



# Ghost Forests, Global Warming, and the Mountain Pine Beetle (Coleoptera: Scolytidae)

Outbreaks of the mountain pine beetle are an important part of ecological cycles in western pine forests and have provided researchers with insights into both the beetle's and the forest's evolutionary adaptability

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The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a significant ecological force at the landscape level. The majority of the life cycle is spent as larvae feeding in the phloem tissue (inner bark) of host pine trees. This feeding activity eventually girdles and kills successfully attacked trees (Amman and Cole 1983, Furniss 1997). Outbreaks of this insect can be truly spectacular events (Fig. 1A; Amman and Logan 1998). Most western pines are suitable hosts for this insect, but ponderosa pine, *Pinus ponderosa* Lawson, and lodgepole pine, *Pinus contorta* Douglas, currently are the most important host species. The distribution of the beetle generally reflects this

primary host range, although lodgepole pine extends further north and ponderosa pine extends further south than the current geographic range of the beetle. The mountain pine beetle is a native insect, having co-evolved as an important ecological component of western pine forests. The inter-relationship between beetle-caused mortality and subsequent fire has resulted in a basic ecological cycle for many western forests (Schmidt 1988).

Some pines species, such as lodgepole pine, are maintained by periodic disturbances. The lodgepole pine forest-type<sup>1</sup> typically is an essential monoculture of even-aged trees that were initiated by a catastrophic, stand-replacing fire. Without the influence of fire (Fig. 1B), lodgepole pine would be lost over much of its native range (Brown 1975, Lotan et al. 1985). Fire serves to prepare the seedbed, releases seeds from the serotinous cones (triggered to release seeds by heat of a fire), and eliminates more shade-tolerant species such as spruce or fir that would eventually out-compete and replace the early seral lodgepole pine.

The mountain pine beetle plays an important regulatory role in the fire ecology of lodgepole pine. In the first few years after an outbreak, the dead needles provide a highly combustible source of fine fuels. Later, the standing dead trees provide "fire ladders" that serve to conduct ground fires into the canopy, resulting in the stand-replacing crown fires that favor lodgepole pine reproduction. Then, as the killed trees begin to fall, the accumulated

**Fig. 1.** (A) Adair ridge in Glacier National Park, MT. All of the red lodgepole pine trees in this photograph were killed during one season by the mountain pine beetle. This landscape is typical of the last great outbreak episode of the late 1970s to early 1980s in the northern Rocky Mountains.

(B) Mountain pine beetle-killed trees provided the fuel for a subsequent round of large-scale fires, including the Yellowstone, WY, fires of 1988 (photograph courtesy of National Park Service, Yellowstone National Park).

This photograph is in the public domain and can be downloaded from the Bureau of Land Management website (<http://www.firepix.net>).



<sup>1</sup>A summary of characteristics for the major forest types in western North America is discussed in most forestry textbooks (e.g., Young and Giese 1990, table 14.1). Also, see Eyre (1980) for a discussion of forest-cover types including characteristics of the lodgepole pine-cover type.

dead vegetation provides the high fuel load required to carry a stand-replacing fire. Finally, as the downed trees decay and rot, they provide a source of ignition maintenance for lightning strikes. Once ignited, decaying logs are capable of smoldering for weeks, or even months, waiting the time when prevailing conditions (hot, windy, and dry) are conducive for expansion into a full-blown forest fire. In fact, such a scenario occurred during the Yellowstone fires of 1988. The mountain pine beetle may further play a regulatory role through an interaction between beetle-caused mortality, fire, and forest pathogens; however, the basic conclusion remains the same – mountain pine beetle outbreaks are an important component in the disturbance ecology of lodgepole pine forests. Mattson (1996) has termed such a relationship a “normative outbreak” in which the outbreak is “part and parcel of the normal plant biology.”

Other pine ecosystems in the west, however, have not coevolved a normative relationship with the mountain pine beetle. In particular, although the five-needle pines found at higher elevation<sup>2</sup> are suitable hosts for the mountain pine beetle (Amman 1982), these high-elevation habitats are too harsh for mountain pine beetle populations to flourish. Among other stresses of high elevation<sup>3</sup>, such habitats lack sufficient thermal input for the mountain pine beetle to complete its life cycle in one season. Univoltinism appears to be basic to maintaining an appropriate seasonality for this beetle and, therefore, population success (Amman 1973, Safranyik 1978).

Over much of the interior west, the coniferous habitat is partitioned into lower elevation pines (e.g., lodgepole or ponderosa pines), a mid-elevation zone of nonhost spruce/fir; and, finally, five-needle pines at higher elevations. The primary region of mountain pine beetle activity is, therefore, restricted to the lower elevation pines that are separated elevationally by a wide band of nonhost species from the high-elevation pines. The large amount of vertical relief in the Rocky Mountains translates, quite literally, into hundreds of miles of horizontal climatic separation.

High-elevation five-needle pines are among the definitive components of Rocky Mountain ecosystems. They include the oldest documented living organisms (i.e., bristlecone pine, *Pinus longaeva* D. K. Bailey). These ecosystems are critical in the distribution of snow and, therefore, water, the most vital resource in this arid region (Fig. 2A). The high-elevation five-needle pines, as a group, provide essential habitat for wildlife, often being the major source of cover in high elevation environments. Whitebark pine, *Pinus albicaulis* Engelman (Fig. 3A), is somewhat unique in that it is inexorably

<sup>2</sup> The five-needle pines found at higher elevation in the Rocky Mountains include whitebark pine (*Pinus albicaulis* Engelman), limber pine (*Pinus flexilis* James), Rocky Mountain and Great Basin bristlecone pines (*Pinus aristata* Engelman and *Pinus longaeva* D. K. Bailey, respectively), and foxtail pine (*Pinus balfouriana* Greville & Balfour).

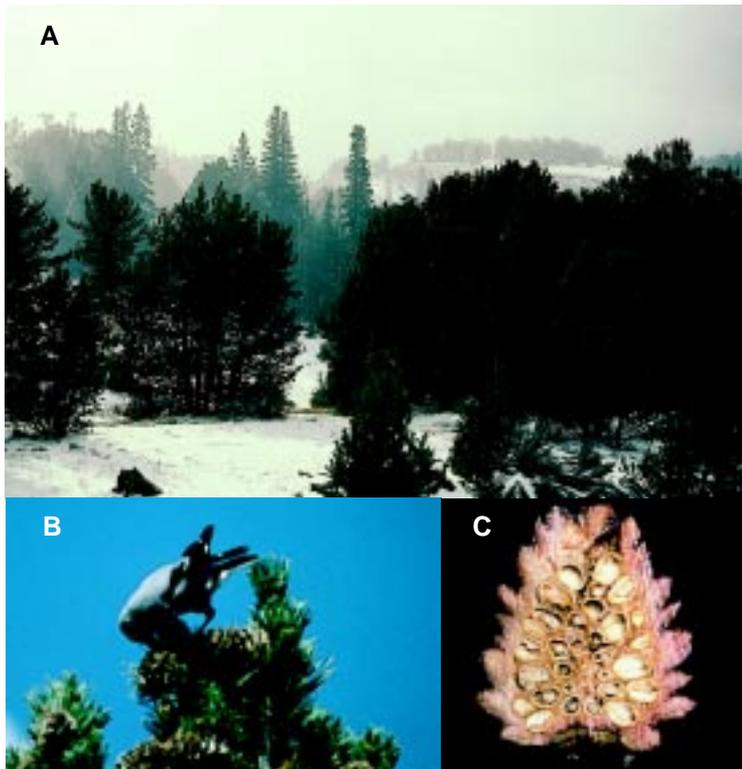


**Fig. 2.** The ecological services provided by whitebark and other high-elevation pines are many and varied. (A) The Rocky Mountains serve as headwaters for major rivers in North America. Most water accumulates as winter snow. As can be seen from the “windrows” of snow captured by the snow-fence effect of these limber pines, the high-elevation five-needle pines are important factors in the conservation and distribution of water. This ecological benefit is nowhere more appreciated than the arid west. (B) Many species of wildlife are dependent on the high nutritional quality of whitebark pine seeds, including the endangered grizzlies of the Greater Yellowstone Area. In years of poor seed production, the number of adverse encounters between the great bear and humans increases significantly (Mattson et al. 1992) (photo courtesy of Barrie Gilbert).

linked to Clark’s nutcracker, *Nucifraga columbiana* Wilson (Fig. 3B). This bird specializes on exploiting the large, fleshy, highly nutritious whitebark pine seeds (Fig. 3C). The pine, in turn, is dependent wholly on Clark’s nutcracker for seed dispersal and subsequent seedling recruitment. Clark’s nutcracker and whitebark pine are keystone mutualists, with the integrity of an entire ecosystem dependent on this mutually beneficial relationship (Lanner 1996).

Whitebark pine provides nutrition not only for Clark’s nutcracker but also for a variety of other species. Red squirrels, *Tamiasciurus hudsonicus* (Ercleben), for example, cache large quantities of the pine’s seeds. Grizzly bears, *Ursus arctos* L., in turn, raid squirrel caches. The cached seeds provide a high quality source of fats at a critical time during which bears are storing nutritional reserves necessary for hibernation. This particularly is true for mated females. Without sufficient fat reserves, implantation of the fertilized ova will not occur (Mattson and Jonkel 1990, Lanner 1996). Anything that disrupts the symbiotic relationship between tree and bird will have cascading effects with diverse impacts ranging from watershed protection to threatened and endangered species (Fig. 2B). The high-elevation five needle pines, themselves, are of high intrinsic value, contributing immeasurably to the biodiversity of the generally species-poor Rocky Mountains. Perhaps no other tree

<sup>3</sup> “High elevation” is a relative concept. In coastal British Columbia, for example, 1,000 m (≈3,000 ft) would be considered “high elevation,” whereas in the Rocky Mountains of southern Colorado, “high elevation” might start around 3,000 m (≈10,000 ft). Differences in the concept of “high elevation” generally reflect the increase in timberline as one travels from north to south. Lanner (1996) provides a highly readable discussion of the classification of the genus *Pinus* with respect to elevational distribution in the western United States.



**Fig. 3.** (A) Whitebark pine stand in central Idaho, Railroad Ridge, White Cloud Mountains. The Mountain Pine Beetle project of the USDA Forest Service, Rocky Mountain Research Station, has maintained high resolution, microhabitat weather sites in this area for several years. At 3,280 m (10,000 ft) elevation, this site seems particularly well adapted for whitebark pine. The oldest documented whitebark pine is near the location of this photograph, and the site has yet to be significantly impacted by whitepine blister rust. Many of the trees occur in clusters, which typically are clone mates of residual seeds from a Clark's nutcracker cache. (B) Clark's nutcracker in characteristic pose, feeding on whitebark pine seeds (photograph courtesy of Ronald Lanner). (C) A cross section of a whitebark pine cone. The cones are closed and covered with pitch that serves to protect the large wingless seeds that must be actively dispersed, principally by Clark's nutcracker (photograph courtesy of Ronald Lanner).

embodies the sense of the American West to quite the extent of a gnarled, 1,500-year-old whitebark pine clinging to life under some of the harshest conditions on the continent.

One hypothesis for the limited spatial distribution of whitebark pine is that it is at a competitive disadvantage with other pines when faced with the onslaught of insects and pathogens that occur in more benign environments. Adaptations to the harsh, high-elevation environment include a long-lived reproductive life (seed viability apparently does not decrease with age of the individual, even for extremely old individuals) and high investment in individual reproductive units. In this, it is a classic "K" selected species. At any rate, the massive outbreaks of mountain pine beetle that occur in lodgepole pine are antithesis to the whitebark pine survival strategy. Although the mountain pine beetle occasionally may infest single trees (or clone mates), outbreaks of the beetle in whitebark pine are not the normative outbreaks typical of lodgepole pine.

However, as we shall see, the relationship between the mountain pine beetle and whitebark pine may be changing.

The existence of whitebark and other high-elevation five-needle pines, unfortunately, is imperiled by inadvertent human activity. First, a pathogen (white pine blister rust, *Cronartium ribicola* J. C. Fischer) introduced on seedlings from Europe during the early 1900s has become widespread with devastating consequences (Keane and Arno 1993). Other management activities, such as fire suppression, have favored more shade-tolerant species such as spruce and fir. More insidiously, global warming may result in increased mountain pine beetle activity. These direct and indirect effects potentially have devastating consequences for whitebark and other high-elevation pines. Will global warming improve the success of the mountain pine beetle in high-elevation systems? In an attempt to answer this question, we first will consider some important aspects of mountain pine beetle biology. We then will combine an empirical model of mountain pine beetle thermal ecology with detailed temperature observations at one high elevation, whitebark pine site. Past outbreak events as well as future scenarios will be evaluated within the context of predictions from this model. Finally, implications for whitebark pine restoration will be discussed, as will the broader implications for invasive species in general.

### Mountain Pine Beetle Ecology

To evaluate the potential for the mountain pine beetle invasion induced by climate change, we must examine some components of the beetle's seasonal life cycle that are particularly responsive to the influence of climate. Two of these components are timing and synchrony. Timing is an obvious and universal requirement for insects living in seasonal environments where critical life history events must be timed appropriately with environmental cues and resource availability. The adaptive problem for the mountain pine beetle is for adult emergence to occur early enough to allow the maximum time for oviposition but late enough to avoid lethal spring (or early summer) temperatures. Adaptive timing is, therefore, a balance between maximizing ovipositional potential and minimizing mortality probability. The second component, synchrony, arises from the fact that the mountain pine beetle differs from most phytophagous insects in that it must kill its host to reproduce successfully. Pine tree hosts are far from passive victims; they have evolved significant defensive chemistry that serves to protect them from beetle attack (Shrimpton 1978, Raffa and Berryman 1987). The mountain pine beetle, in turn, has evolved a mass-attack strategy that overwhelms tree defenses through sheer number of attacking beetles. Success of this strategy is contingent upon large numbers of beetles being simultaneously available for attack (Raffa and Berryman 1987). As a result of the mass-attack strategy, fitness is first an increasing function of population at low densities, and then decreases at high densities due to intraspecific competition for the spatially lim-

ited phloem tissue (Berryman and Pienarr 1973, Berryman 1976). The resulting nonlinearity in the derivative of the population growth rate curve is called an Allee effect (Allee 1931) and is not uncommon for a small weak predator attacking a large, dangerous prey. In the case of the mountain pine beetle, the Allee effect results in a strong selection pressure for both timing and synchrony, the appropriate combination of which results in an adaptive seasonality.

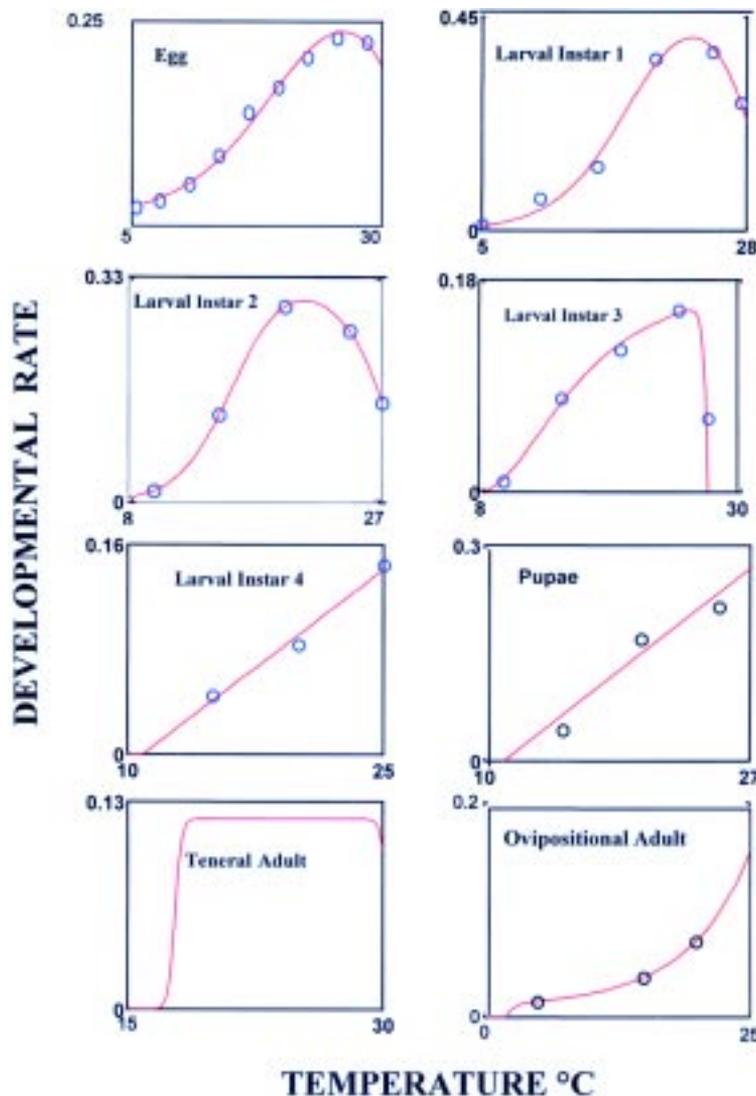
Diapause is a widely expressed aspect of insect physiological ecology that serves, among other things, to maintain an adaptive seasonality. In effect, diapause resets and synchronizes the seasonal clock each year. Given the strong ecological requisite for seasonality in the mountain pine beetle, it is somewhat surprising that extensive rearing experience has failed to suggest diapause or any other physiological timing mechanism. Apparently, all aspects of seasonality are controlled directly by seasonal temperature patterns alone (Logan and Bentz 1999, and references therein).

Direct control of seasonality raises two important questions: (1) what is a mechanistic explanation for direct temperature control, and (2) how are the conflicting selection pressures for a pro-

longed ovipositional period (maximizing recruitment) reconciled with the need for a narrowly focused adult emergence (requiring synchronization)? Answering these two questions poses a significant challenge, particularly when placed in the context of climate change, an event projected into the future [although compelling evidence is mounting that anthropogenic global warming is already taking place (Crowley 2000)]. We have used computer models to assess possible future scenarios for this complicated system.

### Model Development

For modeling purposes, an insect life cycle can be represented by  $N$  life phases. A life phase in this context may, but does not necessarily, correspond to a life stage or instar. For example, the adult life stage may conveniently be broken into three life phases, pre-oviposition, oviposition, and postoviposition. Because we are interested in general patterns reflected by the median phenology of the population, we consider the mountain pine beetle adult stage to be comprised of two phases, pre-oviposition and oviposition (the time beginning with oviposition and lasting until the median egg is oviposited). The complete life cycle is, there-



**Fig. 4.** Plots of developmental rate (the inverse of time in days to complete a life-phase) curves used in the mountain pine beetle model. Developmental rates [the  $r(T)$  in the blue bordered text box] were derived by fitting an appropriate functional form (Logan 1988) to data obtained from constant temperature experiments. The developmental rate for teneral adults is based on anecdotal information only; the shape is consistent with the observation that teneral adult development primarily is a feeding response. A detailed description of data for these developmental rate curves is provided in Logan et al. (1995).

fore, measured from median oviposition date in one generation to median oviposition date of the next (egg to egg). The model represents the temperature-dependent developmental response of eight ( $N = 8$ ) life phases: egg, four larval instars, pupae, pre-ovipositional (teneral) adult, and ovipositional adult. The developmental rate curves we used to model these life-phases (applying the methodology described in the blue bordered text box) are given in Fig. 4. Applying this model using any observed or hypothetical temperature regime allows us to evaluate resulting effects of the thermal environment on seasonality.

### Dynamical Properties of the Model

We previously have used the mountain pine beetle phenology model to evaluate seasonality in lodgepole pine ecosystems (Logan and Amman 1986, Bentz et al. 1991, Logan et al. 1995, Logan and Bentz 1999). Bentz et al. (1991) demonstrated that differential developmental thresholds could serve to synchronize a range of ovipositional dates. The way in which this occurs is described in the

red bordered text box. This work has reinforced our confidence in the basic ecological credibility of the model. Simulations using the model indicate that reasonable climatic conditions iterated over many generations converged to either a single Julian date of adult emergence (fixed point) or a repeating cycle of emergence dates over a period of years (limit cycle). Logan and Allen (1992) provide an introduction to dynamical system concepts of fixed points and limit cycles in an entomological context. See the green bordered text box for an explanation of how fixed points and limit cycles arise naturally from the interaction between the circle map (blue bordered text box) describing the mountain pine beetle life cycle and the seasonal pattern of annual temperature. As indicated in the green bordered text box, a fixed point with a mean generation time of 1 year, and an acceptable emergence date, satisfies our conditions for an adaptive seasonality, whereas a cycle of ovipositional dates does not.

Logan and Bentz (1999) speculated that the dynamical properties of the model could be determined uniquely by starting from an arbitrary initial con-

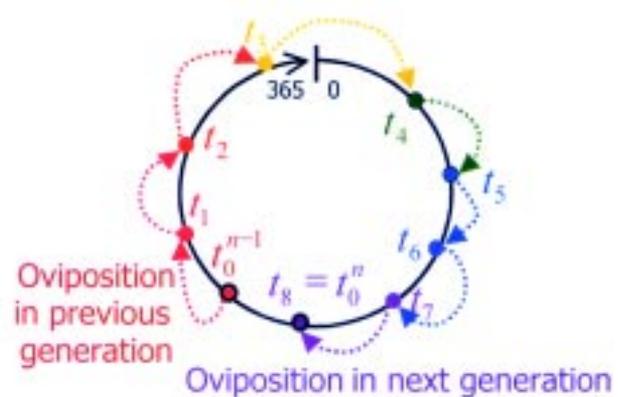
### Modeling Insect Phenology

For each of the eight life phases of the mountain pine beetle, we define a **developmental index**,  $a_j(t)$ , measuring the fraction of life phase  $j$  that has been completed at time  $t$ . The developmental index satisfies a differential equation involving the environmental temperatures,  $T(t)$ , and the developmental rate curve for life phase  $j$ ,  $r_j(t)$ ,

$$\frac{d}{dt}a_j(t) = r_j(T(t)), \quad a_j(t = t_{j-1}) = 0 \Rightarrow \Delta_j a_j = \int_{t_{j-1}}^{t_j} r_j(T(t)) dt = \text{developmental increment.}$$

The life phase begins at  $t_{j-1}$ , which is the time of completion of the previous life phase (as indicated by the initial condition of the differential equation above). The differential equation defines **developmental increments**,  $\Delta_j a_j$ , by integration of the right hand side over short time intervals,  $\Delta t$ . Integration of this differential equation continues until  $a_j = 1$ , which indicates completion of life phase  $j$  and defines  $t_j$ , the end of the life phase.

$$\begin{aligned} \int_{t_0}^{t_1} r_1(T(t)) dt &= 1, \\ \int_{t_1}^{t_2} r_2(T(t)) dt &= 1, \\ \int_{t_2}^{t_3} r_3(T(t)) dt &= 1, \\ \int_{t_3}^{t_4} r_4(T(t)) dt &= 1, \\ \int_{t_4}^{t_5} r_5(T(t)) dt &= 1, \\ \int_{t_5}^{t_6} r_6(T(t)) dt &= 1, \\ \int_{t_6}^{t_7} r_7(T(t)) dt &= 1, \\ \int_{t_7}^{t_8} r_8(T(t)) dt &= 1. \end{aligned}$$

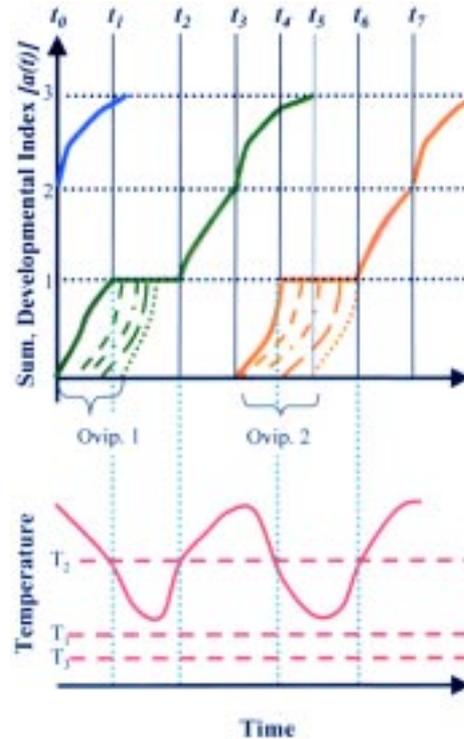


The time at which adult gallery construction and oviposition is completed,  $t_8$ , becomes the oviposition date in the next generation and the beginning of a new sequence of developmental milestones. From the standpoint of understanding whether or not a temperature regime is adaptive for the mountain pine beetle life cycle, what is most important about the date of oviposition is not the particular year but the time of year. Oviposition must occur consistently in late summer/early fall so that cold-hardened life phases develop in time and persist long enough to weather winter's cold. Next year's emergence also must be timed for warm temperatures to facilitate the search for new hosts and subsequent mating. To see what time of year oviposition dates occur, we interpret developmental milestones on a cycle from 0 to 365 days, which then repeats. Thus, the developmental mapping from one oviposition date to the next is a **circle map** from the circle of 0 to 365 days back to the circle of 0 to 365 days.

## Developmental Stops and Synchronized Emergence Dates

The rate curves, as shown in Fig 4, can be complicated nonlinear functions of temperature, and in practice the eight integrals must be evaluated numerically. For sake of example, we consider only three life phases; egg, immature, and ovipositional adult. Developmental increments are added cumulatively until the sum exceeds one. When this occurs, the time of completion,  $t_j$ , is noted, marking the end of one life phase and the beginning of the next (see blue bordered text box). Developmental rate curves (the  $r[T]$  in the blue bordered text box) may have phase-specific thresholds in temperature below which development halts, implying that the developmental index is constant for these low temperatures. When these phase-specific thresholds differ, synchronization of the life-cycle can occur. The impact of this situation is illustrated at right.

Oviposition begins at time  $t_0$  by adults from the  $n-1$  generation (blue line) and is completed shortly after time  $t_1$ , when the developmental index for adults in the  $n_0$  generation equals one. These eggs develop as indicated by the various green trajectories. At time  $t_1$ , temperature drops below the developmental threshold ( $T_2$ ) for the immature life phase. Because temperature is below the  $T_2$  threshold, but above the  $T_1$  threshold, development continues for the eggs but is arrested for immatures. At time  $t_2$ , all individuals have completed the egg phase, temperature once again exceeds the  $T_2$  threshold, and all individuals entering the population during time period Ovip.1 have been synchronized to form a cohort of identically aged immature individuals. This cohort continues to develop through the immature and ovipositional phases. Adults from the  $n_0$  generation begin oviposition at time  $t_3$  and continue to time  $t_5$  (various orange trajectories). At time  $t_4$ , temperature again drops below the  $T_2$  developmental threshold, and synchronization of the  $n_1$  generation eggs occurs by the same process as that for the  $n_0$  generation eggs.



dition (oviposition date). Motivated by this conjecture, Powell et al. (2000) provided a mathematical proof that either a fixed point or a limit cycle characterized the dynamical properties of the mountain pine beetle phenology model. They further derived the general structural characteristics of phenological models that were sufficient for such predictable behavior. Gurney et al. (1994) and Grist and Gurney (1995) previously had arrived at similar conclusions for theoretical populations with two life-phases. Mathematical characterization of the long-term dynamics of mountain pine beetle phenology provides a powerful analytical tool because it is only necessary to follow one arbitrary starting ovipositional date to characterize the adaptiveness of a particular thermal regime (see green bordered text box). This makes it possible to perform an analysis of emergence pattern as temperature is changed. As the mean annual temperature is increased (or decreased) by small amounts,

the dynamical properties of the resulting seasonalities can be plotted (Fig. 5). This process provides a way to evaluate the adaptiveness or suitability of seasonal temperature patterns as the climate is either warmed or cooled.

When the dynamical properties of mountain pine beetle phenology are plotted, an interesting pattern unfolds. As thermal energy is increased, regions of synchronous seasonality are separated by regions of asynchronous seasonality (Fig. 5, orange bordered text box). The regions of asynchronous seasonality form thermal habitat barriers to range expansion. These barriers affect both the potential for, and the nature of, possible invasion into high elevation habitats.

## Implications for Invasion of High-Elevation Systems

In a previous paper, Logan and Bentz (1999) explored the thermal response of mountain pine

### Seasonality, Synchrony and Fixed Points

Yearly temperatures move through seasonal cycles of highs and lows, tied to the yearly cycle of calendar dates. Bark beetle development, directly controlled by temperature, receives strong periodic forcing according to the time of year. Each individual in generation  $n$  starts at an oviposition date,  $t_0^n$ , and goes through a sequence of developmental phases, each of which is completed at a specific date,  $t_1, t_2, t_3, \dots, t_7, t_8$ , for the first, second, third, ..., seventh and eighth life phases, respectively. Completion of the eighth life phase culminates with oviposition for the next generation. Because every oviposition date results in a unique emergence date,  $t_8$ , (and subsequent oviposition date,  $t_0^{n+1}$ , in the next generation) we think of the sequence of developmental milestones,

$$t_0^n \rightarrow t_1 \rightarrow t_2 \rightarrow \dots \rightarrow t_7 \rightarrow t_8 = t_0^{n+1},$$

as a function from the yearly circle back to itself:

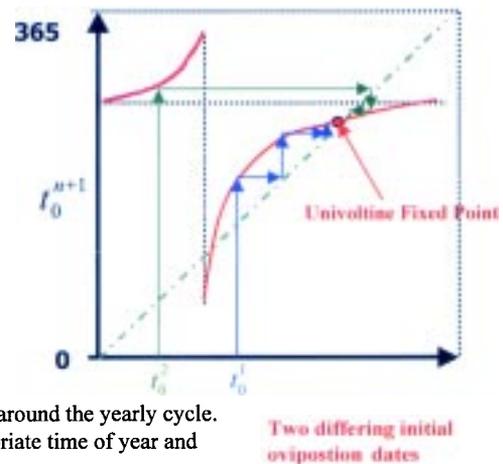
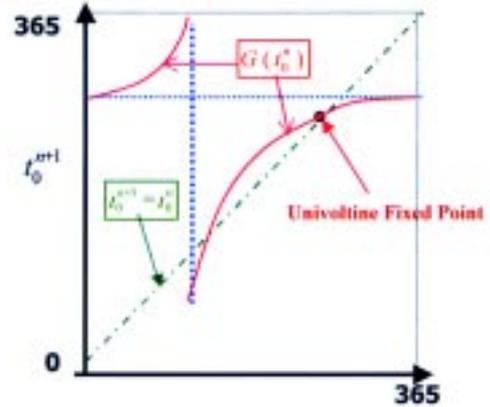
$$t_0^{n+1} = G(t_0^n)$$

Where the graph of  $G$  (solid red line) crosses the fixed point line  $t_0^{n+1} = t_0^n$  (so that the oviposition dates are the same in one generation and the next), a **fixed point** is generated. Seasonality is established if a sequence of oviposition dates,

$$t_0^1, t_0^2, t_0^3, \dots, t_0^n, \dots$$

eventually converges to a fixed point at an appropriate time of year. This means that iterations of the map,  $G$ , which can be thought of as alternate horizontal and vertical 'bounces' between the graph of  $G$  and the fixed point line, spiral in to the fixed point. Equally important to the mountain pine beetle life cycle is synchrony, which assists individuals in mass-attacking new hosts and finding mates.

Synchrony is established if individuals with differing oviposition dates in one generation eventually give rise to progeny with essentially the same oviposition dates. **Stable** fixed points, which have the property that nearby solutions are attracted, are thus the mathematical equivalent of seasonality and synchrony. When no stable fixed points exist, progeny resulting from similar oviposition dates rapidly develops divergent oviposition dates. With no stable, attracting fixed points to establish seasonality, oviposition dates in future generations oscillate around the yearly cycle. Eventually oviposition will occur at an inappropriate time of year and the developing insect will die.



beetle seasonality in one geographic region of a lodgepole pine forest. They found that the thermal ecology of this beetle was relatively resilient to normally expected variation in seasonal temperature patterns. However, they also found that either cooling or warming beyond typical variability could result in disruption of adaptive seasonality. An interesting result was that the region of adaptive seasonality spanned a range of approximately  $2.5^\circ\text{C}$  in mean annual temperature (see Fig. 5, region C). Given the approximate width of the mountain pine beetle thermal niche, Logan and Bentz (1999) briefly mentioned the potential for invasion of high elevation systems. We further explore this potential for one intensively studied high elevation site.

We have maintained a high-resolution weather monitoring system since 1996 at a high elevation

site in the White Cloud Mountains of central Idaho. This site (Railroad Ridge, Livingston Creek Quadrangle,  $44^\circ 8'$  latitude,  $114^\circ 34'$  longitude) is a broad west/east running ridge that gradually slopes from almost 3,200 m (10,500 ft) on the west to about 2,900 m (9,500 ft) on the east. Weather stations have been established on top of the ridge and on south-, north-, and east-facing aspects.

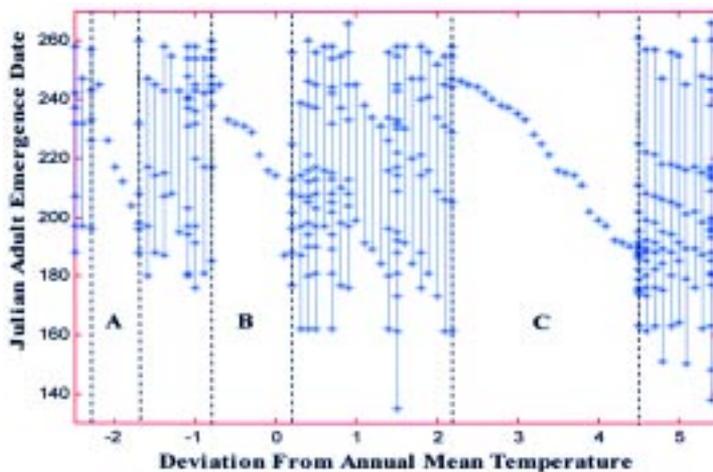
Although Railroad Ridge generally is above the elevational distribution of mountain pine beetle at these latitudes (Amman 1973), substantial beetle caused mortality has occurred in the past. During the widespread mountain pine beetle outbreaks of the 1930s, beetles killed many clusters of whitebark pines (Ciesla and Furniss 1975, Perkins and Swetnam 1996). The slow decomposition rates in the arid high elevation habitat has left most of these

dead trees standing as weathered skeletons, the so-called “ghost forests” (Fig. 6). The ghost forests pose an interesting question: did this mortality result primarily from wind-transported beetles from a concurrent outbreak in lower elevation lodgepole pine, or was the outbreak self-generated within the whitebark pine stands? To address this central question, we conducted a dynamical analysis of the mountain pine beetle phenology model under Railroad Ridge conditions.

Because temperature is the driving variable for our simulation model, we needed to measure the appropriate temperature that reflects the thermal environment experienced by the developing brood. In this respect, ambient temperature is not so important as the actual microhabitat phloem temperature of a successfully attacked tree. The difficulty in measuring microhabitat temperature of attacked trees in high-elevation systems is the rarity of the event; successfully attacked trees are exceedingly rare under current climatic conditions. Fortunately, we were able to establish our north site near a cluster of whitebark pines (clone-mates) that was undergoing a successful attack. We, therefore, were able to concurrently measure ambient and phloem temperature of the attacked trees. To capture the sense of a typical condition, we used the averaged north and south side phloem temperatures [measured at 1.37-m (4.5 ft)<sup>4</sup> on the bole of the tree] to drive our model.

It is interesting that phloem temperature is almost always higher than ambient temperature, particularly on sunny summer days (Fig. 7; Powell 1967). The elevated phloem temperature results primarily from radiant thermal energy absorbed by the tree bole. The additional temperature input to the phloem tissue is critically important during the summer, the effective time for mountain pine beetle development. The predicted time required to complete the life cycle using ambient temperature is 4 years, whereas the time required using phloem temperature is 2 years (i.e., semivoltine). This example illustrates the importance of considering the microhabitat temperature that the organism actually experiences.

As can be seen in Fig. 8, a warming of average annual temperature of a little over 2°C resulted in shifting a semivoltine population to a synchronous univoltine population. Previous observations (Amman 1973, Safranyik 1978) have indicated that population success of the mountain pine beetle is strongly related to univoltinism and an adaptive seasonality. These results are, therefore, consistent with both the climatic limitation of the mountain pine beetle at high elevation under current condition, and the shifting of a thermally hostile habitat to a thermally benign habitat by temperature increases well within those predicted under a CO<sub>2</sub> doubling scenario<sup>5</sup>. The shift from semivoltine to univoltine separated by a maladaptive band of asyn-



**Fig. 5.** This figure was obtained by simulating 30 years of emergence dates starting from an arbitrary initial ovipositional date (JD 240). The average annual temperature at the Railroad Ridge, north site, was increased by adding the amount shown on the x-axis to each hourly temperature. The effect is to increase mean annual temperature by the value on the x-axis. For example: when  $x = 0$ , the simulation was run for 30 years with the observed hourly temperatures; when  $x = 0.1$ , the simulation is run for 30 years with 0.1° C added to each hourly temperature. The cycle length was then computed for each resulting simulation, and the list of emergence dates in the cycle was plotted on the y-axis. A fixed point that resulted in a single value being plotted indicates synchronous emergence. A cycle that resulted in several points being plotted indicates lack of synchrony in emergence. (A) In this region, emergence is synchronous with a 3-year life cycle. (B) Region of synchronous, semivoltine emergence. (C) Region of synchronous, univoltine life cycle (also, see green and orange bordered text boxes).

chronous, fractional voltinism is consistent with the general dynamical attributes of the model. In ecological terms, this translates to the sudden emergence of a problem. As temperatures warm, the thermal environment actually would become less favorable for the mountain pine beetle until a threshold was reached, at which point the thermal environment suddenly would become dramatically more favorable for the beetle. This prediction is ominous in that increasing temperatures could unexpectedly release an endemic or invading mountain pine beetle population in whitebark pine with little or no warning.

The question still remains - how consistent is the prediction of climatic release of mountain pine beetle populations with empirical evidence and, in particular, with the observed mortality that created the ghost forests during the 1930s? Fig. 9 is a plot of mean July temperature for Idaho NCDC<sup>6</sup> Division 8. July temperatures are the most closely related to whitebark pine growth on Railroad Ridge

<sup>5</sup> The 1990 Intergovernmental Panel for Climate Change (IPCC) (Houghton et al. 1990) “best guess” is a warming of 2.5°C with CO<sub>2</sub> doubling. A doubling of carbon dioxide is the generally used benchmark for comparing global warming predictions. This value is used because the effects of other greenhouse gasses can be calibrated relative to CO<sub>2</sub>. The combined result is an effective doubling of CO<sub>2</sub>, an event that will occur by about the year 2030, based on the IPCC “Business-as-Usual” scenario for greenhouse gas-emissions.

<sup>4</sup> This height on the bole of the tree is a standard forestry measurement (e.g., diameter at breast height [dbh] is measured at 4.5 ft).

### Adaptive Bands of Seasonality

Seasonal fixed points for univoltine oviposition are created when the oviposition map,  $t_0^{n+1} = G(t_0^n)$ , crosses the fixed point line  $t_0^{n+1} = t_0^n$ . The location of the graph of  $G(t_0^n)$  depends on the environment, moving toward earlier ovipositional dates as mean temperatures increase.

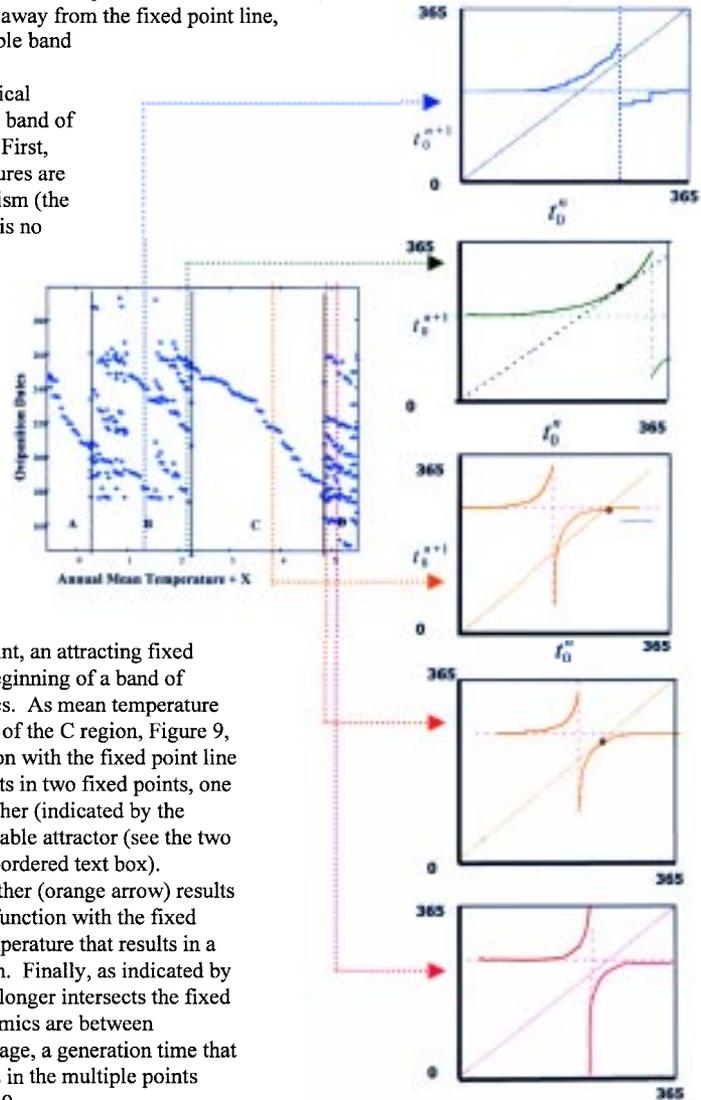
Above a critical temperature threshold, univoltine solutions exist and persist for a range of temperatures. As temperatures increase further, the graph of  $G$  is forced to move away from the fixed point line, terminating the thermally favorable band of univoltine fixed points. As an

example, we consider the dynamical properties of seasonality near the band of univoltine solutions in Figure 9. First, consider the case when temperatures are below that required for univoltinism (the blue arrow). For this case, there is no intersection of the  $G$  function with the fixed point line (see green bordered text box).

Because no fixed point exists, synchronization will not occur. Plotting oviposition dates in such a situation will result in the multiple points for each mean temperature in region B, Figure 9. As temperature increases, the graph of  $G$  approaches the fixed point line until an intersection occurs (green arrow). At this point, an attracting fixed point is formed, indicating the beginning of a band of synchronous, univoltine dynamics.

As mean temperature increases into the central portion of the C region, Figure 9, two intersections of the  $G$  function with the fixed point line occur (yellow arrow). This results in two fixed points, one that is locally unstable and the other (indicated by the yellow point) that is a globally stable attractor (see the two trajectories plotted in the green bordered text box).

Increasing mean temperature further (orange arrow) results in a single intersection of the  $G$  function with the fixed point line, indicating the last temperature that results in a synchronous univoltin population. Finally, as indicated by the red arrow, the  $G$  function no longer intersects the fixed point line, and the seasonal dynamics are between univoltine and bivoltine (on average, a generation time that is less than one year. This results in the multiple points plotted in the D region of Figure 9.



(Biondi et al. 1999) and are, coincidentally, the most important determinant of mountain pine beetle seasonality. The temperature trend line (red line, Fig. 9) during the entire 1930s was higher than normal, including the highest mean July temperature on record. As indicated by this line, average temperature was over 2°C warmer than the 105-year normal, approximately the amount predicted to result in a shift from semivoltine to univoltine. Our model predictions are consistent with the interpretation that large-scale outbreaks at high elevation during the 1930s could have been self-sustaining without transport of beetles from lower elevation pines.

### Management Implications

There has been a concerted effort to collect blister rust resistant whitebark pine seeds from survi-

vors in stands suffering high white pine blister rust mortality. These efforts have progressed to the point of field implementation, and resistant stands of whitebark pine are being planted at various high elevation sites (Tomback et al. 2001). It would be

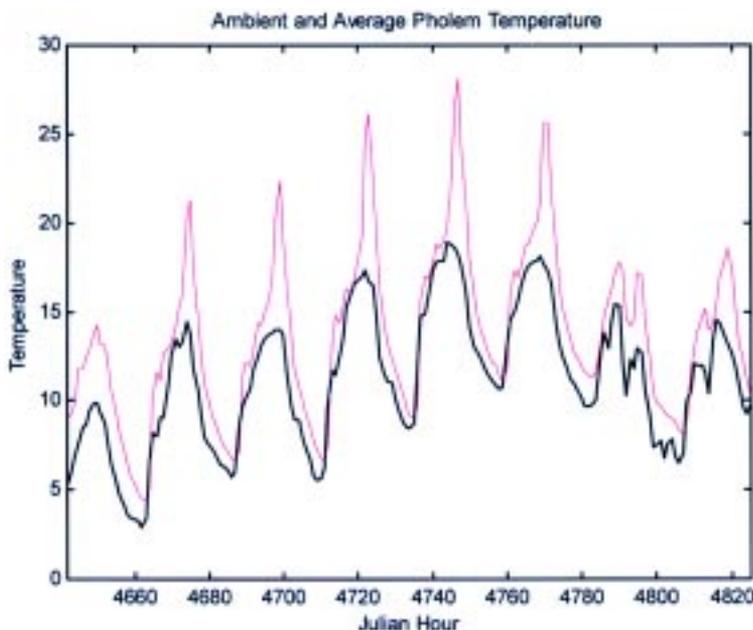
<sup>6</sup> The National Climate Data Center (NCDC) maintains a valuable historical climate database. A continuous record of monthly averaged weather data beginning in 1895 is available. Summarized data (e.g., temperature, Palmer drought index) is computed by averaging records for all reporting weather stations within a particular climatic division. Divisional boundaries are based on areas of similar climatology. Consistency over time in these divisions allows for historical comparisons and trend analyses. Maps of the state divisions and summary data can be downloaded (<http://www.ncdc.noaa.gov/onlineprod/drought/main.html>).



**Fig. 6.** Ghost forest near Railroad Ridge. The standing, weathered trees were killed during the widespread mountain pine beetle outbreak of the 1930s. Landscapes throughout the northern Rocky Mountains experienced substantial mountain pine beetle mortality during this period. These outbreaks were similar in scope to those that occurred in the same region 40 years later. However, the later outbreak event was restricted primarily to lodgepole pine ecosystems. As evidenced in this picture, the 1930s event also was widespread in high elevation ecosystems. The mountain pine beetle currently occurs on Railroad Ridge, resulting in an occasional redtop tree diagnostic of beetle mortality, but at extremely low population levels. The behavior of the beetle also is different at high elevation than in the more benign lodgepole pine habitat. For example, we have observed this beetle occupying downed trees, an occurrence that is rarely observed in lodgepole pine (photograph courtesy of Dana Perkins).

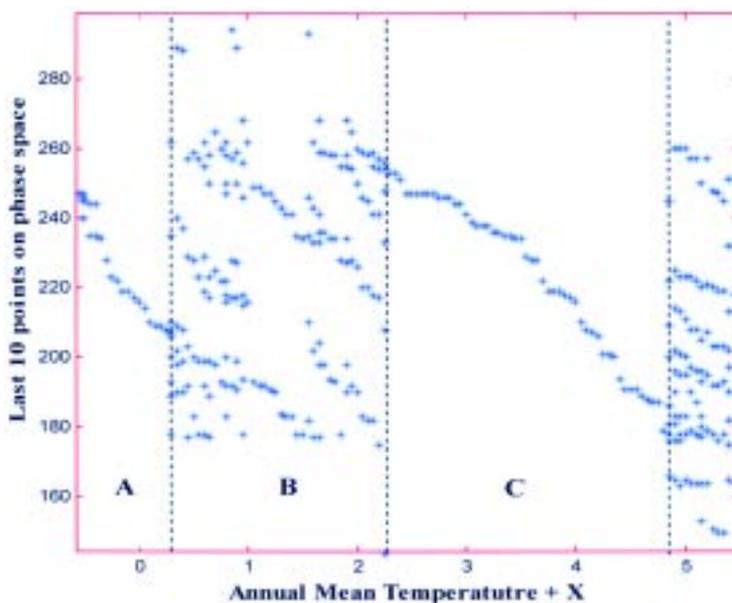
tragic if these resistant stands were restored only to be devastated by mountain pine beetles 50 years later. From previous work with susceptibility and risk assessment, we know (in general terms) stand characteristics that lead to susceptibility in lodgepole and ponderosa pine systems (Amman and Logan 1998). Some of these characteristics can be extrapolated to whitebark pine. There also is the opportunity to use existing information as a reference framework for research evaluating stand conditions as they existed during the outbreak episode of the 1930s. Some high-elevation stands were heavily impacted whereas other nearby stands were relatively untouched. This situation has provided an opportunity to determine which stand attributes are associated with susceptibility to the mountain pine beetle (Perkins 2001).

As we indicated previously, an increase in temperature translates to a northerly latitudinal shift as well as a higher elevation shift. The question becomes, then, how does an increase of approximately 2.5°C translate to a northerly shift in thermal habitat? To answer this question, we analyzed ground temperatures for the summer months (June, July, and August) simulated from the CGCM1 model (Canadian Centre for Climate Modeling and Analysis, data available at the website: <http://www.cccma.bc.ec.gc.ca>). Five years of mean monthly "control" temperatures were obtained for six latitudes ranging from 36.00° N to 63.68° N at longitude 112.5° W. We analyzed these data by using a generalized linear model (SPSS 1998) with

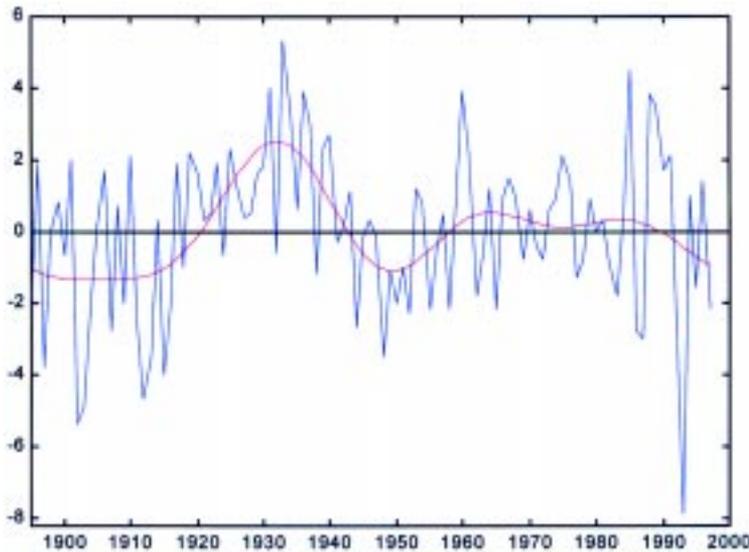


**Fig. 7.** Averages of phloem temperatures recorded from the north and south sides of a successfully colonized whitebark pine (red) versus ambient air temperature (black), Railroad Ridge, north site. The dates covered are 13-20 July 1997.

year considered a random effect, month a fixed effect, and latitude a co-variate. Neither year nor month effect was significant; however, latitude was highly significant ( $F = 222$ ;  $df = 1, 72$ ;  $P < 0.0001$ ). A linear regression of summer temperatures on latitude resulted in an estimated slope of  $-0.3465$ , which translates to a greater than 7° shift north in latitude for a temperature increase of 2.5°C. Fig.

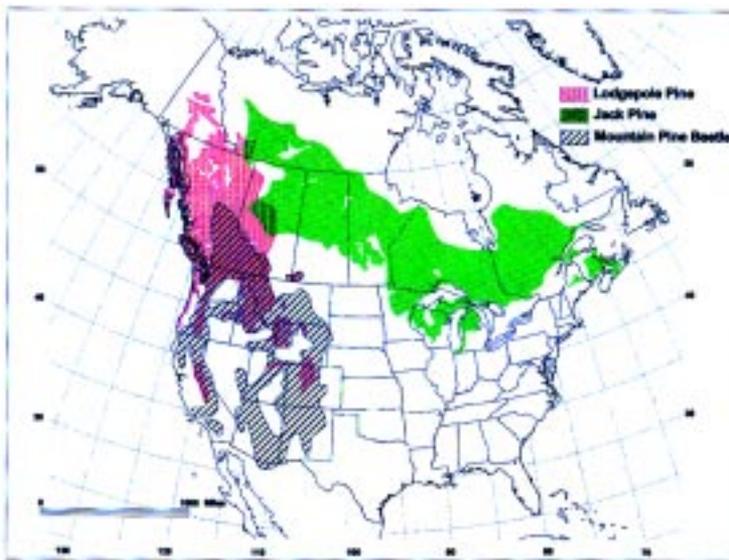


**Fig. 8.** This plot is an enlargement of the ecologically interesting thermal region of Fig. 5. For the observed phloem temperatures on the north site, Railroad Ridge, the observed temperature resulted in a semivoltine, synchronous population (A). Warming by a small amount resulted in complex cycles of asynchronous, fractional (between semi- and uni-) voltinism (B). However, warming of only slightly over 2°C resulted in a synchronous, univoltine life cycle (C). Timing of adult emergence advanced as temperature continued to warm; however, the significant point is that a broad band of over 2.5°C mean annual temperature exists where an adaptive, univoltine seasonality was predicted.



**Fig. 9.** Deviations (blue line) from mean July temperatures (black line) recorded in Idaho NCDC Division 8 from 1895 to 1998. The temperature observations were averaged for all recording stations in the Region. The trend line (red) is well above the mean for the entire 1930s.

10 shows the approximate current mountain pine beetle distribution. A range expansion of 7° N would not only allow mountain pine beetles to occupy previously unoccupied lodgepole pine habitat (range expansion) but also would allow invasion of previously unattacked jack pine (*Pinus banksiana* Lambert), a commercially valuable species in both Canada and the United States. Jack



**Fig. 10.** Approximate current distribution of mountain pine beetle (hatched), lodgepole pine (red), and jack pine (green). As can be seen in this figure, the Great Plains provides an effective barrier separating mountain pine beetles from the U.S. distribution of jack pine. If this barrier is breached to the north due to a warming climate, then there is no apparent reason why a waterfall effect would not follow, spilling across the North American continent to jack pine in the Great Lakes region. Lodgepole pine and jack pine distributions are from map 21, Little and Critchfield (1969); and Canadian distribution of the mountain pine beetle is adapted from a map that can be found at the British Columbia Ministry of Forests website (<http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/beetle/figure1.htm>).

pine has been found to be a suitable host for mountain pine beetle in both laboratory (Cerezke 1995) and field settings (Furniss and Schenk 1969), and a northern record beetle infestation in lodgepole pine has been reported recently (Alberta Environment 1999). Model predictions are consistent with such a gradual shift north through the continuous habitat provided by lodgepole pine.

#### Implications for Invasive Species in General

Although our analysis is focused specifically on one whitebark pine site in central Idaho, the implications are much broader. The invasion (as opposed to range expansion) of a native species into new habitats is similar in many respects to the introduction of an exotic species. However, instead of the introduced species being physically transported in space, the environment itself is shifted from hostile to benign for a species that already is geographically in place. The net result is the same; the in-place plant community is subjected to influences that are foreign to the co-evolved dynamics of the system. There are important differences as well. For example, it seems reasonable to expect as conditions become favorable for the mountain pine beetle, they will simultaneously become more favorable for its biotic associates. In other words, the associated complex of natural enemies will simultaneously invade the newly expanded habitat. Evaluation of potential impacts for both range expansion and invasion of new habitats needs to take these similarities and differences into account. For the mountain pine beetle in particular, and perhaps for eruptive species in general, past experience has shown that natural control agents are ineffective population regulators if conditions of the habitat are favorable for population expansion (Amman and Cole 1983).

The approach we used is of general value for evaluating the invasive potential of exotic as well as native species. Application of a model that uses species-specific developmental rate parameters is a step beyond the simple climate matching that has been applied widely to evaluate invasive potential. Computer programs currently are being developed and/or expanded that facilitate landscape expression of species-specific seasonality models (Régnière 1996). The important question becomes—is the perceived threat great enough to warrant the research expenditure necessary to estimate developmental parameters? Some species, such as the Asian strain of the gypsy moth, *Lymantria dispar* (L.), in the western United States, present a clear and present danger warranting such research expenditure. Developmental information already exists for other important potential invaders. Given this information, the approach we have used here could help evaluate not only the present risk of establishment but also the projected risk as global warming or other climatic change occurs.

Our theoretical work involving the mountain pine beetle as a special case has resulted in some guidelines for evaluating potential invaders with respect to an adaptive seasonality. First, is it known

or suspected that diapause maintains seasonality of the potential invader? If not, then direct temperature control of seasonality can be assumed. For direct temperature control, there are three conditions that are sufficient for synchronous univoltinism: (1) sufficient seasonal variability in the annual temperature cycle, (2) sufficient thermal energy to complete all life phases in a season, and (3) at least one developmental threshold significantly higher than the mean developmental threshold (Powell et al. 2000). This latter condition provides the strong synchronizing force necessary for adaptive seasonality (see blue bordered text box). If diapause is known or suspected, the timing conditions obviously depend on the specific diapause mechanism. However, independent modeling results (Hilbert et al. 1985, Gray 2001) have indicated similar criteria for modeling diapause (i.e., a multiphase process with at least one developmental threshold significantly higher than average). At any rate, a reasonable research priority is to identify critical life phases with high relative developmental thresholds.

Our results also invite speculation about the adaptive significance of diapause. The conditions sufficient for adaptive seasonality without diapause are not particularly restrictive for environments with a strong seasonal temperature cycle. In fact, the ease of meeting these conditions leads one to question the adaptive advantage of diapause as a timing mechanism. One possible interpretation is that diapause is a bet-hedging strategy that buffers the system against variable temperatures (i.e., the organism is not "fooled" by an unusual warm spell in winter). The cost of diapause is loss of adaptability (i.e., diapause is a relatively inflexible timing mechanism that does not allow the organism to rapidly take advantage of changing conditions such as a warming climate). If this interpretation has merit, then it follows that insects like the mountain pine beetle with direct temperature control of seasonality are preadapted to take advantage of a warming climate. 

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