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Assessing the Effects of Changing Climate on Mountain Pine Beetle Dynamics

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Climate and weather have profound effects on insect life systems. As poikilothermic organisms, essentially all life processes are directly related to temperature. Other weather related climatic variables also influence population performance and ultimately determine persistence as a species. In temperate climates, basic adaptations such as maintaining an appropriate seasonality must be keyed to prevailing weather. Any changes in weather, and in particular climate, should be of basic interest to insect ecologists. Given this importance, it is somewhat surprising that relatively few publications have seriously treated the potential effects of climate change on specific insect populations (e.g. Sutherst, 1989; Porter et al., 1991). Perhaps one of the reasons for this dearth of entomological research is that empirical demonstration of climate change is difficult indeed. In the northern Rocky Mountains, for example, the summer of 1993 will be remembered as all-in-all a pretty mild winter. This, of course, during a time of supposed global warming. The world is a noisy place, and the global climate system is exceedingly complex. Both of these facts render empirical, statistical differentiation of long-term trends from short-term cycles to be essentially impossible. This creates an interesting dilemma. We cannot state, with any degree of certainty, that climate change is actually taking place. On the other hand, the issues in question are so basic to life on earth, can we afford to wait for irrefutable empirical confirmation? In general terms, both the world scientific and political communities have determined that the magnitude of risk justifies expenditure of substantial resources to address this potential ecological peril.

As a direct result of the difficulty of empirical experimentation with a system as unwieldy as the global climate, a significant and basic foundation to global climate research has been the development of models to predict the effects of factors such as anthropogenic greenhouse gases. The role of models in situations of high uncertainty and high risk may be to provide the best chance of a crystal ball that in some sense portends the future. Models of global climate [the so called Global Circulation Models (GCMs)] have, in fact, proliferated over the past few years. At the present time, there are at least 20 major GCMs (Kickert, 1993). Given the complexity of the modeled system, it is not surprising that so many models have been developed. It is also of little surprise that these models disagree in many important predictions. In particular, there are substantial differences regarding patterns of climatic variability, rainfall and moisture distributions, modified seasonality, etc. All of these models, however, have one important commonality. They all agree that substantial global warming will take place, and that this warming will occur at an unprecedented rate.

The GCMs, imperfect though they may be, must be considered in aggregate to

represent the best, current knowledge of atmospheric science. As such, a consistent prediction of global warming cannot be ignored. A survey of model output, combined with current and projected production of greenhouse gases results in a reasonable estimate of the magnitude of global warming to be in the neighborhood of 3°C by mid next century. This estimate is based on the assumption of a doubling in CO₂ by 2050, and as such is often referred to as the 2XCO₂ scenario. A global change in mean temperatures of this magnitude corresponds to that which occurred during the mid Pleistocene. Changes in Pleistocene climates resulted in substantial shifts in both plant and insect populations in the Rocky Mountain region of the U. S. (Elaeis, 1991). The major difference between global warming during the Pleistocene and the current situation is the projected rate of change, approximately 10 times that which occurred during the last interglacial (LaRoe, 1991). The disruptive potential is, therefore, much greater than that documented during the Pleistocene, perhaps orders of magnitude greater.

In view of the impacts that insects have on forest ecosystem structure and function, a legitimate question is: what are the impacts of global climate change on important insect species? A review of the limited literature on climate change effects on insect populations reveals the conventional wisdom is that pest problems will be exacerbated. This consensus results primarily from analysis of the effects that temperature have on individual life history traits. Porter et al. (1991) provide a thoughtful review of these impacts. Of the ten attributes they considered, eight will likely enhance insect population success, and only two are ambiguous, with populations either positively or negatively affected. Review of the geological/fossil record tends to corroborate these conclusions. The rich diversity in insect species has apparently not resulted from a particularly high rate of speciation, but rather from an exceedingly low rate of extinction (Labandeira & Sepkoski, 1993). Extinction rates were relatively unaffected even during the late glacial and Holocene changes that were greater in magnitude (but not rate) than the 2XCO₂ scenario (Elaeis, 1991).

Additional insights may be gained by considering survival strategies of contemporary insect species to prevailing climate. For example, every year, many lepidopteran species in the Eastern U.S. migrate north far beyond the limits of typical overwintering success. In effect these insects "gamble" on the chance that unusually favorable weather conditions will allow expansion of the population into new habitats and/or expansion of geographic ranges. This gamble is an indication that insects routinely withstand the loss of significant biomass without suffering adverse evolutionary consequences. In the evolutionary game, insects often gamble on variation in weather events, and are often successful.

In the few computer simulation studies that have been performed with insect models, global warming has generally resulted in improved performance of the insect populations at the expense of the plant resource. Simulation studies performed by Stinner et al. (1989) indicated increased problems with potato leafhopper, black cutworm, green cloverworm, and corn earworm when various global warming scenarios were simulated for the mid-western agricultural region of the U.S. Finally, as an example by counter-example, in our work with mountain pine beetle, population decline, including collapse of outbreaks, have been attributed to unusually cold weather (e.g. Safranyik, 1978). Conversely, at least to our

knowledge, reports of similar occurrences due to unusually mild or warm weather have not been reported.

An inescapable conclusion, given the current evidence, is that conventional wisdom is correct. In general terms, global climate warming will result in exacerbated insect pest problems. This is not to say, however, that the effects of every current pest species will increase under global warming. There will be winners and there will be losers. After all, pest populations are limited in their Southern distribution as well as in their Northern distribution. Projections regarding a particular pest species need to be made on a case-by-case basis. For example, mountain pine beetle (MPB) populations (*Dendroctonus ponderosae* Hopkins), would benefit from global warming due to reduced winter mortality. Conversely, global warming may interfere with the maintaining of an appropriate seasonality for this non-diapausing species. Addressing such species response to modification of a basic ecological driving variable such as climate is a complex issue. Difficulty in dealing with this issue is further compounded by the fact that direct evidence is lacking and system level experimental manipulation is prohibitively expensive. These constraints are exactly those cited for difficulty in dealing with the physical aspects of climate change, and the proposed response is also the same. Computer models and the techniques of system analysis can provide a cost-effective way to evaluate population level and/or ecosystem level responses in anticipation of future events. In the remainder of this presentation we will first describe in general terms the climatic adapted ecology of MPB and a computer model designed to represent important aspects of that ecology. Next we describe the important habitat component of mountain weather on MPB population performance and a landscape-level approach to modeling this critical driving variable. Finally, we describe a research application that uses these models to evaluate the potential of MPB outbreaks as an indication of forest health in high-elevation pine forests.

Climate and Weather Affects

The MPB is economically the most important bark beetle in western North America (Wood, 1963; Gibson, 1988). Although a wide range of *Pinus* species are suitable hosts, MPB is economically most important in lodgepole (*Pinus contorta* Douglas var. *latifolia* Engelman) and ponderosa pine (*Pinus ponderosa* Laws) forests. These two species are among the most widely distributed conifers in western North America. Periodically, large landscapes become vulnerable to mountain pine beetle outbreaks. For example, between the years of 1979 to 1983, over 4 million acres per year in the western United States were infested, resulting in mortality of over 15 million trees each year (McGregor, 1985). Although MPB is a serious competitor with humans for valuable natural resources, it has also been a major component of western pine forests for millennia. Mountain pine beetle outbreaks are an important component of the mechanism that maintains disturbance regenerated species such as lodgepole pine (Flint, 1924; Evenden, 1943; Roe & Amman, 1970; Amman, 1977; Peterman 1978). In fact the role of natural disturbances as determinants of ecosystem scale and pattern over large forested landscapes is becoming generally recognized (Hobbs & Huenneke, 1992). Mountain pine beetle populations can therefore be

legitimately considered as either a serious pest or a critical component of western forest ecosystems. The challenge is to build a sufficient knowledge base to differentiate between outbreaks which are a pathologic symptom of an unhealthy ecosystem from those that are an essential component of a healthy, functioning ecosystem. A mechanistic understanding of the role that climate and weather play in determining population success is essential to such a knowledge base.

The effects of climate and weather are among the most important determinants of MPB population success. These effects are expressed directly through critical population constraints such as winter mortality. Cold temperatures in the winter have accounted for the greatest identifiable source of mortality in life-table studies (Cole, 1974; 1975). Apparently, a relatively narrow phenological window of larval stages are cold hardy, and an intensive research effort is currently underway to determine the mechanistic basis underlying cold-hardiness (Bentz, *in press*). Weather and climate also have more subtle effects on MPB population dynamics. Timing, and particularly synchronous adult emergence, are crucial for successful attack by a small weak predator (MPB) on a large, dangerous prey (pine trees). The significant defense mechanisms of pine trees to MPB attack can only be overcome through a mass attack strategy that numerically overwhelms the tree's defense mechanisms.

From the above two examples, it is apparent that any climatic change has the potential for significant impact on MPB populations, including the increased likelihood of large-scale outbreaks. It is also clear that the effects of climate change may be counterintuitive. For example, a warming climate would favor over-winter survival, but at the same time could have a disruptive effect on maintaining the appropriate seasonality required for coincident adult emergence. The relevant question is what are the specific impacts of various climate change scenarios on the expression of population success and/or outbreak potential? As a initial step toward addressing this question, we have begun development of landscape level models that couple population dynamics with landscape expression of climate and weather.

Mountain Pine Beetle Population Model (MPBMOD)

In order to address both the direct and the indirect effects of climate and weather on MPB populations, it is necessary to represent (1) the full population phenology from egg deposition through adult oviposition, (2) oviposition and recruitment, (3) likelihood of weather related mortality. In addition to these basic processes, addressing questions of climate change requires expression of population dynamics over the complex mountainous terrain that to a large degree determine the proximate weather experienced by the population.

Phenology. Temperature dependent phenology is generally recognized as the basis for representing the life system of poikilothermic organisms in seasonal environments. This is particularly true for insects such as the MPB that lack a true diapause. An appropriate seasonality is apparently maintained entirely through the relationship between developmental rates and developmental thresholds (Bentz et al., 1991). Egg phenology is modeled by the relationships described in Logan & Amman (1986). Larval and pupal phenology are

represented by relationships from Bentz et al. (1991). Parameters defining these relationships are included in the original publications.

A function describing the temperature dependent development of pre-ovipositional (POP) adults was derived from experiments that were conducted in "phloem sandwiches" (as described in Bentz et al., 1991). Constant temperature experiments were conducted at 6 temperatures, ranging from 17.5 to 30 °C. These data are summarized in the original publication. The developmental rate function for POP adults is interesting in that it is essentially temperature insensitive for all but the lowest temperatures. Although small sample size, particularly at higher temperatures, compromises this data set, inclusion of the POP stage is necessary for system continuity and integrity. Sensitivity analysis with a complete life cycle model should provide an indication of the adequacy of the current functional form.

Oviposition. Recruitment is a basic population process necessary for continuity of the species. The magnitude of recruitment sets the ultimate constraint on population growth potential, and as such, is a fundamental component of the outbreak process. Additionally, since the ovipositional period is the functionally important time in the adult life-stage, the function can be used to model adult phenology. The rate and duration of the ovipositional period is temperature dependent, and therefore, weather driven. In addition to temperature dependency, oviposition is also age dependent. For this reason, oviposition was modeled as a three step process requiring two functions; the first describing cm of gallery produced as a function of temperature, and the second relating fecundity to cm of gallery produced.

Temperature dependency of recruitment was determined by computing cm of gallery produced as a function of temperature [$g(T)$]. Data from Amman (1972) was used to construct such a function. In the original publication, a nonlinear function was fitted to data describing average inches of gallery produced per day as a function of temperature. Subsequently, we have used a modified exponential curve since the original function was not defined at temperatures below 7 °C, and oviposition has been reported at lower temperatures (Reid, 1962). Parameters for the exponential function were determined by first generating values from the relationship in Amman (1972), assuming a lower temperature threshold of 2 °C (Reid reported oviposition at 1.67 °C) and then using these data for parameter estimation. This procedure resulted in

$$g(T) = 0.635(e^{0.0008 T^{2.54}} e^{-\tau}). \quad (1)$$

for $T = (T_o - T_b)$; $\tau = T/0.8$; T_o = observed temperature; and $T_b = 2.0$. The functional form of Eq. (1) is empirically motivated, and similar to a previous function used to model ecological data with lower temperature thresholds (Logan et al., 1979).

The relationship used to describe brood production as a function of cm gallery length was based on data contained in Amman and Bartos (1991), Table 1, Group II and III. Data from this table were converted to rates by dividing the raw data by 15.2 cm, the linear length

of the "bark strips" described in the original publication. X-coordinates used for curve fitting were determined as the mid-points of the five bark strips. Therefore, the resulting function has dimension of brood per cm gallery. The functional form fitted was piece-wise linear given as,

$$\begin{aligned} b &= 0.984 + 0.00248c_m && \text{for } c_m < 33.1 \\ &= 1.66 - 0.018c_m && \text{for } c_m \geq 33.1. \end{aligned} \quad (2)$$

The intersection of the two phases occurs at 33.1 cm, which corresponds to the estimated maximum rate of brood production. The X-intercept for the declining phase is 92.2 cm. In other words, the productive life of the female is 92.2 cm of gallery production. In order to determine total, potential brood production, the piece-wise linear function was integrated from 0.0 to 92.2, resulting in maximum recruitment of 65.4. Since the dependent variable is brood produced, background egg mortality is included in this estimate.

Simulation of recruitment and aging for ovipositional adult cohorts proceeds in the following manner. Step 1: compute the inches of gallery constructed during one day (G) as,

$$G = \frac{1}{24} \int_{t=0}^{24} g[T(t)] dt \approx \frac{1}{24} \sum_{t=1}^{24} g[T(t)]. \quad (3)$$

where $T(t_i)$ is Temperature at time i . Step 2: compute the physiological age (the proportion of the life stage completed) accumulated during the i th time step as $a_i = G / (92.2)$, i.e. the proportion of the total potential gallery construction complete during the i th day. The physiological age at the end of the time step (A_i) is then computed as,

$$A_i = a_i + A_{i-1}, \quad (4)$$

for $A_0 = 0$. The ovipositional life stage is completed for a cohort when $A_i = 1$. The aging function, A_p , corresponds to the typical integration of the developmental rate curve (e.g. see Fig. 2 in Logan, 1988). Step 3: include age dependency of oviposition by integrating Eq. (2) for the cm equivalent of the physiological age elapsed during the simulation time step, i.e.

$$E_i = \int_{92.2A_{i-1}}^{92.2A_i} b(c_m) dc_m. \quad (5)$$

This final integral results in brood produced (E_i) by the cohort for the simulation time step. Total egg recruitment is simply computed as the sum over all cohorts.

Mortality. Since long before Malthus, it was generally recognized that the biotic potential of any population far exceeded the earth's capacity to sustain that population (see Hutchinson, 1978 for an enlightened review). This basic principle of population ecology is the reason why so much of insect ecological research has focused on attempts to identify the key mortality agents operating in targeted populations. Although winter temperatures account for the greatest, identifiable mortality in MPB populations (Cole, 1981), little research has been focused on understanding the mechanisms involved. The likelihood of survival during winter months, as well as spring and fall, is a complex process that depends on the interaction of several factors including the frequency, severity, and duration of exposure to cold temperatures, and the cold-hardening capacity of the life stages present. Yuill (1941), Wygant (1942), and Somme (1964) investigated cold tolerances for mountain pine beetle larvae, although these studies were not instar specific. Reid and Gates (1970) and Safranyik and Whitney (1985) observed low temperature tolerance of MPB eggs. Information from these studies tend to be general in nature, and detailed studies of the interactions between low temperature, seasonality, and phenology are lacking, although investigations in progress should provide an understanding of the mechanistic basis for these important processes (Bentz, *in press*).

Since information is not yet available for a mechanistic model of winter mortality, we incorporated expert opinion to develop a rule based approach to modeling winter mortality. The resultant rule base was then re-evaluated within the context of existing data for inconsistency. Expert opinion was on stage specific mortality rules independently derived from interviews with G. D. Amman, L. A. Rasmussen, and B. J. Bentz. Combined expertise represents approximately 70 years of observational history in a wide variety of MPB habitats. The rule-base development procedure was to individually state simple mortality rules for each life-stage, and then jointly negotiate differences in the rules. The mortality rule consisted of a base temperature at which mortality would first begin to appear, and the temperature at which 100% mortality would occur. Each of these two limits was based on the daily observed minimum temperature, and the level of mortality between these two end-points was assumed to be linear. The mortality rule-base is summarized in Table 1.

TABLE 1. Mortality rules based on "best guesses" of experts.

MORTALITY RULES		
Life Stage	Temperature at which mortality begins	Temperature at which mortality is 100%
Egg	-18°C	-18°C
Larvae 1	-23°C	-29°C
Larvae 2	-23°C	-34°C
Larvae 3	-29°C	-40°C
Larvae 4	-29°C	-40°C
Pupae	-18°C	-34°C
PreOviPositional (POP) Adult	-23°C	-34°C
Adult	-23°C	-34°C

Model Formulation. The Pest Model Design System (PMDS; Logan , 1988) was used to develop a computer simulation of the MPB model described herein. PMDS uses a robust cohort-based approach to model phenology. In addition, the computer generated code produced by PMDS is flexible enough that recruitment and mortality rules were easily implemented. A distinct advantage to utilizing the PMDS system for development of phenology based models is the user-friendly front-end that is automatically included. This user interface allows options for running the model with different temperature regimes, convenient modification of model parameters, etc. Copies of the executable and source (C language) code for MPBMOD may be obtained from J.A.L.

Including the Spatial Complexity of Orographic Influences on Climate and Weather

Most population models to date do not explicitly include a spatial component. The reason for this is not a perceived lack of importance, but due to the difficulty in modeling spatial phenomena Liebhold (*in press*) identified spatial complexity as one of the new frontiers for insect and disease models in forest pest management. Unquestionably, MPB population dynamics are played out in an exceedingly complex topographic arena. Mountainous terrain profoundly impacts both climate and weather, and any attempt to evaluate the affect of climate change by necessity must deal with the confounding problem of spatial complexity introduce by orographic influences on climate.

The influences of mountains on weather, as it impacts MPB population processes, occurs at four levels of organization. First is the synoptic level. At this level of organization, global circulation and global cycles come into play, as do continental super-regional processes such as position of the jet-stream, prevailing winds, and frontal systems. The

spatial scale is large, global to super-regional, and the influence of the processes at work impinge more on mountain weather than do mountains on the processes, although mountain influences can extend for considerable depth into the upper atmosphere. Synoptic influences operate at the seasonal, decade or century temporal scale. The second level is regional, involving dynamically and thermally induced wind systems. At this level, we are primarily considering the orographic influence of mountains on synoptic processes. These include those that result from the orientation and magnitude of the mountains themselves. The spatial scale is regional and the temporal scale ranges from seasonal to daily. The third level of influence is meso-scale and primarily dependent on the effects of slope and aspect. The spatial scale is local, in the range of tens to hundreds of meters and the temporal scale is on the order of daily cycles. The final level of organization is micro-meteorological processes that operate within the tree. The spatial scale of these processes is less than that of the bole and depends on exposure (N, S etc.), height of the bole, etc., and their temporal scale is less than twenty-four hours.

In our modeling efforts, we are not attempting the synoptic scale. Such problems are best left to the physical meteorologists and their GCMs. However, the three lower levels of organization, and in particular the last two, fall into the realm of biometerology and are of immediate interest. Modeling the orographic influence on temperature patterns presents three distinct challenges. First is simply the measurement of weather variables in a harsh mountain environment. Second is the problem of projecting a point source of information over a complex topography. And finally, the problem of reducing the complexity of the landscape to a manageable level. We will discuss each of these challenges separately.

From perusal of a map showing United States National Weather Service (NWS) reporting stations, it becomes obvious that major blanks exist which correspond to the high mountain regions. Even in mountainous regions of the western United States, standard weather stations tend to be located in the valleys. The reason for this is simple, people don't, as a general rule, live in the high mountains. The severe conditions of high mountains are hard on both people and equipment. As a result of this inadequate spatial coverage, simple statistical approaches to landscape modeling, such as Kriging, are inadequate for representation of mountain weather. A Kriged surface would resemble an elevated Great Plains. The rich mountain surface responsible for orographic influences would be lost. Fortunately, the situation with respect to monitoring mountain weather is changing due, in large part, to increased interests in mountain recreation and advances in meteorological instrumentation. We now have the motivation, both economically and ecologically, to measure mountain weather combined with the instrumentation that is capable of withstanding the rigors of high elevation environments. For example, the United States Department of Agriculture Soil Conservation Service (SCS) has recently established a comprehensive network of high elevation weather stations in the western United States. This network is a godsend for people interested in mountain environments, and in particular for those interested in mountain weather. This system is highly complementary to the NWS network, and significantly increases our empirical data base on high altitude weather and climate. Additionally, the data base (SNOTEL) is maintained on-line and is made available to legitimate users through the SCS national computer system.

Although recent developments, like the SNOTEL network, have significantly advanced our ability to monitor mountain weather, the challenge of effectively projecting this point data across the complex terrain of interest still remains. The solution to this challenge involves modeling the effects of terrain on temperature. Our basic approach is to combine readily available digital elevation models (DEM) with the empirical analysis of historical weather data. Once stand (level 3) daily maximum and minimum temperatures are modeled, phloem temperatures (level 4) are predicted to actually drive the simulation model.

Phloem temperatures are modeled in three stages. First stand air temperatures are projected, based on known maximum and minimum air temperatures at one or more "base" locations. Projections incorporate elevation and horizontal differences between base measurement and projected locations. Aspect and slope effects are also incorporated, e.g., higher maxima for steep southern exposures and lower maxima for steep northern exposures. Second, phloem maxima and minima are modeled for "shade" (north) and "sun" (south) portions of the bole. Finally, hourly temperatures are interpolated from these maxima and minima from an existing model (Parton & Logan, 1981). The first step uses the model:

$$Tmax_s = Tmax_b + \Delta H \cdot Lx_m + Imax \cdot Ex_{s,m} \cdot \frac{\Delta T}{\Delta T_{95}} \quad (6a)$$

$$Tmin_s = Tmin_b + \Delta H \cdot Ln_m \quad (6b)$$

Where $Tmax$, $Tmin$ are daily maximum and minimum temperature, the subscripts s , b , and m indicate stand, base, and month, ΔH is the difference between stand and base elevation, Lx_m and Ln_m are average monthly vertical lapse rates for maximum and minimum temperatures, $Imax$ is maximum exposure-caused temperature increase, $Ex_{s,m}$ is an exposure index computed from slope and aspect $(RS - Rflat)/(Rmax - Rmin)$, where R is calculated monthly average potential diffuse plus direct solar radiation integrated from minus one to plus three hours of solar zenith assuming 21 km clear sky (Hottel, 1976) and adjusted for slope and aspect (Swift & Knoerr, 1973), ΔT is daily $Tmax_b - Tmin_b$, and ΔT_{95} is historical 95 percentile $Tmax_b - Tmin_b$. The last term added in calculating $Tmax_s$ adjusts for warming due to cloudiness (i.e. sunny or cloudy day). The differential warming of western and southwestern exposures can exert a significant influence on orographic generated weather patterns.

The microhabitat temperature were predicted from modeled site maxima and minima by:

$$TPmax = Tmax_s + \Delta Pmax_{s,m} \cdot \frac{\Delta T}{\Delta T_{95}} \quad (7)$$

where $TPmax$ is south-side phloem maximum temperature, $\Delta Pmax_{s,m}$ is maximum temperature increase for the stand and month (values derived from Schmid *et al.*, 1992), and the remaining terms are as previously defined. South side phloem temperature minima and north side maxima and minima were assumed to be the same as air temperature maxima and minima (Schmid *et al.*, 1992).

Even with an adequate model that allows temperature projection from one point in the landscape to another, the challenge of representing phenology over the continuous landscape still remains. A solution that simply uses a pixel-by-pixel simulation is not practical for computational reasons, particularly when this approach would also require running the simulation model on the same basis. The solution to this problem is provided through Geographic Information Systems (GIS) interpretation of the landscape and subsequent classification into a manageable number of ecologically similar units. Classification begins by obtaining a Digital Elevation Model (DEM, available from the United States Department of Interior United States Geological Service) representation of the landscape in question. Classification rules are then devised based on slope, aspect, and elevation. In our experience, classification rules that divide aspect into 16 classes (22.5° increments), slope into 10 classes (ranging from 0° to $\geq 45^\circ$), and elevation increments of 100 m have provided sufficient ecological resolution. The classification rules are implemented through a GIS (we are currently using IDRISI, Eastman 1993). For a typically complex mountainous landscape (7.5 min Quad spatial scale), classification results in approximately 50 landscape units. Although these landscape units are spatially disjunct, model predictions from landscape units classified the same will be identical (i.e. a lower elevation north-east facing slope may be the same as a higher elevation south-west facing slope). Further, once a landscape sufficiently large to include essential ecological characteristics has been classified, then the number of units required becomes independent of spatial scale. Scale independence might appear to be a self-evident result of classification, but the computational implications are significant. For example, if we were to attempt running the simulation model on strictly a spatial scale, a landscape resolution of 30 m seems ecologically reasonable. With this spatial resolution, landscape level simulation of a 7.5 min Quad would require running MPBMOD on the order of 200,000 times. Furthermore, an increase in spatial scale would result in a linear increase of the number of simulations required to capture the landscape. Although evaluation of various classification rules remain an active research interest, and results to date must be considered preliminary, coupling GIS analysis with simulation results in a computational savings of at least several orders of magnitude.

Model Integration. Work with the objective of integrating MPBMOD with the landscape temperature model is currently in progress. Our goal is provide a flexible front-end that allows convenient projection of selected population attributes over complex,

mountainous landscapes.

Interesting Hypotheses Relating to Mountain Pine Beetle Ecology

The Mountain Pine Beetle project of the US-Forest Service was initiated during the early 1960's in response to the large volume of timber that was being lost to this pest at that time in the western United States. The early emphasis of the project was protection of these timber values, although the approach was always to understand the basic ecology of MPB as a basis for development of management strategies. More recently, in response to shifting societal and US-Forest Service priorities, the research emphasis of the project has evolved from that of protection ecology to one of disturbance ecology. Although protection of short-term timber value remains of interest, perhaps even more important is attempting to understand the ecological role of MPB disturbance in western coniferous forests. In particular, disturbance frequency and intensity is a major determinant of subsequent forest ecosystem pattern, structure, and function. Disturbances and changes in disturbance patterns may also be a key symptom of forest health and an indicator of larger ecological issues such as global climate change. It is in the role of basic disturbance ecology that mountain pine beetle becomes of interest in high-altitude, 5-needle pine forests.

Mountain pine beetle is a potentially important component of sensitive, high elevation pine systems, such as whitebark pine (WBP) forests. In contrast to the dynamics exhibited in lodgepole pine (LPP), MPB populations in WBP typically operate as a fugitive species. Due to the high elevation climate characteristics of WBP ecosystems, MPB populations are typically semivoltine and asynchronous (Safranyik, 1978). Populations of MPB in WBP, therefore, do not exhibit the predictable (Schmidt, 1989) cycle of beetle outbreaks and fire typical of lodgepole systems. Adverse effects of severe climate on population performance are primarily responsible for maintaining mountain pine beetle populations in a sub-outbreak phase in high elevation forests (Amman et al., 1977). Climate effects are expressed in several related ways. Heat accumulation is not sufficient for completion of the typical univoltine life cycle and, as a result, populations are semivoltine. Stretching the life cycle over two years results in severe mortality consequences. Only a relatively narrow phenological window of life stages are cold resistant (larval instars three and four) and those life stages older or younger should suffer extreme mortality. In addition to mortality, the two year life cycle slows the chronological clock with respect to the insects physiological clock. As a result, critical life history events are prolonged and events that are synchronous in univoltine population would be temporally dispersed in a semivoltine population. Temporal dispersion could result in disastrous consequences for a species utilizing a mass-attack strategy to overcome host resistance. In this view, self-sustaining outbreaks of MPB in WBP would be unlikely and tree mortality from MPB should be temporally sporadic and spatially diffuse, with only the occasional weakened tree taken out. At least two exceptions to this generalization are possible. First, prolonged periods of unusually warm temperatures might allow population release and subsequent build-up of MPB populations within the WBP stand. The potential for climatic release of the population is particularly problematic given global warming scenarios. The second possibility results from movement of substantial numbers of

MPB into WBP stands from adjacent LPP stands undergoing an outbreak. Such occurrences have been documented in forests with a contiguous intergradation of LPP into WBP (Bartos & Gibson, 1990).

The high elevation 5-needle pine forest ecosystems of the western United States are unquestionably of high intrinsic and esthetic value. They are some of the oldest organisms in the interior west of the U.S., and as a consequence contain a lengthy biological record of climatic influence on ecological systems. Ecologists are becoming increasingly aware of the connectedness of ecosystems, and high elevation 5-needle pine ecosystems are no exception. For example, WBP seeds comprise an important component in grizzly bear diets during the critical time they are preparing for hibernation. Interestingly enough, conflicts between humans and bears increases significantly during years of poor WBP seed production (Mattson & Jonkel, 1990). High elevation ecosystems can be thought of as existing on the extremes. These type of systems, those that maintain themselves under consistently adverse or harsh conditions, are typically thought of as prime candidates for indicators of environmental change (Danks, 1992). With respect to the role that high elevation forests might play as "canaries of ecological peril," there is apparent evidence that high elevation forests are systems under siege. A good example are the so-called "ghost forests" of WBP found in various high elevation sites throughout the west, including the Sawtooth National Recreation Area (SNRA) near Stanley, Idaho. The name for these forests arise from the large number of standing dead trees, which weather to a grey, ghost-like color. The real question of interest is; are the high mortality observations in the ghost forests an indication of pathologic change in the ecosystem, or are they simply a normal aspect of a healthy functioning ecosystem?

Motivated, at least in part, by the potential for an indicator of forest health, a US-Forest Service (Intermountain Research Station) project has been cooperatively funded with the Laboratory of Tree Ring Analysis at the University of Arizona (D. L. Perkins and T. W. Swetnam) to investigate mortality causes in the WBP ghost forests in the SNRA. In these investigations, it is becoming increasingly evident that significant, often catastrophic (over a period of 10 or less years) mortality, has resulted from MPB attack. This result is surprising because of the isolation (separation by non-host spruce-fir) of WBP from LPP. As previously noted, mortality could "spill-over" from an ongoing outbreak in an adjacent LPP stand (Bartos & Gibson, 1990), but the occurrence of outbreaks in ecologically isolated stands is enigmatic. **Three possible hypotheses for this enigmatic observation seem possible. (i) Our understanding of weather effects on MPB population dynamics is seriously in error. (ii) Unusually mild weather patterns over several years resulted in self-sustaining outbreaks. (iii) Some, as yet unknown, transport mechanism resulted in import of sufficient beetles to cause catastrophic mortality.**

The first hypothesis is currently a primary focus of the Mountain Pine Beetle Project of the USDA-Forest Service Intermountain Research Station. Predictions from the previously described model are being rigorously validated in field experiments at a variety of geographic locations in the western United States (see B. J. Bentz, *in press*). The second hypothesis is being tested by reconstruction of site-specific weather patterns using the previously described

landscape model and historical records. This work is in progress for the MPB mortality events identified from tree-ring analysis to have occurred during the 1920's. Temperature model projections will be corroborated through tree-ring analysis of growth patterns for the time period of interest. To test the third hypothesis, we first need to identify a long-range transport mechanism. From the location of the ghost forests, and from prevailing orographic generated weather phenomena, we have hypothesized a potential mechanism that is a consequence of the combined action of prevailing continental air-mass flow and thermally induced summer winds.

The first component of the hypothesized long-range transport mechanism became apparent during a late summer visit to one of the ghost forest sites. Even at the time of the visit (August) a sizable residual cornice remained above the site, indicating the extent of snow loading during winter storm events. The prominence of this cornice emphasized the direction of prevailing winds and suggested a beetle transport mechanism similar to the catchment and deposition that is responsible for snow wind-loading during a winter storm. The potential catchment area, far below the intervening band of non-host forest type, was also apparent: a large valley-basin of monoculture LPP. Of course, while the mechanism suggested by the cornice is a winter phenomena, hardly suitable for transport of flying beetles, it is an indication of the predominant west-to-east continental air-mass flow (see Fig. 1).

A summer orographic weather phenomena that could serve to transport MPB from a spatially-separated outbreak in LPP up into high-elevation WBP habitat results from the summer "valley-winds" (Barry, 1992). In the western United States, almost all mountain ranges have a north-south orientation resulting in predominantly east and west facing aspects. The summer valley-winds result from thermal warming of east/west facing slopes and subsequent up-slope winds created by the rising warm air. In the mountainous United States, the typical situation is that gentle easterly breezes result as the morning sun begins to warm the east facing aspects. As the sun gains altitude and intensity, substantial warming occurs during the afternoon on the west facing aspects. In contrast to the gentle breezes characteristic of the morning easterly's, the afternoon westerly's are often powerful winds. As the thermally warmed air rises, it is compressed between the mountain ridge-line and the upper atmosphere resulting in increased wind velocity across the ridge top. Sudden deceleration on the lee side creates turbulent flow on the east facing slopes below the ridge line. The resulting turbulence is analogous to eddies formed as a river flows past a rock or other barrier. Beetles transported by westerly valley winds would be "sucked" into the east-facing deposition zone by the turbulent flow, and once deposited, would tend to be held there by the resulting eddy lines (see Fig 2). These strong afternoon winds correspond temporally with the time of beetle emergence and flight.

The transport mechanism that we have described results in several predictions. The first, and most obvious is a MPB temporally coincident outbreak in an appropriate LPP stand. For the SNRA, "appropriate" means forests on the western aspect of east facing WBP stands. For example, MPB episodes in the Sawtooth mountains should be correlated with outbreaks in the Payett drainage, whereas those in the White Cloud mountains should be correlated with outbreaks in the Salmon river drainage. Lack of temporal correlation with an appropriate

outbreak would be evidence to falsify the long-range transport hypothesis. Conversely, there should be a lack of correlation with MPB outbreaks to the east of ghost forest sites. Attempts are currently underway to locate the appropriate historical records required to evaluate these spatial predictions. Another prediction would be lack of correlation between unusually mild weather and MPB caused mortality. This prediction can be tested by running MPBMOD for prevailing weather patterns reconstructed from historic records during the time of the MPB outbreaks. Lack of suitable high-elevation weather, as predicted by poor population performance from the model, during a mortality episode would tend to corroborate some transport mechanism. Finally we should be able to predict catchment and deposition zones from a combination of topographic maps, forest cover types, and records of MPB outbreaks. These types of predictions can be automated through use of rule-based reasoning combined with GIS analysis of corresponding DEMs. Validity of these predictions can be ground-truthed as a measure of the predictive power of the hypotheses. The main point is, hypotheses regarding the mechanism of catastrophic mortality events in WBP result in testable predictions.

Determining the relative plausibility of competing hypotheses for the high-elevation ghost forests is important for several reasons. The critical question is: Did the observed MPB mortality result from unusually warm weather conditions, and therefore be a warning of potentially exacerbated impacts of climate change due to increased MPB activity. Conversely, if the ghost forest mortality resulted from long-range transport of beetles, then it may well be that such occurrences have been a part of the WBP ecosystem for millennia. If we are to use the occurrence of insect outbreaks as an indication of forest health, the ability to differentiate between pathologic aspects of the system from normal occurrences in a healthy, functioning ecosystem is essential. Monitoring the occurrence of pest outbreaks may be an important indicator of changing climate and deteriorating forest health, but only if we know enough to determine the probable causality of temporal outbreak patterns. A mechanistic understanding of the WBP ghost forests has wider implications than simply for the high-elevation forests of the interior west. WBP and LPP have evolved very different life-history strategies that enable them to adapt to various disturbances. Understanding these adaptations will help us to more fully understand the role of disturbance in forest ecosystem structure and function, and to effectively formulate management strategies in the face global warming or other modifications to natural disturbance regimes.

Summary and Conclusions

In summary, the conventional wisdom that a warming climate will result in increased insect pest problems is probably true. This conclusion results from a variety of life history characteristics that allow insects to effectively adapt to rapidly changing conditions. The demonstrated resiliency of insect populations in face of previous climatic variation reinforces this conclusion. Although in general terms insect pest problems may be exacerbated, it is difficult to make insightful predictions for a particular insect species, there will be winners and there will be losers in a changing global climate. The potential consequences, however, warrant the effort required to make honest attempts at evaluating consequences of climate

change for potentially important pest species. Aggressive bark beetles, such as the mountain pine beetle, have the potential to foreclose evolutionary options of sensitive species such as WBP through mortality that negates the strategy of a long lived species persisting until adverse conditions improve.

The potential role of insects (or insect damage) as biological indicators of environmental stress and forest health is generally recognized. Biological systems serve to integrate the total environment, and as such, they may respond to changes in the physical environment long before the change could be directly measured. This potential is particularly important in situations such as the global climate in which subtle signals are hidden by background noise. It is generally recognized that the most sensitive indicators of ecosystem health are those components of the system that exist under conditions of chronic stress. Alteration in historical disturbance regimes with respect to intensity, duration, or magnitude in these conditions may be an efficient early warning of more widespread impacts in the future. The whole issue of forest health monitoring revolves around these concepts. The challenge is: **Discriminating between ecological disturbance that is a pathologic symptom of an unhealthy ecosystem from those situations in which disturbance is a natural manifestation of a healthy, functioning ecosystem.** The role of mathematical models can aid substantially in this discriminatory process, but only if they include validated representations of key ecological processes.

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ENDNOTES

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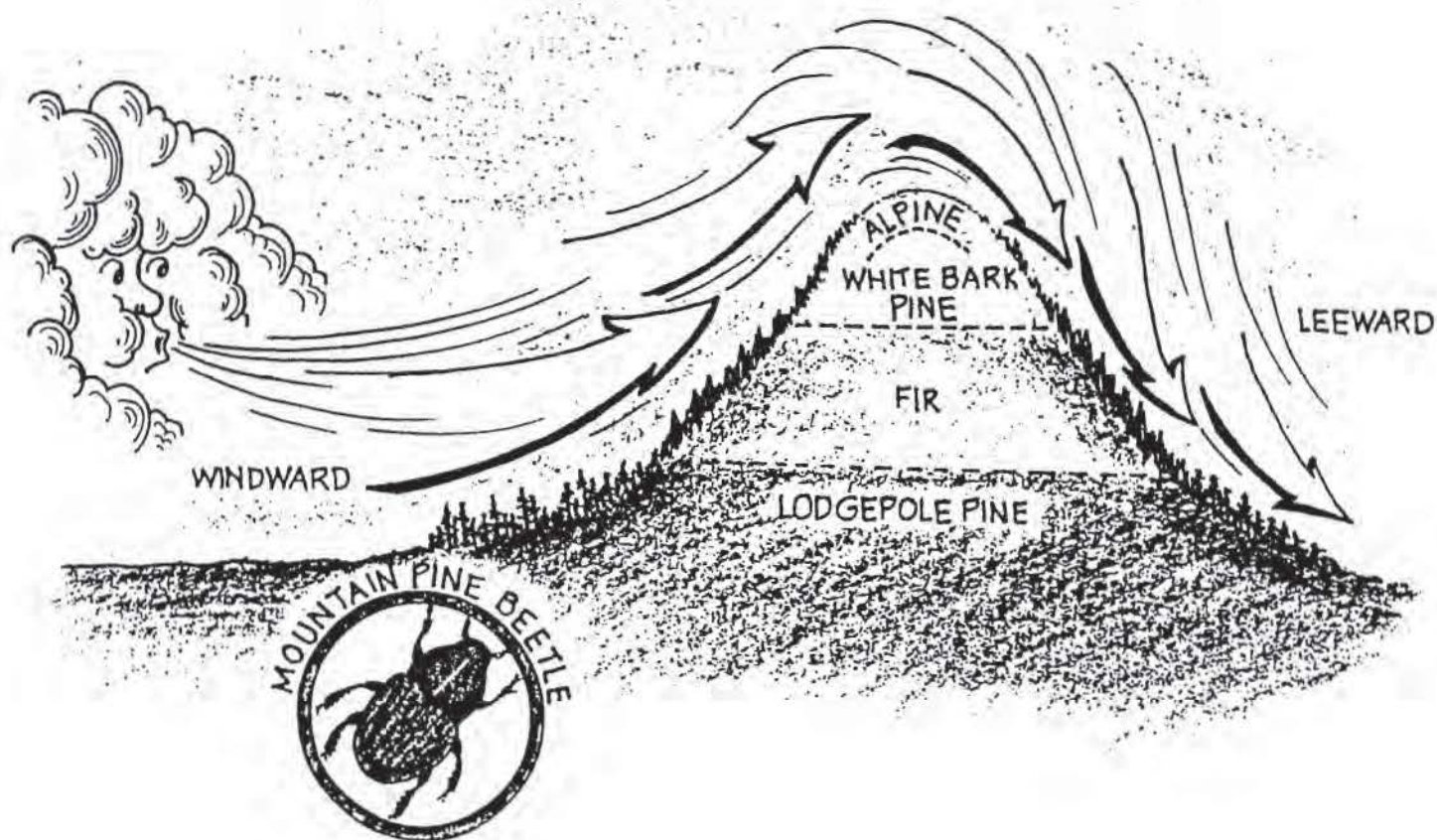


Figure 1. Typical pattern of continental frontal storm patterns. Prevailing winds from the west accelerate on the upslope, windward exposures. A zone of turbulence and abrupt deceleration of the winds occurs on the leeward facing ridge tops. The decreased capacity of particle transport that accompanies the decelerating wind velocities are responsible for wind loading of snow during winter storm events. The obvious cornices that results are evidence of prevailing winds and subsequent transport.

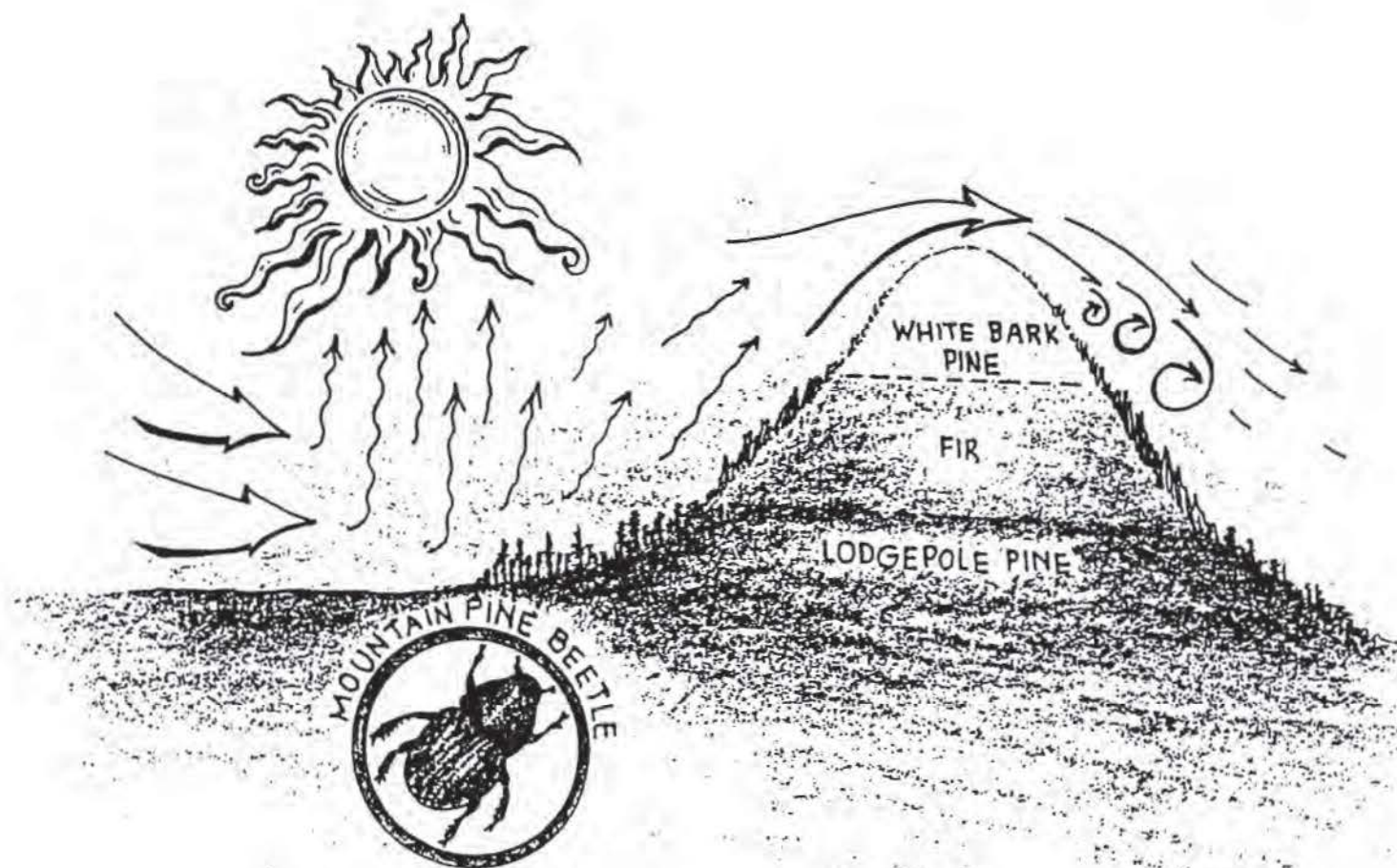


Figure 2 - Typically strong up-slope winds occur on summer afternoons as a result of thermal warming of west facing ridges. Velocities of these thermally generated winds are strong enough to establish standing eddies on the leeward (east facing) slopes. The predictable summer up-slope winds could act as a transport mechanism for mountain pine beetles in much the same way that winter storm patterns act as a snow transport and deposition mechanism. See text for further explanation.