

# Model Analysis of Spatial Patterns in Mountain Pine Beetle Outbreaks

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The mountain pine beetle [MPB, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)] is an aggressive bark beetle, one that typically needs to kill host trees in order to successfully reproduce. This ecological adaptation has resulted in an organism that is both economically important and ecologically significant. Even though significant resources have been expended on MPB research, and a great deal of knowledge exists regarding individual aspects of MPB ecology, some of the most basic questions regarding outbreaks remain unanswered. In our opinion, one reason for the lack of synthesis and predictive power is the inadequate treatment of spatial dynamics in outbreak theories. This paper explicitly addresses the role of spatial dynamics in the precipitation and propagation of MPB outbreaks.

We first describe a spatially dynamic model of the MPB/forest interaction that includes chemical ecology, spatial redistribution of beetles, attack, and resulting host mortality. The model is a system of 6 coupled, partial differential equations with 7 state variables and 20 parameters. It represents an attempt to capture the relatively complex predator/prey interaction between MPB and host trees by including the minimum phenomenological descriptions necessary for ecological credibility. This system of equations describes the temporal dynamics of: beetle attraction as a function of pheromone concentration; the change in numbers of flying and nesting beetles; tree resistance/susceptibility; and tree recovery from attack. Spatial dynamics are modeled by fluxes due to gradients in pheromones and kairomones, and the random redistribution of beetles in absence of semiochemicals.

We then use the parameterized model to explore three issues central to the ecology of MPB/forest interaction. The first of these is in response to the need for objective ways to

compare patterns of successful beetle attacks as they evolve in space. Simulation results indicate that at endemic levels, the pattern of successful attacks are determined almost exclusively by the underlying distribution of susceptible host trees (environmental determinism). As an outbreak develops, the pattern of successfully attacked trees switches to one that is dynamically driven by the self-generated semiochemical landscape (dynamic determinism). This switch from an environmentally determined spatial pattern to a dynamically driven pattern is the hallmark of an outbreak. We discuss the application of a spatial correlation coefficient that can be used to differentiate between the spatial distribution of killed trees in endemic and outbreak phases. The second issue we address through simulation is synchrony in adult emergence. Synchronous adult emergence is critical for the mass attack strategy necessary for overcoming tree defenses. Results from these simulations indicate that the degree of synchrony in adult emergence can have important consequences for assessing the risk of an outbreak. The final issue we investigate through simulation is the effect of spatial pattern of nurse trees (those successfully attacked the previous year) on outbreak potential. Simulations indicated that the spatial proximity of nurse trees was an important determinant of subsequent successful attacks.

We conclude with a discussion of the general implications of our simulation experiments.

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## INTRODUCTION

Terrestrial ecosystems exhibit spatial variability at scales ranging from centimeters to kilometers. Spatial complexity results from both underlying patterns of the physical environment and complex biotic interactions. Even in an initially uniform environment, spatial heterogeneity would soon evolve as different species aggregate and disperse in spatially complex ways. Animals aggregate for a variety of reasons, including defense from predators, improved predation success, and enhanced reproductive success. Plants array themselves in complex patterns due to seed dispersal patterns, herbivore pressure and other factors. Regardless of the reasons for initial aggregation or dispersal, spatial complexity is often self-generating as a result of feedback between organisms and their abiotic and biotic environment (Roberts, 1987). In particular, spatial complexity often arises from nonlinear self-focusing. Individuals aggregate in response to chemical, auditory, visual or other cues. When the dispersing population is itself responsible for the cues which lead to aggregation, nonlinear feedback occurs, creating self-focused groups of individuals. Self-dissipation may also be an important ecological adaptation that helps populations avoid dangerous habitats or over-exploitation of critical resources. The interplay between nonlinear self-focussing and self-dissipating forces leads to a complex variety of new patterns and spatial dynamics, the understanding of which has long been a central theme of applied ecology. Due to the computational and experimental difficulty in dealing with spatial dynamics, spatial analysis remains at the forefront of ecological investigation (Durrett and

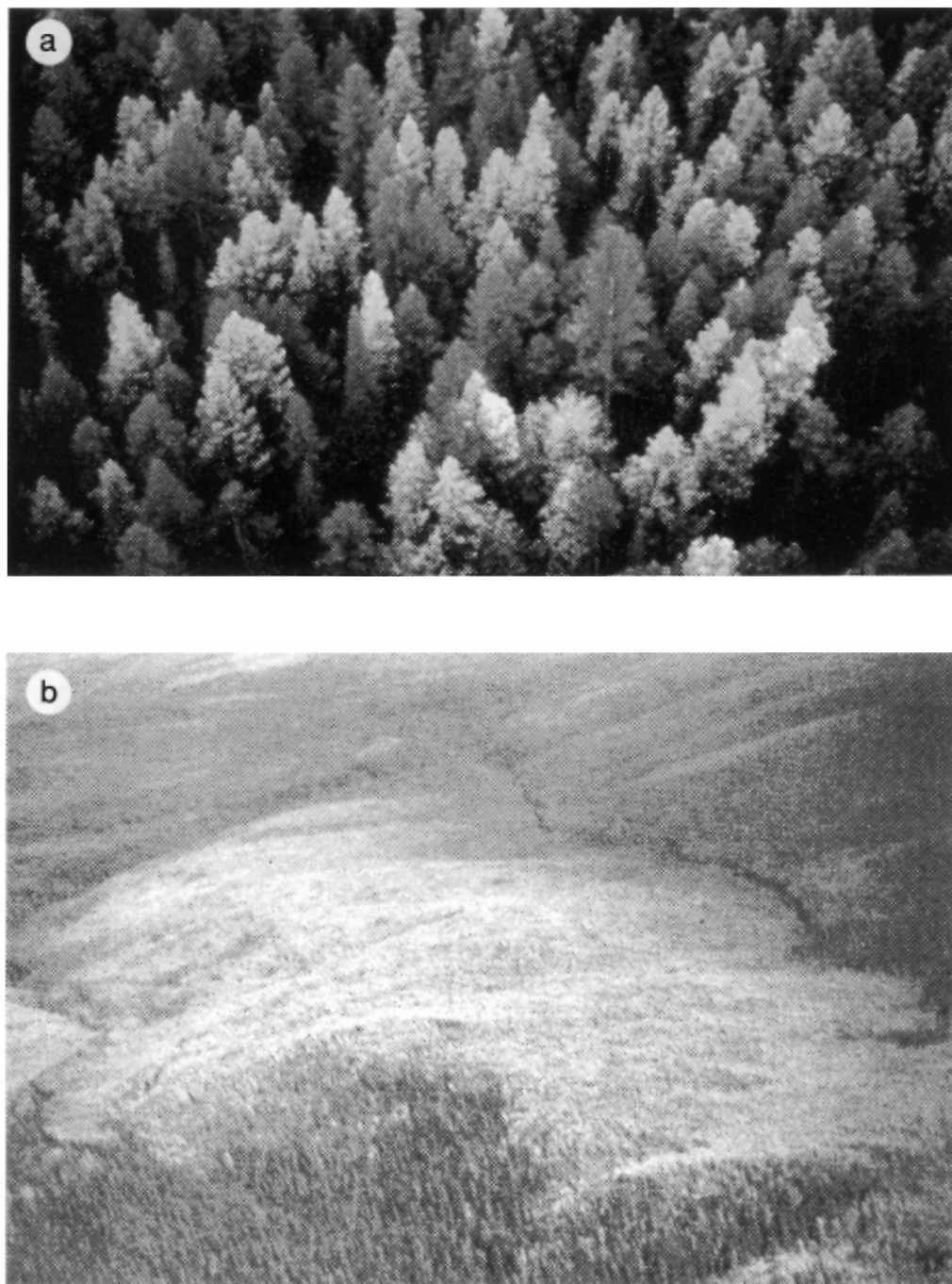
Levin, 1994; Gueron and Levin, 1993; Levin, 1994; Kareiva, 1994).

Self-focusing and self-dissipating considerations are of particular importance for some predators that attack dangerous prey that are, at the same time, easily over-exploited. Such is the case for the mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) attacking pine trees (Berryman *et al.*, 1984). MPB is an aggressive bark beetle that must kill its host to successfully reproduce. In order to accomplish this end, the significant defense mechanisms of the host tree, involving both the primary resin system and induced hypersensitive responses (Nebeker *et al.*, 1993), must be overcome. However, once a tree is overwhelmed, populations are restricted to the phloem layer of the inner bark. Since the phloem layer is relatively thin, the nesting<sup>1</sup> habitat is severely restricted and easily over-exploited (Cole, 1962; Berryman and Pienaar, 1973). In response to selection pressures acting on a small, weak predator attacking a large dangerous prey, MPB have evolved a pheromone mediated mass attack strategy that overwhelms the tree defensive mechanism through large numbers of attacking beetles. This system incorporates both tree-defensive compounds and beetle-produced chemicals to manufacture attractive pheromones of truly prodigious capabilities (Pitman, 1971; Pitman *et al.*, 1968; Hughes, 1973). Likewise, in response to selection pressures for efficient utilization of limited resources, pheromones that send anti-aggregation signals come into play once a tree has been colonized (Borden *et al.*, 1987; Rudinsky *et al.*,

<sup>1</sup> We refer to the complex of within-season activities (feeding, mating, gallery construction, oviposition, and larval maturation, etc.) that occur in the phloem as "nesting."

1974; Hunt and Borden, 1989). The combination of self-focusing and self-dissipating forces leads to a spatial Allee effect (Allee, 1931) in which predator success is enhanced by increasing density at low population levels, and then inhibited by competition at higher densities. As

the population organizes by nonlinear self-focussing and self-dissipation (White and Powell, submitted), the dispersal pattern can become increasingly complex (Fig. 1a). Complex spatial dynamics are thus integral to an understanding of MPB ecology and formulation of



**FIG. 1.** (a) Self generating spatial complexity within an MPB outbreak. The red-top trees have been killed by attacking beetles, while nearby trees have survived. The stand is in an even aged lodgepole pine forest. (b) Aerial photograph of MPB outbreak on Adair ridge in Glacier National Park, 1980. All the red-top trees in this landscape were killed in a single season of the epidemic.

rational management policy regarding this important insect.

The ecological adaptation of MPB as an aggressive bark beetle that must kill its host to successfully reproduce has resulted in an organism that is both economically important and ecologically significant. Outbreaks of MPB can be of truly spectacular proportions (Fig. 1b), with resulting tree mortality that is both intensive (often in excess of 80% mortality) and extensive (sometimes thousands of acres). As a consequence of this economic and ecological significance, a great deal of monetary and intellectual resources have been expended trying to understand the underlying ecological basis of these spectacular outbreak events. This attention has resulted in an impressive knowledge base that is well documented in the scientific literature (e.g., Lessard *et al.*, 1986). In spite of this significant effort, some of the most basic questions regarding MPB outbreaks remain unanswered. Among these are: What actually triggers an outbreak? What determines its intensity and spatial extent? Although several hypotheses have been put forward (Berryman, 1976; Berryman *et al.*, 1984; Cole and Amman, 1980; Amman, 1978; Raffa and Berryman, 1986), a generally accepted synthesis remains an illusive goal. In our opinion, one important reason for the lack of synthesis and ability to predict outbreaks is the inadequate treatment of spatial dynamics in outbreak theories.

Our basic thesis is that outbreak dynamics are inherently dependent on dispersal behavior as well as local population dynamics, and that to understand outbreaks in a large-scale spatial domain one must consider dispersal behavior as well as local conditions. Integrating ecological processes across spatial and temporal scales is a daunting task. First, the very nature of outbreaks leads to a great deal of interest when a raging epidemic is in progress, but interest quickly wanes during periods of remission. As a result, empirical information is skewed towards measurements made after an outbreak is already in progress and much less data exist during the critical times leading up to outbreak initiation. Secondly, it is physically and logistically difficult to conduct experiments in mountainous terrain on the spatial scale that is required. As a result, most empirical experiments have been conducted at the individual tree, or at most, stand level. In response to the difficulties in on-the-ground empirical analysis of outbreak events, we have formulated a mathematical model of MPB chemical ecology and the spatial interaction between MPB and host forests. Analysis of this model is itself fraught with difficulties due to spatial complexity of turbulence resulting from the nonlinearities we have already discussed (Taubes, 1995). Due to these mathematical and computational

difficulties, our work to date (Powell *et al.*, 1996; Powell and Rose, in press; White and Powell, in press) has dealt largely with the analytical and numerical aspects of the model. In this paper, we begin to apply this model in the analysis of ecological questions regarding the nature of MPB outbreaks.

We first describe development of the model in enough detail to provide the reader with a basic understanding of model structure. The level of system description is intermediate between a mechanistic simulation and a completely general, theoretical model. The model can be classified as a system-specific, phenomenological representation. We next briefly discuss the numerical solution approaches used to obtain simulation results. Numerical solutions are then used to explore three issues critical to a more complete understanding of MPB outbreak dynamics. The first of these involves the shift in observed spatial pattern that accompanies the temporal evolution of an outbreak. The second issue is temporal synchrony of adult emergence. Temporal synchrony is an important ecological attribute since large numbers of attacking beetles must be present to simultaneously attack trees in order to overcome defensive tree responses. We finally explore the effect of spatial arrangement of weakened trees (those attacked the previous year) and the role they might serve as "nurse trees" to focus initiation of an outbreak.

## METHODS

### *Description of the Model*

Our objective is to explore some critical aspects of MPB ecology through simulations with a model of chemical ecology, spatial redistribution, attack, and tree mortality. In a sense, we are using the model as a tool for testing hypotheses regarding the sufficiency of certain critical attributes of MPB ecology, especially those pertaining to the self-focusing and self-dissipating effects of pheromone chemistry, as the cause of observed mortality patterns. The motivation for our work is to better understand the causes and consequences of outbreaks rather than to predict the actual sequence of an outbreak in a specific forest. We therefore seek to include only the minimum, reasonable subset of factors impinging on the MPB life-system that are required to capture the spatial redistribution of attacking beetles and their subsequent mortality impact on the forest. Since we are not attempting to recreate the ecological world inside a computer chip, our description of critical components of MPB spatial ecology are phenomenological rather than

mechanistic. In order to facilitate model description, we will describe the temporal evolution of pheromone chemistry, beetle density, and forest dynamics. We will then describe the spatial dynamics of these factors.

### Temporal Dynamics

*Pheromone Ecology.* Female MPB, which typically initiate new attacks, bore into the bark and through a chemically mediated synergistic reaction with host chemicals, release trans-verbenol. Trans-verbenol is an aggregative pheromone attracting both sexes (Pitman *et al.*, 1968; Hughes, 1973; Pitman, 1971). Attracted males produce exo-brevicomin which at low concentrations primarily attracts females (Conn *et al.*, 1983). At higher concentrations exo-brevicomin may act to inhibit aggregation (Borden *et al.*, 1987; Rudinsky *et al.*, 1974). As the attack progresses, verbenone, an antiaggregation semiochemical, is produced through autoxidation of host terpenes, and by enzymatic conversion of yeasts (Hunt and Borden, 1989). The temporal sequence of these complex interactions is: as the resource is originally colonized, attractive pheromones are produced as an increasing function of beetle density; then, as the tree becomes more fully exploited, anti-aggregation pheromones begin to dominate, again as an increasing function of population density. Integration of this temporal sequence results in a second order density-dependent process represented in the model by a composite pheromone that is attractive at low concentrations and repulsive at higher concentrations. Attractiveness as a function of pheromone concentration is controlled by the nonlinear, phenomenological relationship,

$$f(A) = A_3 \left\{ A_0 (A_3 + 1) \ln \left( 1 + \frac{A}{A_3 A_0} \right) - A \right. \\ \left. \nabla f = \frac{A_0 - A}{A_0 + A/A_3} \cdot \nabla A \right. \quad (1)$$

where  $A$  is pheromone concentration;  $A_0$  is a shaping parameter that determines the concentration at which the pheromone ceases to become more attractive, i.e. the maximum attractiveness; and  $A_3$  is a measure of the steepness of decline in attractiveness once concentration exceeds  $A_0$ . The gradient of  $f(A)$  determines the response of a flying beetle at any point in space, pheromone concentration is attractive as long as  $\nabla f(A) > 0$ .

*Flying Beetle Density.* If we neglect spatial redistribution, the number of flying MPB ( $P$ ) decreases proportionally due to a background death rate,  $\omega_1 P$ , and the

number of beetles landing and nesting in a tree,  $r_1 P(R/R_0)(1 + \sigma A)$ . The term  $r_1 P$  represents randomly landing beetles; the term  $r_1 \sigma A$  describes the nesting in response to pheromones as a linearly increasing function of pheromone concentration.  $R_0$  is the initial resin capacity of the tree, and as such is a representation of tree health (resistance).  $R_0$  is also proportional to the surface area of the bole, and consequently  $R/R_0$  measures the uninfested portion of the bole. This ratio allows more nesting (and subsequently, more production) from healthy trees, a consequence in agreement with the interpretation of healthy, thick phloem trees providing a high quality food resource (Amman 1972). This gives the dynamic equation for temporal changes in flying beetle density:

$$\dot{P} = -\omega_1 P - r_1 \frac{R}{R_0} P(1 + \sigma A) + \gamma. \quad (2)$$

The term  $\gamma$  is the emergence rate of flying beetles, and may be both temporally and spatially dependent.

*Nesting Beetle Density.* The nesting population,  $Q$ , grows proportionally at the rate in which beetles are removed from the flying population in response to either random landings or pheromone concentration, i.e.,  $r_1 P(R/R_0)(1 + \sigma A)$ . Nesting beetles have a background mortality of some rate  $\omega_2 Q$ . Beetles are also subjected to mortality from host defenses, represented by resin out-flow ( $S$ ). This latter source of mortality should decrease in proportion to the resin out-flow through boring holes made by attacking beetles ( $H$ ), resulting in  $\beta S(Q/H)$ . This gives an equation for  $Q$ ,

$$\dot{Q} = -\omega_2 Q + r_1 \frac{R}{R_0} P(1 + \sigma A) - \beta S \frac{Q}{H}. \quad (3)$$

*Tree Resistance/Susceptibility.* In order to meet our objectives of a model capable of capturing the qualitative nature of the interaction between MPB and the forest, we need to be able to represent spatial heterogeneity of the forest from the beetles perspective. We do this by including a relative measure of tree resistance to beetle attack. Describing the explicit mechanistic basis of resistance and/or susceptibility is beyond the scope of this work. We seek the simplest description possible that will allow us to test hypotheses regarding the spatial distribution of susceptible trees. This relative measure of resistance is represented in the model by "resin capacity" ( $R$ ). When  $R \rightarrow 0$ , the tree has exhausted its defenses and is dead. Conversely, a tree of average resistance is scaled to be  $R = 1$ . The rate of change in resin capacity is then proportional to  $R(R_0 - R)$ , where  $R_0$  is the initial, relative tree health. Resin capacity is depleted proportionally to the

number of attack holes and the available resin that can flow out through these holes. These two processes give.

$$\dot{R} = [r_2(R_0 - R) - r_3H]R. \quad (4)$$

*Tree Recovery.* The final critical variable that needs to be represented in the model is a way to account for the temporal recovery of attacked trees. We do this by dynamically modeling the evidence of attack, i.e. attack holes ( $H$ ). The rate of increase in the number of attack holes is equal to the number of beetles that have attempted to nest. On the other hand, tree recovery from attack is represented by resin crystallization and subsequent closing of the hole. This means that  $H$  should be lost at a rate proportional to the amount of resin outflow,  $S$ , which is itself proportional to the number of holes and the available resin capacity,

$$S = r_3HR.$$

A rate equation for  $H$  is then given by

$$\dot{H} = r_1 \frac{R}{R_0} P(1 + \sigma A) - r_4S. \quad (5)$$

This set of equations reflects the temporal dynamics without spatial redistribution, and is similar in many respects to existing models of the same interaction (e.g. Berryman *et al.*, 1989).

### Spatial Dynamics

We include spatial redistribution by considering the effect of various fluxes on the population. Denote the flux vector by  $\Phi$ . There are three basic components to the flux function: (1) flying beetles response to pheromone concentration,  $A$ ; (2) flying beetles response to host compounds,  $C$ ; and (3) redistribution due to random dispersal,  $\rho$ . Thus,

$$\Phi = \phi_C + \phi_A + \phi_\rho,$$

where

- $\phi_C$  is flux along gradients of  $C(x, y, t)$  due to chemical signals from potential hosts,

$$\phi_C = \kappa P \nabla C.$$

- $\phi_A$  is flux due to the beetles' attraction to/repulsion from the composite pheromone  $A$ ,

$$\phi_A = \nu P \nabla f(A).$$

This flux function has the nonlinear effect of attracting beetles for small  $A$ , but with saturable repulsive effect (parameterized by  $A_3$  for  $A > A_0$ , see Eq. 1).

- $\phi_\rho$  is flux due to the beetles' random redistribution in the absence of other influences dependent only on spatial changes in the density of flying beetles, which gives

$$\phi_\rho = -\mu \nabla P.$$

Adding the effects of these fluxes with the temporal dynamics of Eq. (2) results in a spatial-evolution equation for  $P$ ,

$$\begin{aligned} \frac{\partial P}{\partial t} = & -\nabla \cdot \{[\kappa \nabla C + \nu \nabla f(A)]P - \mu \nabla P\} \\ & -\omega_1 P - r_1 \frac{R}{R_0} P(1 + \sigma A) + \gamma. \end{aligned} \quad (6)$$

We will assume that the chemical concentrations,  $A$  and  $C$ , obey standard diffusion laws, but with sources and sinks of their own. For the suite of pheromones released by nesting beetles, sources are proportional to  $Q$ , while losses occur due to chemical decomposition and dispersion through the canopy. These effects give a linear diffusion equation for  $A$ ,

$$\frac{\partial}{\partial t} A = b_1 \nabla^2 A + a_1 Q - \delta_1 A. \quad (7)$$

For host kairomones,  $C$ , the source is resin outflow or other host produced compounds. Again, we expect some loss due to chemical decomposition, giving an equation similar to that for  $A$ ,

$$\frac{\partial}{\partial t} C = b_2 \nabla^2 C + a_2 S - \delta_2 C. \quad (8)$$

Equations (3–8) are a complete spatial-temporal description of the state variables controlling the MPB/host relationship. These equations result in a system of 7 state variables which depend on spatial location,  $x$ ,  $y$ , and time  $t$ . A descriptive list of state variables is provided in Table I. Since they are reaction diffusion type equations, we refer to the model as MPBpde for **M**ountain **P**ine **B**eetle **p**artial **d**ifferential equation.

TABLE I

List and Description of State Variables Used in MPBpode

State Variable	Description
$P(x, y, t)$	Population
$Q(x, y, t)$	Population of alive, nesting beetles
$A(x, y, t)$	Concentration of composite pheromone
$C(x, y, t)$	Concentration of volatiles released by host trees (kairomones)
$S(x, y, t)$	Resin outflow (the rate at which tree defenses are depleted)
$R(x, y, t)$	Resin capacity (relative resistance)
$H(x, y, t)$	Number of boring holes made by attacking beetles

### Numerical Simulations

Although MPBpde is far less complex than the typical simulation model of the same interaction (e.g., Raffa and Berryman, 1986), it is more mechanistically detailed than previous models of similar interactions (Turchin, 1989) where diffusivity simply became a population density function. As such, it provides an intermediate step between the ecologically detailed simulation environment and the typically abstract level of purely theoretical models. This level of model complexity is important because it provides a means by which field-oriented ecologists can understand and evaluate our description of the processes while maintaining an acceptable level of mathematical tractability. The model includes both self-focusing (pheromone attraction) and self-dissipating (anti-attraction or pheromone inhibition) terms in addition to random movement. All three are necessary to capture the essence of the chemical ecology described above.

Although our aim is to model MPB chemical ecology at an analytically tractable level, the system of partial differential equations (PDEs) still presents substantial numerical challenges. The most natural way to solve these equations is to attempt numerical solution by discretizing space and solving the resulting ordinary differential equations (ODE). This straightforward approach, however, is not feasible due to the spatial scale of interest, the relatively high dimensionality (number of state variables), and the extreme stiffness of the model. First, the order of magnitude differences in temporal scales of parameters lead to traditional ODE-style stiffness. Secondly, an essential characteristic of the model is the focusing of flying MPB onto very small scales (so that beetles can successfully attack individual trees), resulting in *spatial stiffness*—state variables may vary by several orders of magnitude over short spatial scales. Instances of spatial stiffness occur sporadically, as a population

first focuses on individual trees, are then repulsed from these original focus trees and switch attacks to new trees. Additionally, ecological credibility necessitates the need for “transparent” boundary conditions through which beetles leave the spatial domain of the model.

Computational problems have been successfully addressed through a semi-analytic approach (White and Powell, in press). The fastest scales of the problem occur in Eqs. (6–7), which are also the only two linear equations in the model. In Fourier space these equations have trivial analytic solutions. Consequently, we resolve spatial structures in wave space, and solve the two stiffest equations analytically over whatever time step is required for solution of the rest of the equations. All spatial derivatives are evaluated using the Fourier Transform, and the resulting temporal equations integrated using an adaptive-step Adams–Bashforth–Moulton ODE solver. This solution approach combines high accuracy with the ability to adjust time-steps as the stiffness of the problem varies. Using this approach, we are able to simulate full seasonal emergence/flight/dispersal/attack periods (two to four weeks) with overnight turn around on a work-station level computer.

TABLE II

List of Parameter Definitions Appearing in the Model of MPB/Host Spatial–Temporal Interaction

Parameter	Description
$\kappa$	Measure of the beetles' perception of and attraction to weakened trees
$\nu$	Attractiveness of the composite pheromone
$\mu$	Diffusivity of flying beetles due to randomness
$A_0$	Critical concentration at which composite pheromone become repulsive
$A_3$	Saturation parameter for composite pheromone
$a_1$	Rate of pheromone production by nesting beetles
$b_1$	Rate of pheromone diffusion
$\delta_1$	Loss rate of pheromone
$a_2$	Rate of resin exudation by host tree
$b_2$	Rate of kairomone diffusion
$\delta_2$	Loss rate of kairomone
$R_0$	Local peak resin capacity, a measure of tree health
$\sigma$	Rate of pheromone enhanced attack
$r_1$	Rate of landing and conversion from flying to nesting beetles
$r_2$	Rate of resin replenishment
$r_3$	Rate of resin outflow through holes bored by beetles
$r_4$	Rate of resin crystallization (tree recovery)
$\omega_1$	Background mortality rate of flying beetles
$\omega_2$	Background mortality rate of nesting beetles
$\beta$	Mortality rate of nesting beetles due to tree defenses
$\gamma(x, y, t)$	Emergence rate of flying beetles, spatially and temporally dependent

### Parameter Estimation

Reasonable values for all parameters in the model can be obtained either directly from the literature (Powell *et al.*, 1996), or through a combination of published information combined with a technique of projecting the spatial model onto a local domain (Powell and Rose, in press). Basic parameter values used in simulations are listed in Table III. Individual parameters that were varied in simulations are discussed in the next section.

## RESULTS AND DISCUSSION

### Environmental vs Dynamic Determinism

In response to the need for objective ways to compare outbreak patterns as they evolve in space, White and Powell (in press) suggested using the temporal evolution of spatial correlation between  $Q$  and  $R_0$  (the point-by-point correlation between the values of  $Q$  and  $R_0$ ). The first beetles to emerge (pioneering beetles) encounter a chemical landscape that is devoid of the strong pheromone signals. Dispersal is driven at this time by random events, visual cues, and the relatively weak kairomones that signal weakened trees ( $C$ ) (Gara *et al.*, 1984; Moeck and Simmons, 1991; Hayes and Strom, 1995; Hobson, 1995). At the beginning of emergence, these relatively weak signals are the only non-random forces influencing MPB dispersion, and they are solely a product of the environment. As pioneer beetles begin to successfully attack trees, they begin producing the strong forces of attracting pheromones. If there are enough attacking beetles to overcome tree defenses, the resulting self-generated chemical landscape dominates all other factors. These chemically mediated processes result in temporal evolution of a spatial signature that characterizes the progression of an infestation from endemic to an epidemic. In the endemic phase, beetle distribution is primarily determined by the distribution of weakened trees in the forest. White and Powell (in press) have used the spatial correlation between  $Q$  and  $R_0$  as a measure of the influence of weakened trees on successful attacks. This correlation coefficient is a value between  $-1$  and  $1$ , with  $-1$  corresponding to an exact match in the spatial pattern of low values of  $R_0$  with high values of  $Q$ , and  $1$  being equivalent to  $Q = kR_0 + c$  for some positive constants  $k$  and  $c$ . The correlation coefficient is zero if there is no match in the spatial patterns of  $Q$  and  $R_0$ . When the spatial correlation is close to  $-1$ , the dispersal pattern is environmentally determined, meaning that the pattern of successful attacks ( $Q$ ) is almost completely determined

by the pattern of weak ( $R_0$  small) trees in the forest. Conversely, as attacking beetles switch to healthy trees adjacent to weak "focus" trees, this correlation is lost. A large negative correlation is, therefore, termed "environmental determinism"<sup>2</sup> and the subsequent loss of correlation is termed "dynamic determinism."

*Model Initialization.* As an example, consider a series of simulations with parameters as defined in Table III, with the exception of varying  $\gamma$  to result in increasingly severe beetle pressure. In these simulations,  $\gamma$  was introduced as a uniform background distribution, i.e., no initial spatial complexity to emergence. The rate of emergence ranged from 0.075 (for an integrated total number of beetles equal to 786) to 0.15 (for an integrated total number of beetles equal to 1536). The background forest<sup>3</sup> was randomly generated from a uniform sampling distribution with a mean  $R_0$  of unity and a range of  $\pm 0.5$ . All simulations were allowed to run for 40 beetle flight hours.<sup>4</sup>

*Simulation Results.* Figure 2 illustrates the loss of environmental determinism that occurred at the two highest emergence rates. This figure demonstrates a clear distinction in spatial pattern between the endemic phase where only weakened or stressed trees are overcome (the two lowest emergence rates) and the outbreak phase where healthy trees are overcome by mass attacking beetles. It is also evident that although  $\gamma$  was increased in a smooth, continuous fashion, the increase resulted in a dramatically different spatial pattern for the two higher emergence rates. This threshold effect is an important hallmark of an outbreak, and the spatial correlation coefficient results in standard statistical criteria that can be used to separate an outbreak population from an endemic population. Figure 3 is a time plot of the spatial correlation of the four simulations. The dramatic loss of spatial correlation at the higher beetle densities is evident, as is the outbreak nature of the shift from environmental to dynamic determinism.

*Discussion.* The concept of environmental determinism provides a useful criteria for comparing spatial patterns that result from differing initial conditions, parameter values, or model structure. It therefore

<sup>2</sup> Roberts (1987) used the term environmental determinism to describe any spatial pattern that results from an underlying environmental variability.

<sup>3</sup> The spatial scale of the forest is a  $64 \times 64$  grid, representing a forest of 1.6 Km square.

<sup>4</sup> Flight period for emerging beetle is approximately 4 hrs/day. A simulation of 40 flight hours, therefore, roughly corresponds to 10 days of emergence.



TABLE III

Parameter Values Used in Simulation Runs. We Have Used fh for Flight Hour, hec for Hectare, tmg for Tens of Micrograms,  $R_0$  Is Initial Resin Capacity Scaled to 1 for a Healthy Tree of Average Resistance

Parameter	Value	Units
$\kappa$	8	hec <sup>2</sup> tmg <sup>-1</sup> fh <sup>-1</sup>
$\nu$	10	hec <sup>3</sup> tmg <sup>-2</sup> fh <sup>-1</sup>
$\mu$	1	hec fh <sup>-1</sup>
$A_0$	2	tmg hec <sup>-1</sup>
$A_3$	0.2	—
$a_1$	400	tmg hec <sup>-1</sup> fh <sup>-1</sup> MPB <sup>-1</sup>
$b_1$	50	hec fh <sup>-1</sup>
$\delta_1$	200	fh <sup>-1</sup>
$b_2$	50	hec fh <sup>-1</sup>
$\delta_2$	0.1	fh <sup>-1</sup>
$R_0$	1 ± 0.5	$R_0$
$\sigma$	15	hec tmg <sup>-1</sup>
$r_1$	0.15513	fh <sup>-1</sup>
$r_2$	0.05	$R_0^{-1}$ fh <sup>-1</sup>
$r_3$	0.025	fh <sup>-1</sup>
$r_4$	0.1	$R_0^{-1}$ fh <sup>-1</sup>
$\omega_1$	0.1	fh <sup>-1</sup>
$\omega_2$	0.001	fh <sup>-1</sup>
$\beta$	100	MPB $R_0^{-1}$
$\gamma(t)$	varies	MPB hec <sup>-1</sup> fh <sup>-1</sup>

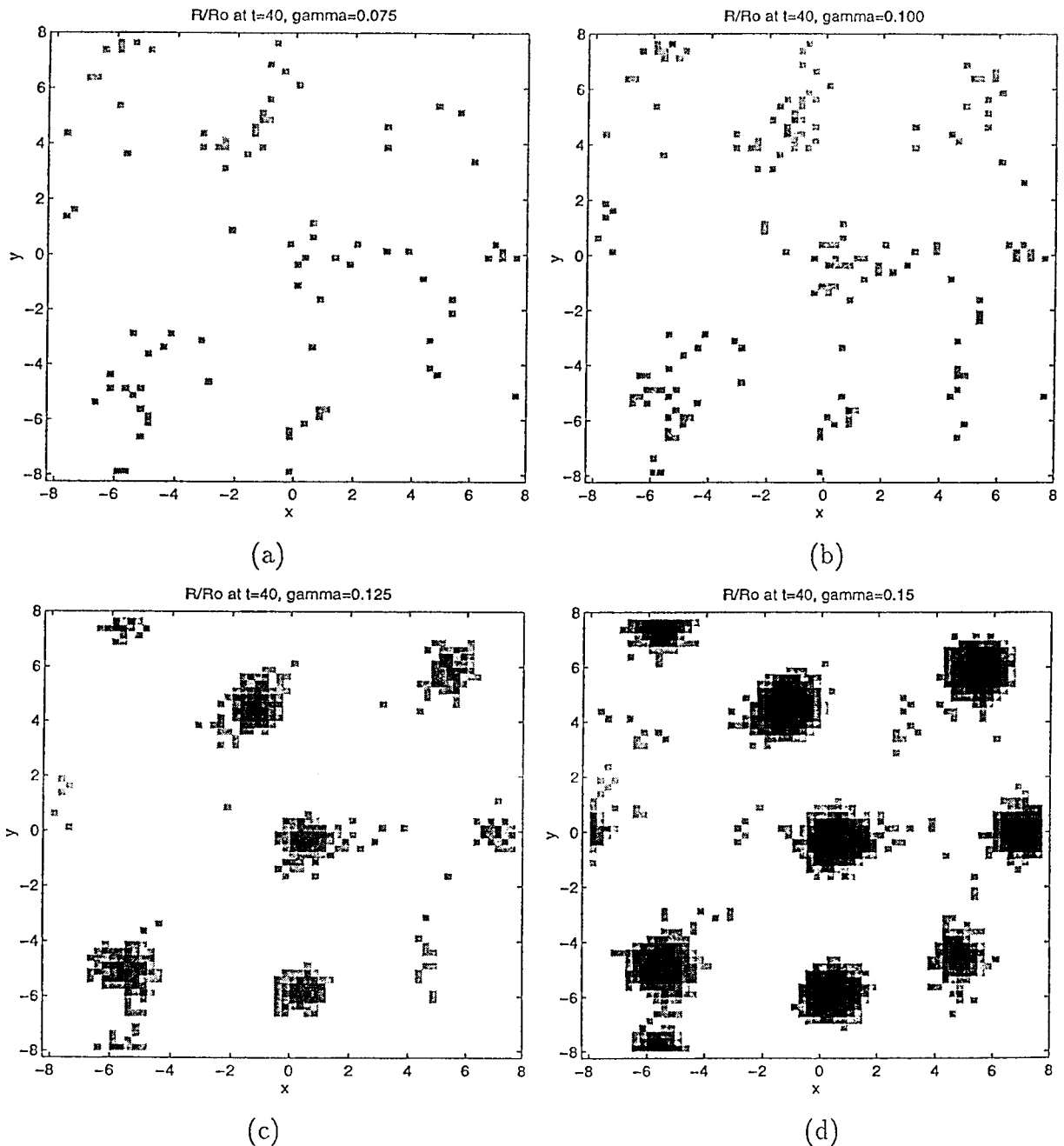
provides one tool that can be used to compare different model runs, or in fact, to test hypotheses through comparison of model runs with field observations. The concept also has important implications apart from a useful way to compare spatial patterns. In particular, a great deal of effort and resources have been expended over the years in attempts to characterize susceptibility of a stand to MPB infestation (Bentz *et al.*, 1993; Shore and Safranyik, 1992) and risk (the probability of an outbreak occurring). In fact, several risk rating schemes have been devised (Amman *et al.*, 1977; Mahoney, 1978; Berryman, 1978; Schenk *et al.*, 1980). Bentz *et al.* (1993) found that when these were applied in a prospective manner, none of them performed much better than could be obtained by flipping a coin. An interesting enigma exists; even though statistically significant relationships can be found between tree/stand characteristics and tree mortality using existing data, the resulting risk rating schemes that are derived from these relationships have little predictive significance. The solution to this enigma is undoubtedly multifaceted, but at least part of the problem is inadequately addressing spatial dynamics. Bentz *et al.* (1993) concluded that major problems existed in interpreting existing susceptibility and risk rating systems because no distinction was made between stand attributes measured during endemic and epidemic population phases. We

note that most of the interest in outbreak insects occurs during times of epidemics, and therefore much of the data is collected during outbreaks. Figures 2 and 3 clearly illustrate that during outbreaks the significant correlation (an inverse measure of susceptibility) relationship between  $Q$  and  $R_0$  is lost.

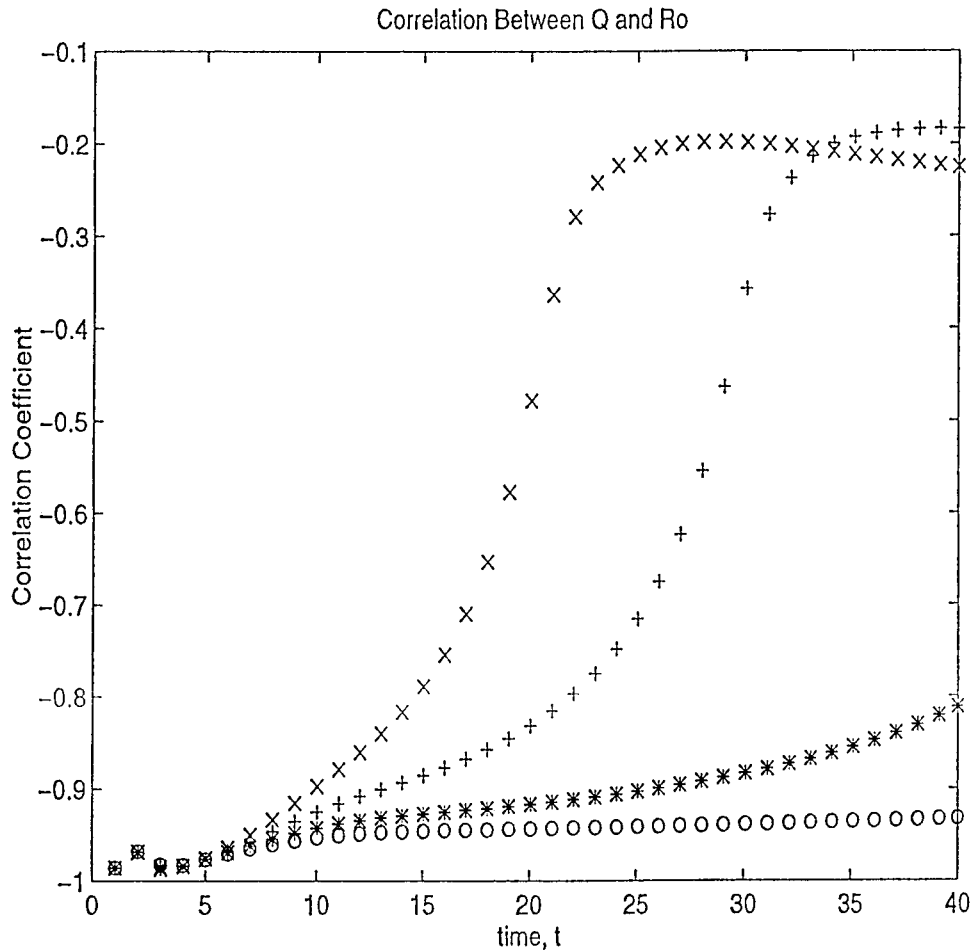
It is easily seen from Fig. 2 that the loss of environmental determinism that accompanies an outbreak would mask the critical effects of tree or stand attributes related to susceptibility. During the endemic population phase, trees that are successfully attacked may well be those that express measurable attributes that could be used to predict susceptibility. This suggests two experimental strategies for susceptibility/risk analysis. The first is to restrict data to endemic phase populations when correlation exists. This approach was taken by Schmitz (1988); however, there are two difficulties with this approach. The first is location of enough attacked trees for a statistically valid sample. Secondly, if only killed “red-tops” (trees killed the previous year) are sampled, then there is no experimental control. A second strategy is to sample in an outbreak setting, but to sample with sufficient temporal and spatial resolution to detect the loss of environmental determinism (Eckberg *et al.*, 1994; McCambridge, 1967; Geiszler and Gara, 1978; Geiszler *et al.*, 1980a).

### Temperature Effects on Synchrony of Emergence

Weather, and in particular the seasonal patterns of temperature, has a profound effect on poikilothermic organisms living in temperate environments. Temperature is recognized as the single most important factor of the physical environment impacting MPB populations (Cole, 1974, 1981; Safranyik, 1978). One critical aspect of temperature is its effect on synchronization of adult emergence. Synchronous adult emergence is critical to a successful mass attack strategy necessary for overcoming tree defenses. The ecological implication of seasonality as manifested by synchronous adult emergence has been recognized for some time (Amman and Cole, 1983; Salom *et al.*, 1987). Weather and temperature effect the synchronization and duration of adult emergence through the annual cycle of phenological events (Bentz *et al.*, 1991; Bentz, 1995), and by the more proximate effect of cool temperatures prolonging and depressing emergence. As a first step toward developing a tool for assessing the impact of seasonal weather on synchronous adult emergence and, subsequently, outbreak potential, we have analyzed results from simulated temporal emergence patterns. The objectives of this analysis were



**FIG. 2.** Results of simulations initiated with increasing levels of beetle emergence. Dark areas correspond to low resin levels and, therefore, areas of high tree mortality. At low beetle population densities (*a*, *b*), the pattern of resin depletion mirrors almost exactly the pattern of weak trees in the initial randomly generated forest. At the two higher population densities (*c*, *d*), self-focusing and switching attack from weak focus trees to nearby healthy trees becomes apparent. Even though the emergence rate ( $\gamma$ ) was increased in each step by a constant 0.025, the resulting pattern shows an obvious discontinuity for the two higher emergence rates. (a)  $\gamma = 0.075$ ; (b)  $\gamma = 0.10$ ; (c)  $\gamma = 0.125$ ; (d)  $\gamma = 0.15$ . Time ( $t$ ) is measured in beetle flight hours.



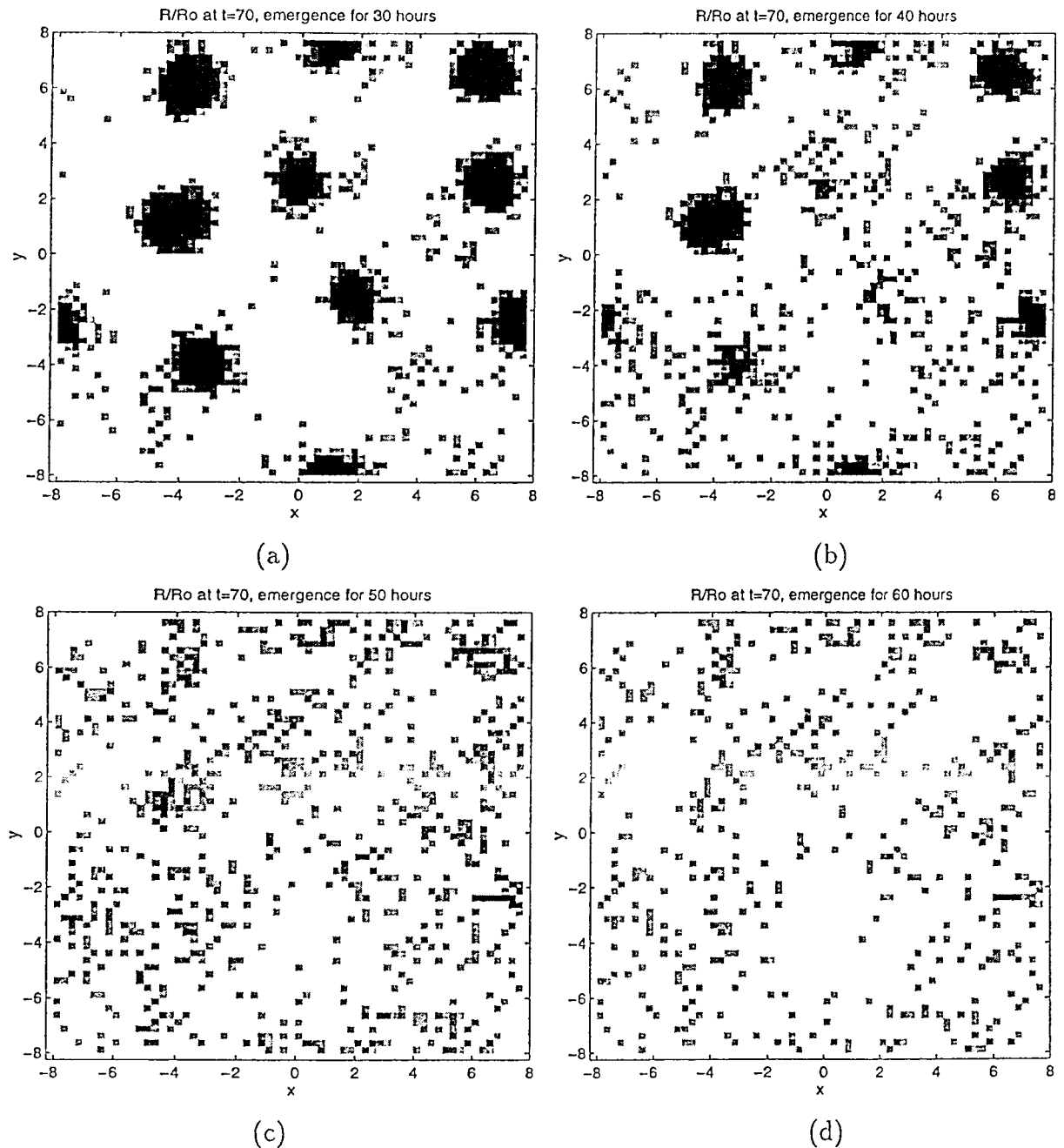
**FIG. 3.** Correlation between infestation of nesting beetles,  $Q$ , and initial tree vigor,  $R_0$ , for the simulations in Fig. 1. As attacking beetles switch from foci which form around weakened trees to nearby healthy trees, the correlation between nesting beetles ( $Q$ ) and original tree health ( $R_0$ ) is lost.

to (1) evaluate the sensitivity of outbreak to synchrony in adult emergence, and (2) begin to develop quantitative criteria for field applications in risk assessment.

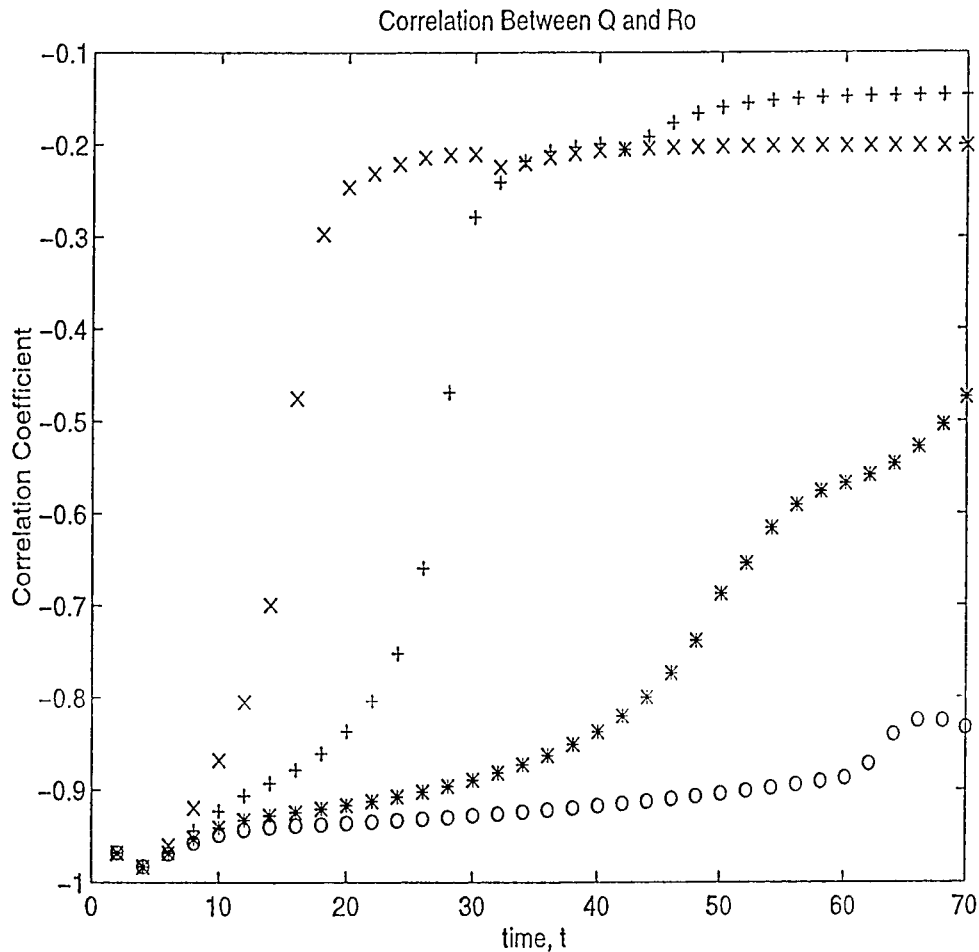
**Model Initialization.** Variation in the degree of synchronous adult emergence could result from either an unseasonable period of cool temperatures during emergence, or as an emergent property of temperature events that occurred earlier during times of phenological sensitivity (Bentz *et al.*, 1991). In order to test the ecological effects of synchronous emergence, we initialized the model with parameters as listed in Table 3, with the exception of  $\gamma$ . As in the previous example,  $\gamma$  was spatially independent, i.e. we provided a constant “beetle pressure” throughout the simulated forest. However, in contrast to the previous example, we varied the temporal magnitude and the duration of  $\gamma$  in such a way that the integrated total number of beetles equaled 1280 in all

cases, but the emergence duration varied from 30 flight hours to 60 flight hours. The net result was a uniform pulse of beetles that varied in duration but not in integrated magnitude. As before, the initial forest was generated randomly from a uniform distribution with mean  $R_0 = 1$  and a range of  $\pm 0.5$ .

**Simulation Results.** Results of these simulation experiments are shown in Fig. 4. This figure illustrates that as synchrony increases, healthy trees near initially weak trees are overcome by the focused attacking beetles. The threshold effect is even more apparent in Fig. 5, which plots the switch from environmental determinism to dynamic determinism that accompanies the increasingly synchronous emergence, and in Fig. 6, which plots tree mortality in each simulation. Even though the time pulse is varied continuously (increasing the emergence period by a constant 10 flight hours), the



**FIG. 4.** End results of simulations with differing levels of synchrony in beetle emergence. Dark areas correspond to low resin levels. Synchrony was accomplished by decreasing the duration of emergence and simultaneously varying  $\gamma$  to result in a constant total emergence of 1280 beetles. All simulations were allowed to run for 70 flight hours, enough time for pattern formation to develop. As the emergence period becomes increasingly protracted, the pattern of mortality is environmentally determined, i.e., the correlation between initially weak trees and mortality is high. When emergence is highly synchronous, the pattern of mortality is dynamically determined, i.e., the correlation between initially weak trees and mortality is low. (a)  $\gamma = 0.167$  for 30 flight hours; (b)  $\gamma = 0.125$  for 40 flight hours; (c)  $\gamma = 0.10$  for 50 flight hours; (d)  $\gamma = 0.083$  for 60 flight hours.



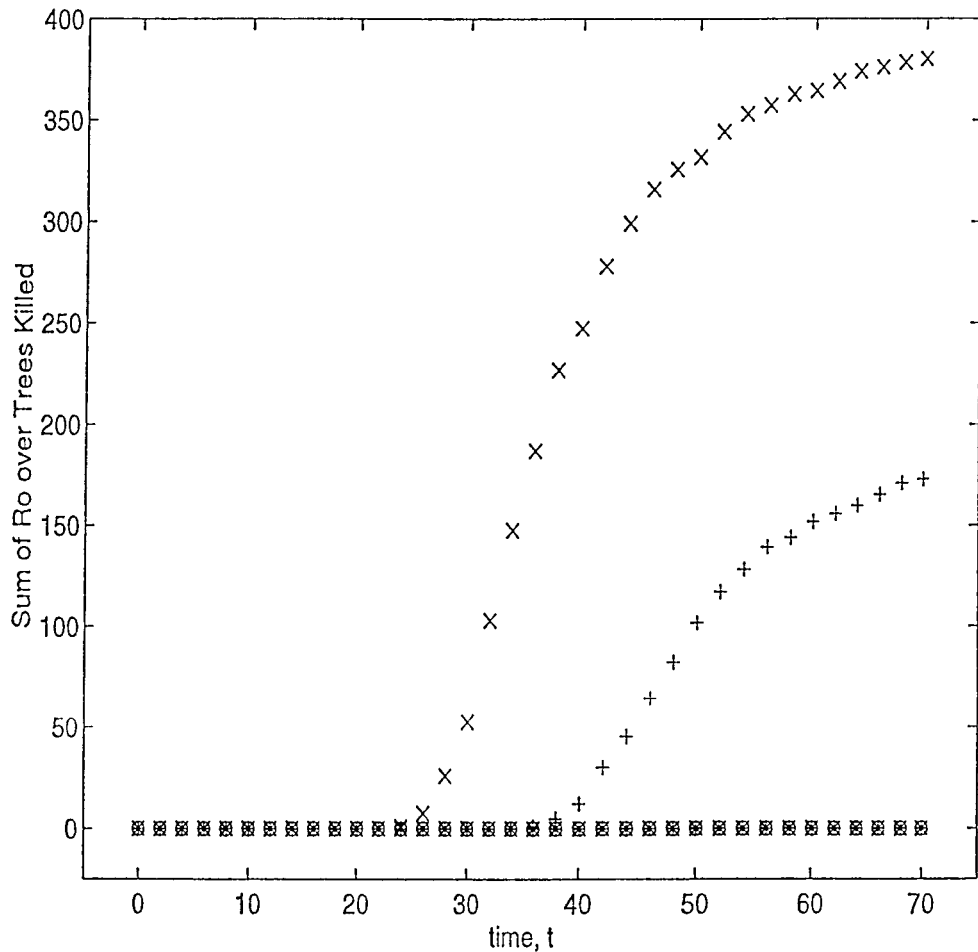
**FIG. 5.** Correlation between infestation of nesting beetles,  $Q$ , and initial tree vigor,  $R_0$ , for the simulations in Fig. 4. As emergence becomes more synchronous, the negative correlation signature of environmental determinism is lost early in the simulation. (x)  $\gamma=0.167$  for 30 flight hours; (+)  $\gamma=0.125$  for 40 flight hours; (\*)  $\gamma=0.10$  for 50 flight hours; (o)  $\gamma=0.083$  for 60 flight hours.

effect is expressed as a discontinuous threshold—an outbreak.

**Discussion.** Results presented in Figs. 4–6 are a striking demonstration of the potential impact of weather mediated synchronous emergence on outbreak potential. These results also considerably expand the interpretation of the importance of temperature on MPB ecology. Bentz *et al.* (1991) demonstrated that differences in low temperature thresholds between instars was primarily responsible for compression of the prolonged ovipositional curve to the synchronous emergence curve. Unusually mild winter temperatures, or a shift in climate, could be disruptive to maintaining an appropriate seasonality. As a consequence, both the average annual temperature cycle (climate) and particular events (weather during the emergence period) are critical determinants of population success (Safraiyik, 1978;

Rasmussen, 1980). Such insights may help to more fully understand climatic limitations to the geographic distribution of MPB, and the potential for shifts in geographic distribution due to factors such as global climate change.

Sensitivity to synchrony in emergence speaks to the need for further research into the mechanisms that result in seasonality and timing. These studies should include empirical investigations of developmental processes in both controlled laboratory settings and through field monitoring. In addition, the complex way in which climate and weather interact to result in seasonal events indicates the importance of building process level models that integrate both factors into seasonal predictions of key population determinants. We have developed, and continue to refine, such a model, MPBmod (Logan, *et al.*, 1995). An application of MPBmod that is central to the topic of this paper is its use to develop production



**FIG. 6.** Accumulated resin depletion for the simulation experiments of Fig. 4. A measure of total mortality is obtained by summing the total resin capacity for all trees that have lost at least 90% of their original resin capacity (90% resin depletion is considered irreversible, i.e., tree death). The effect of synchronous emergence on outbreak potential is apparent. Both synchronous emergences result in significant mortality while zero mortality occurs in both of the prolonged emergences. (x)  $\gamma=0.167$  for 30 flight hours; (+)  $\gamma=0.125$  for 40 flight hours; (\*)  $\gamma=0.10$  for 50 flight hours; (o)  $\gamma=0.083$  for 60 flight hours.

functions ( $\gamma$ ) for input to multi-year simulations using MPBpde.

Our simulation results indicate that including the effect of weather influence on synchrony in could substantially improve risk assessment. One key variable that has been ignored in most susceptibility/risk assessments is the inclusion of estimated MPB population performance (but see Shore and Safranyik, 1992). Synchrony in adult emergence is one such indicator of population performance.

### **Spatial Arrangement of Nurse Trees**

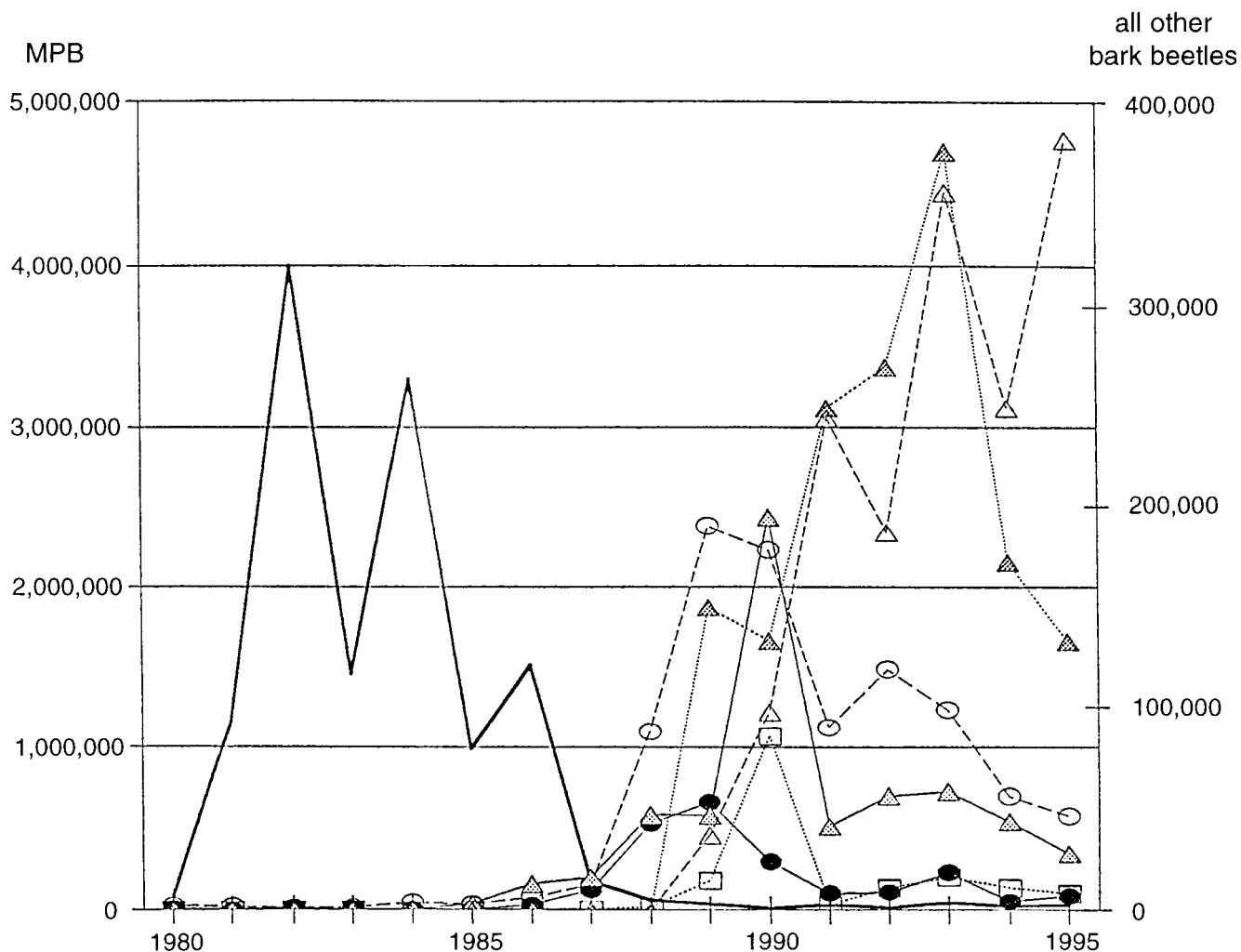
The role that stress plays in precipitating bark beetle outbreaks has been a point of debate for many years. There is general agreement that different sources of stress

(e.g. drought, pathogens) can reduce the defensive capabilities of host trees (see Schowalter and Filip, 1993, for a review). There is less consensus, however, in the role that tree stress may play in precipitation of outbreaks. Some hypothesize that a general stress induced reduction in tree vigor is the primary trigger for an outbreak. According to this hypothesis, an overall reduction in tree resistance due to some stressing factor releases the beetle population from regulation and an outbreak occurs (e.g., Berryman, 1978). Drought is one widespread stressing factor which could cause a rapid decline in stand vigor, and drought is often considered the triggering event for an outbreak (Berryman, 1976).

Although the hypothesis of drought induced stress operating as a triggering event to MPB outbreaks is widely accepted, observations and theoretical arguments

(Lorio, 1993) indicate that other events may be more important. MPB outbreaks in the interior west appear to be more related to periods of moisture abundance than drought (Fig. 7). Even though drought stress reduces tree resistance, the resulting stressed tree is typically not a high quality food resource (e.g., Thompson *et al.*, 1985). Amman (1978) proposed an alternative hypothesis for the switch between endemic and epidemic beetle population phases that is based on a combination of conditions rather than a specific triggering mechanism. These necessary conditions include: (1) a sufficient population of beetles, (2) an abundant high-quality food resource, and (3) weather conducive to population success. Once these conditions exist, chance events (e.g., proximity of

trees weakened by root disease to act as nurse trees) result in enough beetles in an area to overcome healthy trees with thick phloem. High brood production from these healthy trees then induces the outbreak. The major difference between the drought and a "random proximity" hypothesis is the spatial pattern of stressed and healthy trees. A widespread climatic anomaly such as prolonged drought will produce a more homogeneous forest of weakened trees, whereas stresses such as pathogens often result in a patchy forest of intermixed weak and healthy trees. In the latter scenario, endemic populations are supported in the refugia of weaker trees (Tkacz and Schmitz, 1986), while the healthy trees provide the food source necessary for population buildup.

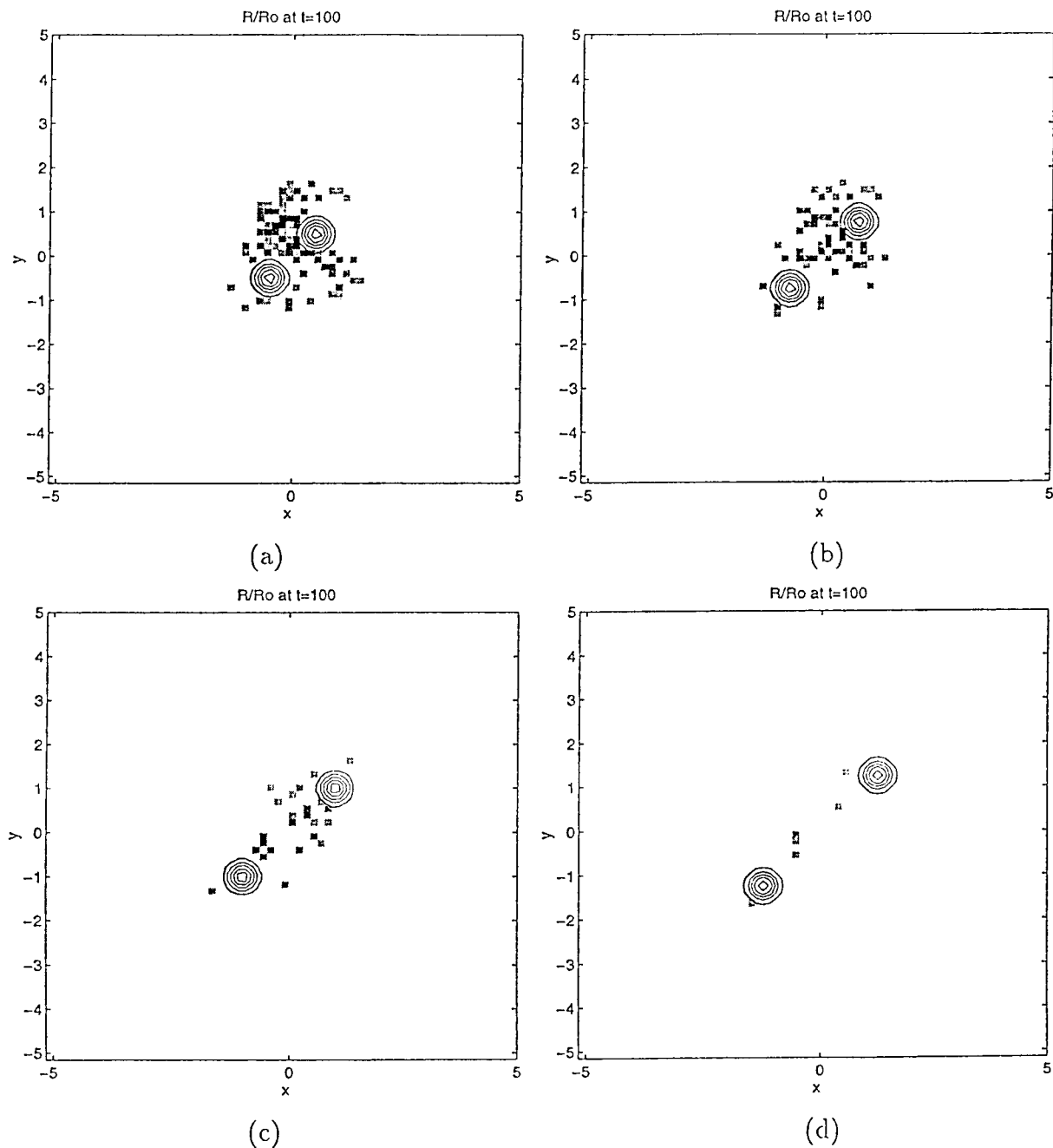


**FIG. 7.** Trees killed by bark beetles in USDA Forest Service Intermountain Region 4 between 1980 and 1994. Note that MPB populations were highest during the early to mid 1980s, a time of moisture abundance in the interior West. Populations of other bark beetles were on the increase during the late 1980s, a time of general drought stress; however, MPB populations precipitously declined during the same time period. Data source, Barbouletos *et al.*, 1995. Solid line, mountain pine beetle; shaded triangles, spruce beetle; open squares, jeffery pine beetle; open circles, douglas-fir beetle; closed circles, western pine beetle; open triangles, western balsam bark beetle.

Although we do not view these two hypotheses as being mutually exclusive, an interesting and important question is: what is the nature of effects that result from proximity of nurse trees during the endemic population phase? As a step towards answering this question, we have performed simulations where we keep both the

density of emerging beetles and the number of sources constant, but we vary the proximity of emerging beetle sources.

*Model Initialization.* The model was initialized in the same manner as the previous example, with the following



**FIG. 8.** Mortality level as a function of proximity to focus trees. The same total number of beetles (80 per spot) were introduced in all four simulations. The spots of source beetles are of radius 0.5 and their centers are 1.41, 2.12, 2.83, and 3.54 units apart (1 unit = 100m) in (a), (b), (c), and (d), respectively. Dark areas correspond to increasing resin depletion.



exceptions. Instead of a spatially homogeneous background of emerging beetles, they were concentrated at two point sources. Integrated beetle densities in all runs were held constant at 80 per spot. The two epicenters were then moved progressively further apart in successive simulations. In all instances, the temporal emergence curve ( $\gamma$ ) was a square wave of 80 time steps (flight hours) duration. Simulations were allowed to proceed for a total of 100 flight hours.

*Results of Simulation.* Simulations were run long enough beyond the end of emergence to allow tree recovery unless it was successfully attacked and killed. Recall, the state variable  $R$  is a surrogate for tree health, and when  $R$  approaches zero, the tree is dead. The effects of proximity are apparent in the pattern of killed trees in Fig. 8. Even more striking is the obvious outbreak effect shown in Fig. 9. In the simulations with beetle sources the

furthest removed from one another, no trees were killed (as measured by at least 90% resin depletion). By contrast, when the trees were in close proximity, significant mortality occurred. It is easy to see how the process could be self-propagating. Weakened trees in close proximity produce enough beetles to overcome even healthy trees. These trees in turn are the producers of large quantities of brood the following year which are again in close proximity (Cole *et al.*, 1985). Such positive feedback potential is symptomatic of instabilities such as outbreaks.

*Discussion.* Although our simulation results neither deny nor confirm any particular hypothesis of outbreak induction, several important points are worth considering. First, the importance of including a measure of the spatial distribution of red-tops in risk assessment during endemic phases is well illustrated. Secondly, our results

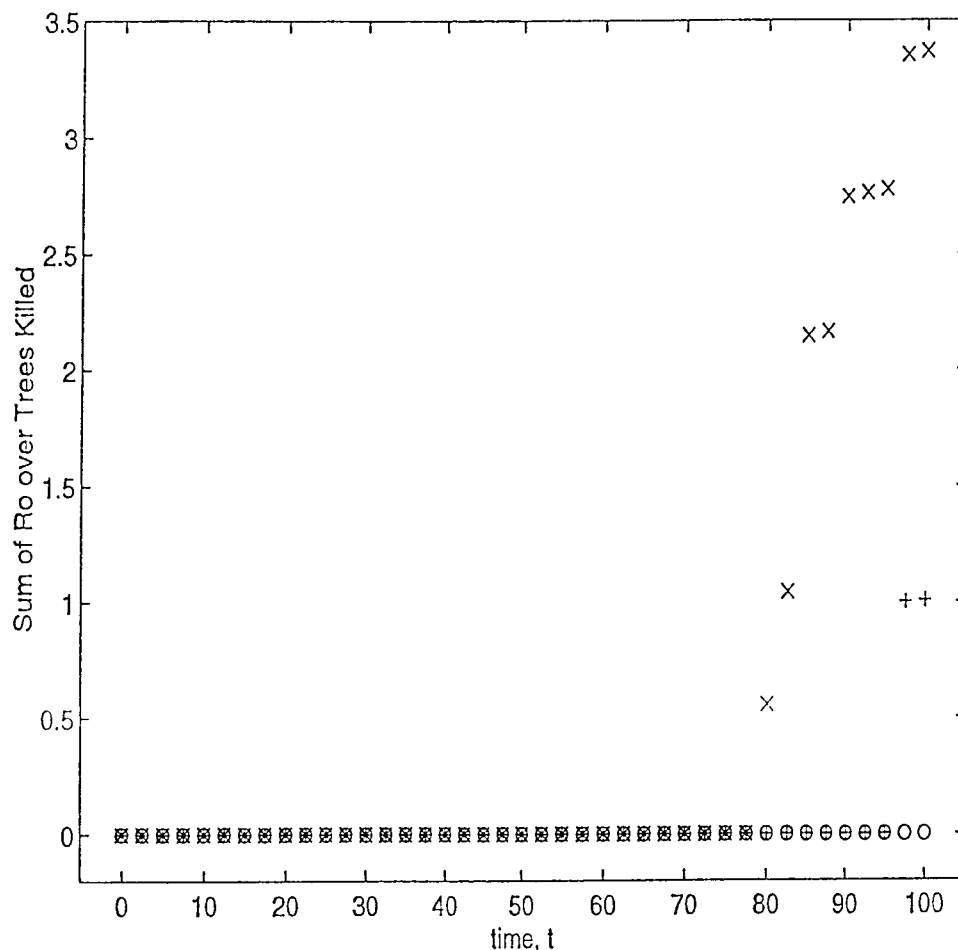


FIG. 9. Accumulated resin depletion for the simulations in Fig. 8. Amount of resin depletion for killed trees using at least 90% reduction in resin capacity as a sign of tree mortality.  $x$  = 1.41 units apart,  $+$  = 2.12 units apart,  $o$  = 2.83 units apart.

indicate the potential for spatial feedback generating an outbreak in the absence of either a wide-spread external modification of the environment (e.g., drought) or in the genetic composition of the population.

The effects of spatial feedback in self-focusing systems indicates the importance of research designed to more clearly elucidate the spatial nature and arrangement of host stress factors. Water-stressed trees are a good example. Drought produces large expanses of water stressed trees, but other sources of water stress can result in spatially complex patterns of water stress without the widespread reduction in host quality that most likely accompanies a general drought. Coniferous/deciduous ecotones between pine and aspen, or edaphic characteristics are good examples of factors that can result in spatially heterogeneous patterns of water stress.

Among other spatially distributed causative agents of stress, root disease or other host pathogens, are probably the most studied (Schmitz, 1988, Schowalter and Filip, 1993). The driving forces behind the spatial distribution of host pathogens may have important implications for MPB outbreaks such as providing epicenters for outbreaks. Indeed, the spatial distribution of host pathogens may well be the driving force behind the periodicity of MPB outbreaks. Geiszler *et al.* (1980b) have hypothesized such a mechanistic link between MPB, fungi, and fire in lodgepole pine ecosystems.

Finally, an interesting question is raised regarding the geometry of killed trees in an endemic setting. Are there particular spatial arrangements that are more conducive to precipitating an outbreak than others? What is the effective distance between killed trees for production of epicenters? MPBpde is a powerful tool that can be effectively used in conjunction with field empirical studies to address such issues.

## GENERAL DISCUSSION

In this paper we have described a spatially explicit model of MPB redistribution and attack of host trees, and the response of the host to attack. We have further applied simulations with this model for analysis of three ecological issues central to MPB outbreak ecology. These simulation experiments have demonstrated that nonlinear spatial effects, namely self-focussing and self-dissipation, can by themselves be responsible for observed attack and outbreak phenomena. In the analysis of simulation results, we have introduced the concept of environmental vs. dynamic determinism that captures the difference between spatial complexity due to environmental

heterogeneity (exogenous factors) and spatial complexity driven by inherent, nonlinear spatial dynamics. A statistical measure was applied, spatial correlation coefficients, which was introduced to discriminate between environmentally and dynamically mediated spatial complexity. Simulation results from these experiments imply that many of the rate-competition issues between tree host and tree attacker can only be meaningfully studied by taking spatial issues into account. As a result, these simulation experiments demonstrate that management activities should include spatial considerations, probably at the landscape scale.

The simulations we have discussed are our first attempts to use the model in a hypothesis testing mode. As such, they are representative of the types of ecological issues we will address in future applications of the model. Such exercises force serious scrutiny of the current literature and available knowledge for parameter estimation. The model is also helping us design field experiments that are of a spatial nature, i.e., determining effective radius of pheromone traps. An interesting question is, how useful would such a model be as a management tool? As we move from the existing paradigm of forest pest management to a more balanced view of incorporating natural disturbance within the ecosystem management of sustainable systems, we will not only need to include meaningful landscapes, but we will also need to address issues of large spatial scale and long time frames. The modeling effort we have described will continue to be a central organizational and conceptual paradigm for our MPB research, and also holds the potential to result in a valuable management tool capable of addressing the critical issues of expanded spatial and temporal scales.

## ACKNOWLEDGMENTS

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