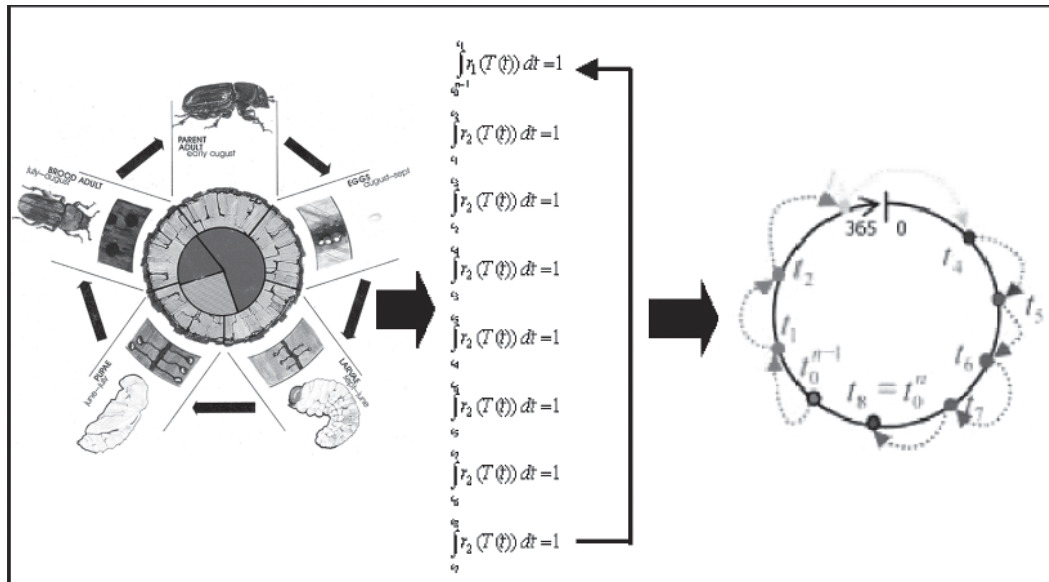


Figure 2. Schematic diagram of the mountain pine beetle model. Development for each life stage is accumulated according to the stage specific development rate curves in Fig. 1. Completion of the final life stage signals the initiation of the first life stage in the next generation. This process is mathematically represented as a circle map, analogous to the cycles of the natural world.

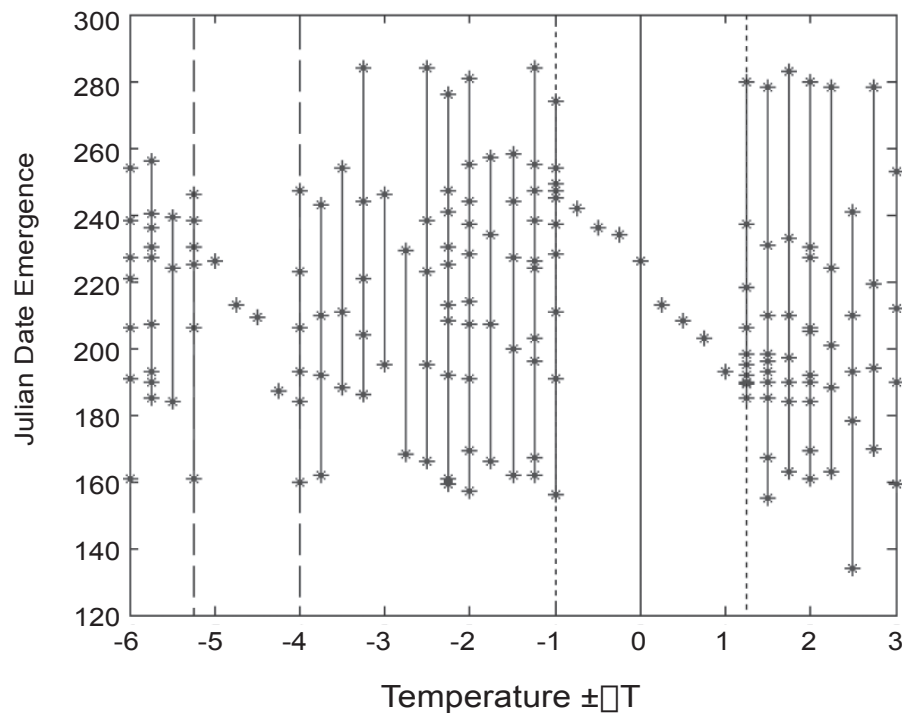


Figure 3. Bifurcation plot of 1995 temperatures for the Ranch site, Stanley, ID, USA. An amount ΔT was added (subtracted) to each hourly temperature in the annual cycle; the model was then initiated and allowed to run for many (20) generations. The last 10 adult emergence dates were then plotted. Plotting of a single point indicates synchrony (good for the mountain pine beetle) while plotting of several points indicates a cycle of emergence dates (bad for the mountain pine beetle). The dashed lines bound the temperature region of synchronous, semi-voltine emergence; the temperature region of synchronous, univoltine emergence is bounded by the dotted lines.

The reader is referred to Logan and Bentz (1999) for details and ecological interpretation of these results. In order to understand how stable, univoltine emergence dates could suddenly bifurcate into multi-date orbits of emergence dates, it is necessary to view phenology as a dynamical system mapping the yearly cycle of possible oviposition dates back to the same yearly cycle (Powell et al. 2000; Jenkins et al. 2001; Logan and Powell 2001).

Defining the G function

There is an inherent circularity in the progression of seasons and the rotation of Julian dates from 0 to 365 and back again. Temperature is also, in broad strokes, a periodic function of the time of year. If we assume periodicity in the temperature cycle from year to year, and interpret the sequence of ovipositional dates modulo 365 according to the Julian calendar, we have constructed a mathematical circle map (see Fig. 4).

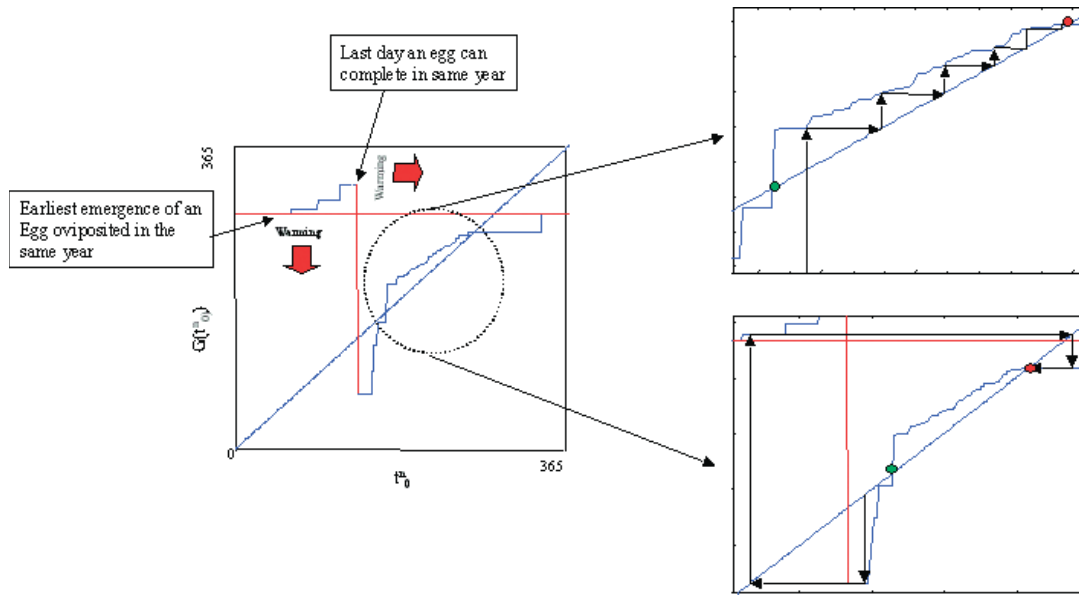


Figure 4. G -function characteristics. The upper intersection of the G -function with the fixed-point line is a stable attractor, as shown by the two trajectories in the two right-hand plots.

By this we mean that, for a given periodic temperature signal, the output oviposition date, t_0^{n+1} , depends directly and uniquely on the oviposition date for the previous generation,

$$t_0^{n+1} = G(t_0^n), \quad (3)$$

where both t_0^n and t_0^{n+1} are Julian dates (not interpreted modulo 365). This function mapping generation to generation, or “ G – function” will be the basis for the mathematical analysis of phenology and seasonality. It generates a circle-map if both t_0^n and t_0^{n+1} are interpreted modulo 365, that is, with respect only to *time* of year, but not year.

When the G function has a fixed point, that is, if there is a day in the year, t^* , for which

$$t^* + 365 = G(t^*), \quad (4)$$

then the population must have a fixed number of generations per year. Perhaps more importantly, when this fixed point is stable (that is, when nearby oviposition dates converge to the fixed point as the map is iterated from year to year), the result is that the entire population will tend to synchronize on an oviposition date near the fixed point, thus satisfying the basic requirement of synchronous emergence for the mountain pine beetle's successful mass-attack strategy. Appropriate timing of adult emergence can be evaluated by determining if a stable, univoltine fixed point falls within a window of allowable dates. The stability of the intersection of a G -function can be determined by the nature of its intersection with the 45° fixed-point line,

$$t_0^{n+1} = t_0^n. \quad (5)$$

If the slope of the G -function at the crossing with the fixed-point line is smaller than one, the fixed point is stable, attracting nearby solutions. Conversely, if the slope at intersection is greater than one, nearby solutions will diverge.

If there is no intersection of the G -function with the fixed-point line, potentially complex cycles result. These cycles violate the definition of adaptive seasonality for two reasons. First, cycles imply asynchronous emergence. Although the resulting cycles may be stable in the sense that they attract and entrain nearby oviposition dates, eggs deposited on different dates will be attracted to different points on the cycle, destroying synchrony. Secondly, these cycles typically involve at least some emergence dates at unacceptable times of the year (i.e., either too late or too early), resulting in increased mortality for some portion of the population.

A graphical interpretation of G -function dynamics is provided in Figure 4. A bifurcation by gradually warming a temperature cycle will result in the downward movement of the horizontal asymptote of Figure 4, and the simultaneous rightward migration of the vertical asymptote. Thus, the G -function will appear to move as a wave from upper left to lower right as temperatures warm. This will first create and then destroy intersections with the fixed-point line. The range of temperatures for which an intersection occurs correspond to the observed regime of attracting (synchronous) emergence dates in Figure 3, while the range of temperatures lacking an intersection corresponds to the region of complex cycles.

Winding number

In the discussion so far we have focused on univoltinism and fixed points of the G function interpreted modulo 365, since the timing and synchrony of one generation per year is important for so many organisms in temperate environments. However, other adaptive seasonalities are possible. Many other important bark beetles go through two or more generations per year (bi-, tri-voltinism, etc.), all of which must be timed with host phenology and resource availability. On the other hand, many important forest insects (for e.g., high elevation populations of mountain pine beetle and spruce beetle) exhibit an endemic state in which a single generation completes every two years (semivoltinism). These voltinisms are also natural, structurally stable consequences of phenological circle maps, as we will discuss below.

An elementary dynamical property of order-preserving circle maps is the *rotation number*. The rotation number is the average number of rotations proscribed by points iterated under the circle map. Given the phenology mapping, $t_0^{n+1} = G(t_0^n)$, for a periodic temperature series and times *not* interpreted modulo 365 (so that the range and domain of G are unbounded), the rotation (or winding) number, W , is defined mathematically by

$$W = \lim_{n \rightarrow \infty} \left[\frac{G^n(t_0)}{365n} \right]. \quad (6)$$

Here $G^n(t_0)$ denotes the n^{th} iterate of G , or the oviposition date in the n^{th} generation, starting with an initial oviposition date of t_0 . As n grows larger and larger, the fraction G^n/n approaches the mean slope of the n^{th} generation oviposition curve, giving an average value in terms of number of days per generation. Dividing by 365 gives average number of years per generation, corresponding to the average number of rotations proscribed by oviposition mappings each year. In the limit, this defines one over the net “winding” of the mapped oviposition dates around the circle.

The winding number is particularly important in the context of insect development because it corresponds directly to the voltinism. Thus, a univoltine life cycle corresponds to a winding number of one, a bivoltine life cycle (two generations per year) to a winding number of one half, and a semivoltine life cycle (a two year life cycle) to a winding number of two.

Results and Discussion

The results from the previous section provide criteria for determining an adaptive seasonality for the mountain pine beetle, namely:

- (1) The G -function has an intersection with the fixed-point line;
- (2) The G -function intersection is at an appropriate time of year;
- (3) The slope of the G -function intersection is less than unity; and
- (4) The winding number equals one.

These four criteria provide a rapid algorithm for evaluating any weather pattern or temperature regime. If all four criteria are satisfied, then the habitat is thermally adaptive for the mountain pine beetle; if not, then it is maladaptive. A MATLAB® program designed to determine adaptive seasonality for the mountain pine beetle can be obtained by contacting Jesse Logan. See Logan and Powell (2001) for an example application of this tool for climate analysis of mountain pine beetle outbreak potential.

The entire issue of mountain pine beetle climate interaction gains increased importance in the face of global warming. We will briefly describe one application of the G -function theory in the Stanley Basin in Central Idaho where we have maintained intensive research on mountain pine beetle population dynamics for almost 15 consecutive years. This area is well within the geographic distribution of the beetle and contains ample forests of lodgepole pine, but for meso-climatic reasons, the historic thermal habitat is only marginally suited for mountain pine beetles. This has two important results: first, instead of the dramatic boom-and-bust outbreak cycles of more benign climates, historical populations tend to be maintained at sub-outbreak levels for prolonged periods. This has allowed for detailed population dynamics research at one site for a prolonged time. Second, climate marginality means that slight variation in annual weather patterns result in immediate and measurable population responses. See Logan and Bentz (1999) for a more detailed description of the Stanley Basin in relation to mountain pine beetle ecology. In spite of the historic marginality of the climate from the mountain pine beetle perspective, the last eight years (1995-2003) have seen an outbreak of major proportions developing in this location.

As an indication of the sensitivity of the mountain pine beetle population response to weather in the Stanley Basin, consider the annual attack densities from the USDA-FS annual Aerial Detection Survey² (ADS) data (Fig. 5).

² Aerial Detection Survey (ADS) data is obtained by flying over a region in a light aircraft and recording red-topped trees on a sketch map. Polygons recorded on the map must enclose at least ten trees, but may be an area of complete mortality. The ADS data is, therefore, difficult to convert into actual number of attacked trees, but give a good idea of total impact by mountain pine beetle.

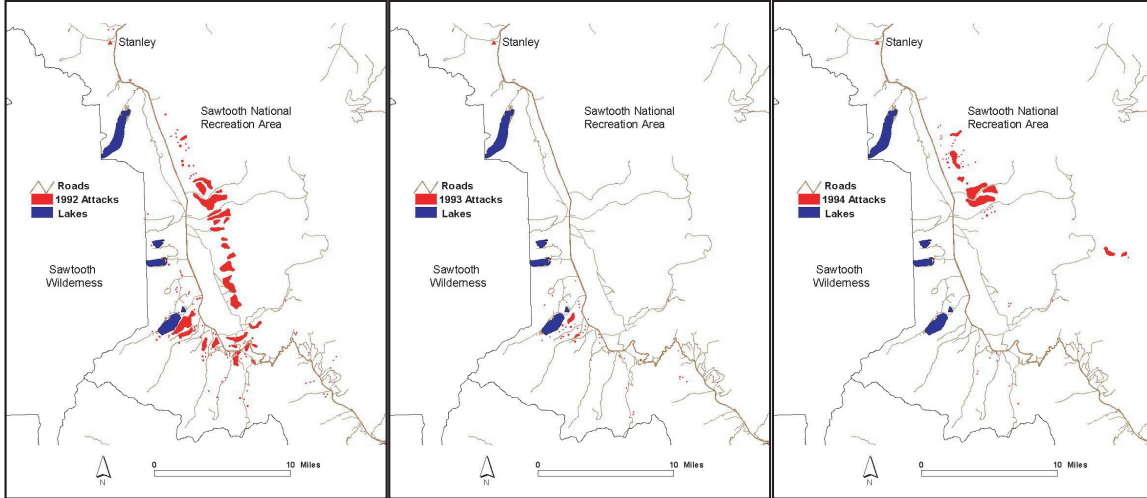


Figure 5. USDA Forest Service Aerial Detection Survey data for the Sawtooth Valley, Stanley, ID USA.
See text for explanation.

From Figure 5 it is apparent that large areas of forest were impacted in 1991-92, but the pulse of beetles resulting from these attacks generated very few successful attacks the following summer (1993). During the summer of 1994, the successful attack cycle was reinitiated, although at a reduced level resulting from the population depression that occurred in 1993. If we consider the concurrent weather data, we see that the summer of 1993 (depressed population) was the coldest summer (June, July, August) on record corresponding to the worldwide impact of the Pinatubo volcanic eruption.

The impact of lowered summer temperatures is evident in the G -function resulting from annual phloem temperatures recorded at our Ranch site, Stanley Basin for 1993. The G -function (Fig. 6A) indicates a maladaptive seasonality: the curve lacks a synchronizing fixed point, oviposition periods occur too late in the year, and emergence times are inappropriate. In contrast, consider the dynamics of the G -function resulting from 1995 temperatures recorded at the same site (Fig. 6B). From this G -function, we see that an intersection with the fixed-point line occurs and that the attractor is at an appropriate time of year, indicating an adaptive annual weather cycle

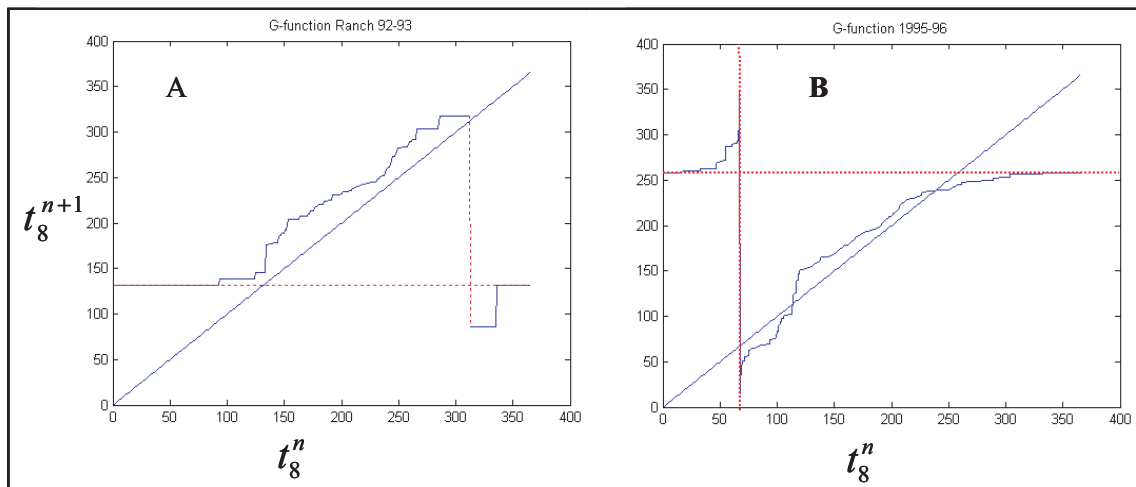


Figure 6. Effect of warming temperatures on G function intersections. A. Calculation using temperatures from the Pinatubo year of 1992-93. B. Calculation using temperatures from 1995-96.

Subsequent years have been even warmer, with results from our study sites consistently predicting adaptive seasonality accompanying an observed exponential growth for acreage impacted by the mountain pine beetle (Fig. 7)

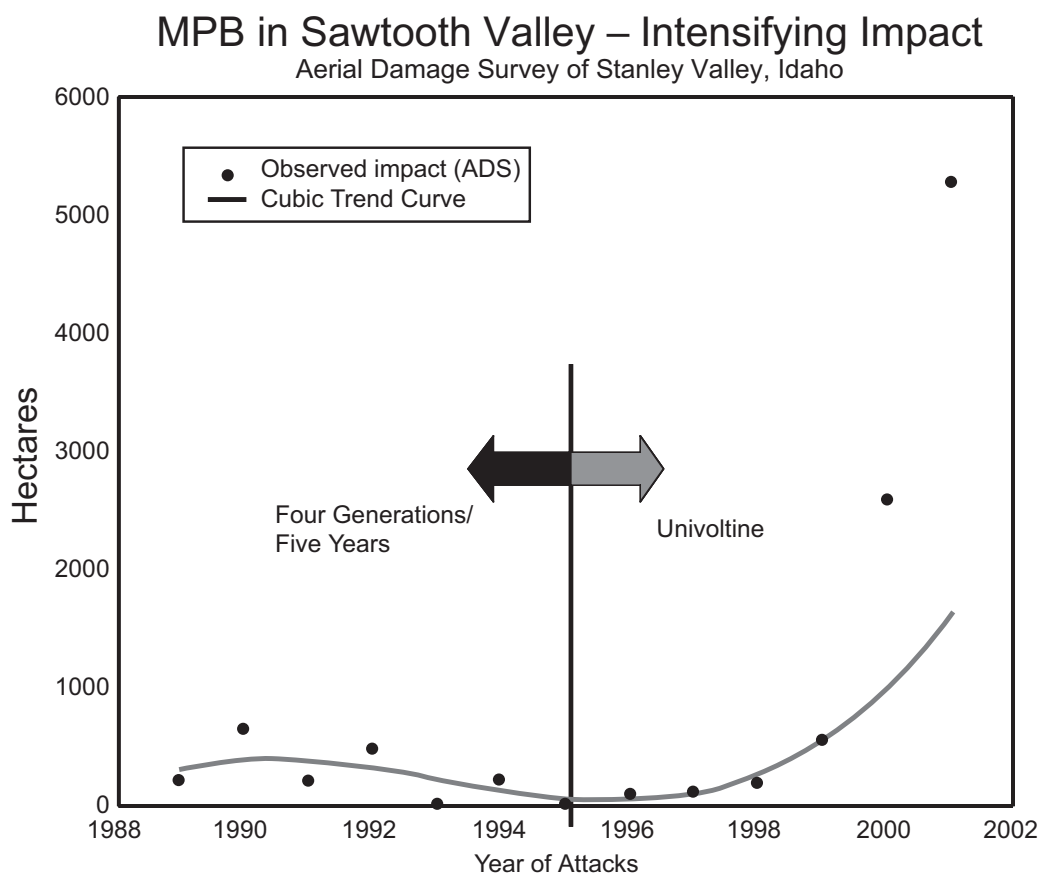


Figure 7. G-function analyses since the summer of 1995-96 have resulted in a predicted univoltine, synchronous life cycle for mountain pine beetles. These predictions have been accompanied with an explosive outbreak (the last mountain pine beetle outbreak in the Stanley area occurred in the late 1920s to early 1930, also an unusually warm period).

If this trend continues, our model predictions are for an increasing proportion of years that are favorable for mountain pine beetle populations, shifting the Stanley Basin from a low- or moderate- to a high-hazard area [see Safranyik’s (1978) definition of a “high-hazard” area].

In addition to impacting the mountain pine beetle disturbance regime in the current (historical) distribution of mountain pine beetle, global warming provides the potential for mountain pine beetle to act as an invasive native species (Logan and Powell 2001). In particular, the northern expansion of mountain pine beetle into previously unoccupied jack pine habitat is discussed by Carroll et al. (2004). We note that the Canadian distribution of jack pine is contiguous not only with jack pine in the Lake States of the U.S., but also with the eastern and southeastern pines as well (Fig. 8).

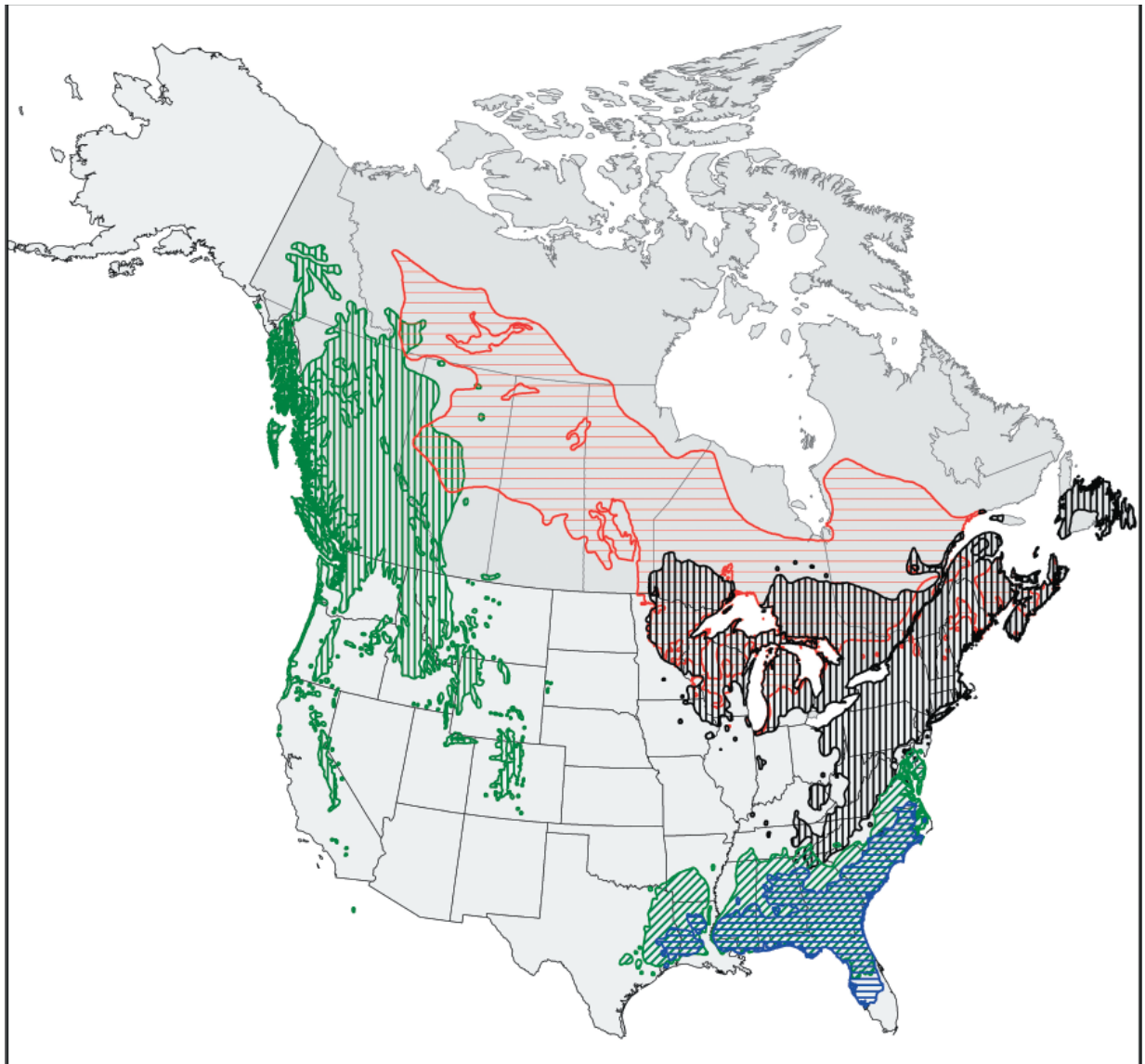


Figure 8. Major pine species connecting lodgepole pine with the eastern USA.

The potential range expansion south along the eastern coast of the U.S. raises the ecologically interesting question of eventual competition between the mountain pine beetle and the southern pine beetle, the two most economically disruptive pine beetles in the U.S. A similar global warming scenario holds for the high-elevation, five-needle pines (Logan and Powell 2001). We have ongoing research at two whitebark pine sites (one 10,000-ft site at Railroad Ridge in Central Idaho, and the other at an 8,000-ft location in western Idaho). The lower elevation site is experiencing a building outbreak, and a switch from endemic to incipient population phase occurred this past summer (2003) at the higher elevation site.

Our mountain pine beetle adaptive seasonality model has been interfaced with the BioSIM modelling system (Régnière 1996), allowing landscape level evaluation of historical events and simulation of predicted future events under various climate change scenarios. This landscape level model is currently being used to evaluate mountain pine beetle response to various climate change scenarios. The results suggest continued northwards expansion and increased vulnerability of pines at high altitude.

Conclusions

Equations (1) and (2) provide the generalized basis for modelling insect phenology; and equations (3), (4), (5) and (6) additionally provide the analytical tools for evaluating adaptive seasonality, given specifically for mountain pine beetle by the criteria:

- (1) The G -function has an intersection with the fixed-point line;
- (2) The G -function intersection is at an appropriate time of year;
- (3) The slope of the G -function intersection is less than unity; and
- (4) The winding number equals one.

This generalized framework is flexible, and can essentially be applied for any forest pest. In fact, it has been applied in a similar way for evaluating establishment probability for gypsy moth in both Canada (Régnière and Nealis 2002; Logan et al. 2003; Gray 2004) and Utah.

Specific applications of the above theory to mountain pine beetle have allowed historical evaluation of weather and climate with respect to geographic distribution and outbreak history. Future applications include the prediction of population responses to global warming. Predictions for mountain pine beetle include:

- Intensification of outbreaks patterns (frequency, intensity) in the historical distribution range;
- Northerly shift in population distribution, eventually connecting with the boreal jack pine distribution;
- Continental scale invasion of jack pine, the rate of which will be determined by dispersion, dispersal, and genetic adaptation;
- Subsequent invasion of pines southward in the eastern US;
- The southern limit of mountain pine beetle distribution shifting north, the degree of shift determined by genetic adaptation for maintaining phenology in a band of adaptive seasonality, and competition with other *Dendroctonus* species; and,
- Range expansion north by Mexican pine beetle, roundheaded bark beetle, and southern pine beetle into expatriated habitat.

The modelling framework we have developed for analysis of adaptive seasonality will be used to evaluate the probability of such events given reasonable climate change scenarios (Logan et al. 2003).

Current events involving bark beetle activity in North America tend to support the predictions in the preceding paragraph. Unprecedented outbreaks of spruce beetle are occurring (or have recently occurred) throughout its range from Alaska to southern Utah. Spruce mortality in some regions of the Kenai Peninsula, Alaska exceeds 95%. The magnitude of mountain pine beetle outbreaks in British Columbia, Canada are greater than at any time in recorded history, and they are occurring further north than previously recorded. Significant mountain pine beetle-caused tree mortality is also occurring in fragile high elevation whitebark pine ecosystems, habitats typically too cold for univoltine populations under pre-climate change conditions. Piñon *Ips* outbreaks are occurring throughout the entire range of the piñon, drastically altering the piñon-juniper ecozone. The occurrence of any one of these events by itself would be noteworthy; the fact that they are occurring simultaneously is remarkable. Drought and other factors undoubtedly play a role in some of these events, but the one commonality across all of these geographically and ecologically diverse phenomena is the series of unusually warm temperatures that begin somewhere in the mid 1980s. As stated in a recent Washington Post³ article, "... Just as we underestimated the rate at which the climate would change, we have underestimated the biological responses to warming and the costs associated with the accompanying weather extremes. Climate change is weakening the hosts and emboldening the pests..."

³ Climate Change is Really Bugging our Forests, by Paul R. Epstein and Gary M. Tabor, Sunday, September 7, 2003; page B05.

Acknowledgements

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