



Local Projections for a Global Model of Mountain Pine Beetle Attacks

JAMES A. POWELL[†], JESSE A. LOGAN[‡] AND BARBARA J. BENTZ[‡]

[†] *Department of Mathematics and Statistics and* [‡] *Logan Forestry Sciences Laboratory, USDA Forest Service Intermountain Research Station and Department of Forest Resources, Utah State University, Logan, Utah 84322, U.S.A.*

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We derive a system of nonlinear partial differential equations describing the phenomenon of mountain pine beetles attacking lodgepole pine *en masse*. A methodology for projecting the behavior of these partial differential equations onto purely local ordinary differential equations is discussed and implemented. The behavior of this system of equations is analysed and compared heuristically with observations.

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1. Introduction

Mathematical reasoning has played a central role in ecological theory and application for at least the past 70 years [dating from the independent rediscovery of Verhulst's (1845) work by Pearl & Reed in 1920]. From the very beginning of these applications, there has been an appreciation for the role that spatial dynamics play in ecological issues [see Holmes *et al.*, (1994) and Turchin (1989), for recent reviews]. Irrespective of these early attempts to include spatial considerations in ecological models, the preponderance of mathematical modeling applications have involved analysis of spatially independent, ordinary differential (difference) equation (ODE) models. This results not from the lack of perceived importance of spatial effects, but from the conceptual and procedural difficulty in dealing with partial differential (difference) equations (PDE), particularly in describing complex ecological interactions. The increased computational power offered by modern computers has resulted in a resurgence of interest and research on spatial dynamics in ecological phenomena. Indeed, the inclusion of spatial dynamics in

meaningful ecological models has been termed the “last frontier” in ecological theory (Kareiva, 1994).

Spatial dynamics typically play a central role in the community dynamics of highly mobile insects (Turchin & Theony, 1993). For example, dispersal is one of the most important, yet least understood, factors of bark beetle population biology (Anonymous, 1989). Current research with mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins), indicates that spatial dynamics play a crucial role (Preisler & Mitchell, 1993; Mitchell & Preisler, 1991; Safranyik *et al.*, 1992). MPB has long been considered a major pest in western forests. As an aggressive bark beetle (one that kills its host), eruptions of this species are impressive events. Outbreaks can be both intensive (up to 80% or greater mortality) and extensive (covering thousands of contiguous acres), resulting in serious economic consequences. It is also becoming recognized that disturbances, such as MPB outbreaks, may be central to maintaining the structure, function and health of western forests.

Interpretation of MPB in this dual role as a serious economic competitor and as a co-evolved component of the ecosystem presents an interesting challenge. One important method we are incorporating to help address this challenge is development and analysis of

[†] Author to whom correspondence should be addressed.

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quantitative models. Aggregation on and dispersal from a host are of such over-riding importance to MPB ecology that including spatial dynamics in model representations is essential for ecological credibility. For many bark beetle species, including MPB, dispersal is only one part of the sequence of events necessary for successful population establishment and expansion. The self-focussing and self-dissipating aspects of the species chemical ecology are also integral components affecting population spatial dynamics. Others have developed quantitative models of bark beetle dispersal and aggregation (Burnell, 1977; Berryman *et al.*, 1989; Safranyik *et al.*, 1989; Polymenopoulos & Long, 1990; Turchin & Theony, 1993), which we are building on to develop a large-scale (e.g. forest-sized) reaction-diffusion PDE model of the spatial interaction between the MPB and its host trees, including critical components of this species' chemical ecology. The mathematical motivation for this model is fully described below. We refer to the explicit, spatially dynamic model as the "global model" because it attempts to capture the full spatial extent of MPB pheromone ecology. From this modeling endeavor, we have observed that even starting with a completely homogenous environment, the positive and negative feedback generated by attacking beetles soon results in a rich, spatially dependent chemical landscape that tends to modify future events.

The spatial ebb and flow of beetle-produced pheromones is a striking aspect of the predator/prey interaction between MPB and pine trees. However, due to the computational difficulty of PDEs, continued formulation of the global model is proving difficult. These difficulties arise primarily from three sources: estimating parameters for a global model that are based on data from "local" or point analysis of beetle chemical ecology, computational intractability of the PDE global model, and inaccessibility of the global model to both the mathematical and ecological team members. In response to these difficulties we have developed an ODE projection of the global PDE model. We refer to this model as the "local projection" because it includes the global spatial dynamics in only an implicit way. The local projection model provides a tool for focussing on single-tree processes, but simultaneously includes local consequences of large-scale spatial dynamics. Objectives

for development of the local projection model are:

- (1) Providing a model that can assist in interpretation of published empirical studies on the chemical ecology of MPB and the use of this data for estimating of spatial parameters.
- (2) Addressing the computational difficulties associated with numerical solution to PDE models. Our intent is to provide a meaningful model in which numerical solutions can be obtained in a reasonable amount of time on a 486 level PC.
- (3) Facilitating collaboration between mathematicians and ecologists analysing the chemically mediated spatial ecology of MPB interactions in western forest ecosystems.

The local model will not only assist in understanding MPB/host dynamics, but also address issues which enhance collaboration between ecologists and mathematicians.

To produce this local, implicitly spatial model, we must first have a mathematical description of the MPB/pine system. This will be accomplished through the medium of nonlinear reaction-diffusion PDE. While these are complicated to solve directly, we can use them to determine how to project the dynamics onto local spatial modes. This amounts to choosing a heuristic spatial description for the spatially active variables which has just enough degrees of freedom to depict local dynamics. We will choose Gaussian modes as one way to parametrize the local spatial behavior. The complicated governing PDE will then be used to determine how Gaussian parameters evolve in time, thus producing an ODE description of PDE behavior. In the final sections of this paper we will examine the qualitative behavior of these local models and draw some conclusions about the utility of our results.

2. Derivation of the Global Model

2.1. BEHAVIOR OF THE PINE BEETLE/HOST TREE SYSTEM

Because of its economic impact, MPB population dynamics has been the subject of sustained research efforts dating from the early 1900s, focussed primarily on protection of valuable forest resources. Although this insect spends most of its life cycle under the bark feeding on phloem tissue¹, the relatively short phase of the life cycle in which emergence and attack of new hosts occurs is essential for continuing the population. It is during this time that complex spatial dynamics come into play.

¹ Several processes occur while beetles are in phloem tissue. These include feeding, pheromone production, mating and gallery construction. We use the term nesting to include all of these activities.

The MPB is typically a univoltine species which attacks living pines. Unlike most phytophagous insects, successful reproduction is contingent upon death of all or part of the host (Sheppard, 1966; Wood, 1972). Host trees, however, have evolved effective response mechanisms to defend themselves against bark beetle attacks (Smith, 1963, 1966; Reid *et al.*, 1967; Nebeker *et al.*, 1993; Raffa *et al.*, 1993). Almost all trees are capable of responding to bark beetle attacks, but only those with a rapid and sustained reaction are likely to survive. If many beetles attack the same tree over a short period of time (e.g. mass attack), they can exhaust the trees' defensive mechanisms. The final outcome of a bark beetle dispersal and colonization attempt is, therefore, dependent upon a series of competing rate reactions which regulate both beetle arrival and host response (Raffa & Berryman, 1979; Safranyik *et al.*, 1989).

The evolved relationship between the MPB and its host trees has resulted in an elaborate chemical communication system. Through a chemically-mediated synergistic reaction with host chemical compounds, female beetles attacking a tree release trans-verbenol, which, when mixed with α -pinene, is an aggregation pheromone attracting both sexes (Pitman *et al.*, 1968; Pitman, 1971; Hughes, 1973). At higher concentrations of trans-verbenol, higher proportions of males are attracted (Renwick & Vita, 1970). Attacking males produce exo-brevicomin which at low concentrations primarily attracts females (Conn *et al.*, 1983). This system of chemical communication results in mass attack on a single focus tree. However, the tree is a finite food resource that can be over-exploited by too many beetles. Verbenone, an epidietic¹ pheromone, is released by attacking males and inhibits the landing of additional beetles at high concentrations (Borden *et al.*, 1987). Once the concentration of verbenone sufficiently exceeds the concentration of aggregating pheromones, flying beetles in the area switch to nearby host trees (McCambridge, 1967; Geiszler & Gara, 1978; Geiszler *et al.*, 1980). When the incoming beetles switch, the new tree often has greater attack rates and is colonized more rapidly than the original focus tree (Rasmussen, 1974). The switching mechanism provides a means for efficiently utilizing the available population of attacking beetles.

Although density-dependent beetle pheromone responses play the dominant role, kairomones produced by the tree may also play a part (Hunt *et al.*,

1989). At low population densities, attacking MPB selectively attack trees weakened by disease or other stresses (Tkacz & Schmitz, 1986; Schmitz, 1988; Schowalter & Filip, 1993). It is hypothesized that stressed trees release a kairomone signal which attracts MPB flying in the vicinity, providing primary attraction to a particular tree (Roe & Amman, 1970; Gara *et al.*, 1984; Moeck & Simmons, 1991). An alternative hypothesis is that new hosts are found using a combination of random landings guided by visual cues (Schonherr, 1976; Sheppard, 1966) followed by chemical and tactile cues once on the host tree (Hynum, 1980; Raffa & Berryman, 1979). Most likely, both situations occur. Although the combination of factors that signals a weakened tree remains an open question, enough evidence exists for the effect of host compounds on beetle behavior (Norris & Baker, 1967; Raffa & Berryman, 1982; Raffa, 1988) that models of MPB spatial dynamics should include some representation of host volatiles, as well as beetle-produced pheromones.

The complex chemical cues in the MPB/pine tree interaction act as self-focusing and self-dissipating forces. The interaction of these forces results in a nonlinear density dependent response that results in complex spatial patterns of resource utilization. Although the explicit spatial feedback is critical to the ecological association of MPB with its hosts, there is no spatially explicit model of the interaction. In the next two sections we will discuss the construction of a spatio-temporal mathematical model of the MPB/host spatial ecology.

2.2. LOCAL DYNAMICS

Building on previous models of the temporal dynamics of MPB attacks [and in particular Berryman *et al.* (1989)], we define the following variables, which depend on the spatial location, x , y and time, t :

$P(x, y, t)$ = population of airborne beetles.

$Q(x, y, t)$ = population of (alive) nesting/feeding beetles.

$A(x, y, t)$ = concentration of beetle-produced pheromones.

$C(x, y, t)$ = concentration of volatiles released by host trees.

$S(x, y, t)$ = resin outflow from attacked trees.

$R(x, y, t)$ = resin capacity of host trees.

$H(x, y, t)$ = number of MPB attack holes.

The number of flying beetles is monotonic (when we neglect terms describing in-flux of flying MPB), and decreases in proportion to the death rate ($\omega_1 P$) and the number of beetles who land and attempt to

¹The term epidietic describes specific sorts of animal behavior which are used principally for population density regulation (Prokopy, 1980).

nest in a tree ($r_1P(1 + \sigma A)$). The term r_1P models random attack by flying MPB, while $r_1\sigma AP$ models attack rate enhancement in the presence of pheromones. This gives a dynamic equation for changes in flying MPB density:

$$\dot{P} = -\omega_1P - r_1P(1 + \sigma A).$$

Every beetle who attempts to nest is (at least temporarily) a living, nesting beetle, and so the population Q must grow proportionally to $r_1P(1 + \sigma A)$. They will also die at some rate (much smaller than the death rate of flying MPB), ω_2Q . Finally, beetles will be killed by the natural defense mechanisms of the host tree, resin pitch-out and toxins. However, only that portion of resin flowing out through holes occupied by living MPB will kill nesting beetles, and so the population of nesting MPB should decrease in proportion to the resin out-flow through occupied holes, $\beta_1S(Q/H)$. This gives an equation of motion for Q ,

$$\dot{Q} = -\omega_2Q + r_1P(1 + \sigma A) - \beta_1S\frac{Q}{H}.$$

This equation is similar to eqn A2, in Berryman *et al.* (1989), which also models the density of attacking beetles, with one important conceptual difference. The Berryman model includes the effect of beetle-produced pheromones as a quadratic function of resin levels. In our model, the differential effect of pheromones arises from the concentration of the suite of beetle-produced pheromones, A . As this increases beyond some threshold, the suite of pheromones becomes anti-aggregative (see the discussion of fluxes, below). The concentration of A grows proportionally to the density of nesting beetles (Schlyter *et al.*, 1989). Thus, differentiation between attraction and anti-attraction in our model is an attribute of the beetle and not the host. Both representations are first-order approximations to a process that involves both host- and beetle-produced chemicals.

The rate at which the number of attack holes increases is precisely equal to the number of MPB attempting to nest. On the other hand, as resin flows through galleries it crystallizes, slowly closing the hole. This means that holes should be lost at a rate proportional to the amount of resin out-flow, S , which itself is proportional to the number of holes and the available resin capacity, HR . Therefore, the rate of change of H is given by

$$\dot{H} = r_1P(1 + \sigma A) - r_4HR.$$

Explicitly modeling the dynamics of attack holes, H allows us to incorporate the effects of the temporal distribution of attacks. Much of the hypothesized selection pressure for evolution of the chemical communication in bark beetles is to overcome tree defenses by numerically overwhelming tree defenses, the so-called ‘‘mass attack’’ strategy. Focussing attacks over a short period of time is critical to a successful attack because of the capacity for the tree to recover if its defense mechanisms are not exhausted rapidly enough. Probability of tree mortality is not simply a function of total attacks but is highly dependent on the time frame over which these attacks occur. In this context, H functions as a mechanism for incorporating attack synchrony.

It remains to be determined how the local resin capacity and the amount of resin outflow vary with time. We assume that an unstressed tree would stabilize its resin capacity at the reservoir capacity, R_0 , and that small deviations from this capacity would die away at a characteristic relaxation rate. If, on the other hand, the resin capacity is driven to zero no replenishment is possible. Consequently, the rate of change of the resin capacity should be proportional to $R(R - R_0)$. On the other hand, the resin capacity is depleted at a rate proportional to the number of attack holes and the available amount of resin which can flow out through the holes. These two processes give an equation of motion:

$$\dot{R} = r_2(R_0 - R)R - S.$$

Modeling resin capacity in this way is similar to the approach of Berryman *et al.* (1989), with the slight difference in interpretation that in the Berryman model R is the amount of resin in the average beetle gallery, and in our interpretation R is the whole tree reservoir. Both interpretations are consistent with the idea of resin, and resultant tree resistance, being reduced as resin is drained from the tree due to beetle attacks (Raffa & Berryman, 1983a, b). The amount of out-flow is assumed to be in proportion to the number of attack holes drilled and the amount of resin available to flow through those holes, giving a constitutive equation for S :

$$S = r_3HR.$$

This gives a complete set of equations reflecting behavior in the absence of dispersal and aggregation:

$$\dot{P} = -\omega_1P - r_1P(1 + \sigma A) \quad (1)$$

$$\dot{Q} = -\omega_2Q + r_1P(1 + \sigma A) - \beta_1r_3QR \quad (2)$$

$$\dot{R} = [r_2(R_0 - R) - r_3H]R \quad (3)$$

$$\dot{H} = r_1 P(1 + \sigma A) - r_4 HR \tag{4}$$

$$S = r_3 HR. \tag{5}$$

These represent host response to attack and the effect of MPB attack on a single tree, ignoring interactions at large space scales.

2.3. SPATIAL REDISTRIBUTION OF BEETLES AND FOREST DYNAMICS

At low population levels a successful strategy for MPB is to attack trees weakened by some stress factor (e.g. weather, disease, less aggressive associated bark beetle ssp.). As population levels increase many beetles are able to focus their efforts on trees which are currently under attack. At low population levels, in our model we assume pioneer beetles respond to kairomones (the variable C) released by a host tree. As the population attacking the host tree grows, concentrations of attracting pheromones (the variable A) increase, and soon becomes the dominant factor affecting spatial redistribution of flying MPB. Because host kairomones are important synergists and precursors to MPB pheromones, the kairomone concentration, C , is important at all population levels. Currently, for simplicity we only explicitly use the kairomone concentration as a means to initialize the nonlinear attack mechanism, mimicking a stressed or unhealthy tree. Depending on the concentrations of A and C , the population of flying MPB will redistribute themselves to take advantage of weakened groups of trees. It is this redistribution that is essential to capturing the dynamics of mass attack, which we address here.

Our mechanism for understanding spatial redistribution is to consider mass balances in some arbitrary spatial domain, Ω . The total number of beetles in that domain is

$$N = \int_{\Omega} P dx dy,$$

and can change only due to movement of beetles across the boundary of Ω (flux) or loss/emergence of beetles within Ω (sinks/sources). This gives us a simple law,

$$\frac{d}{dt} N = \text{Flux into } \Omega - \text{Flux out of } \Omega + \text{Source Terms} - \text{Sink Terms} \tag{6}$$

The source and sink terms are all of those terms which we analysed above, comprising the local, temporal dynamics of the system, integrated over the

domain Ω . For brevity we will denote these terms as $f(P, A, x, y, t)$, and note that

$$\text{Source Terms} - \text{Sink Terms} = \int_{\Omega} f dx dy.$$

The flux terms will quantify how the population of flying MPB moves.

We will denote the flux vector by $\vec{\phi}$, and assume that it has three basic components, reflecting the beetles' recognition of potential hosts, their response to pheromones and the degree of randomness in their behavior. Thus,

$$\vec{\phi} = \vec{\phi}_A + \vec{\phi}_C + \vec{\phi}_P,$$

where: $\vec{\phi}_A$ is flux due to the beetles' attraction to/repulsion from the suite of pheromones, A . The summed response of these pheromones is attractive in small concentrations, anti-aggregative in higher concentrations, and the pheromones are released only by nesting/feeding beetles. Let A_0 be the concentration at which the pheromone becomes anti-aggregative. We presume that the net beetle population will move in the direction of pheromone gradients, and that the number moving into Ω will be proportional to the local population density, giving

$$\vec{\phi}_A = vP(A_0 - A)\nabla A(x, y, t).$$

Here the parameter v is the constant of proportionality.

$\vec{\phi}_C$ is flux due to the beetles' recognition of potential hosts, dependent on $C(x, y, t)$ and the local density of flying beetles. Thus, beetles will move in a direction in which they perceive some spatial change in the volatiles emitted by damaged trees. The rate at which they move will be proportional to the local density of flying beetles and the strength of their perception. Thus, we write

$$\vec{\phi}_C = \kappa P(x, y, t)\nabla C(x, y, t).$$

The parameter κ is the constant of proportionality.

$\vec{\phi}_P$ is flux to the beetles' random redistribution in the absence of other influences, dependent only on spatial changes in the density of flying beetles. Given a population of randomly moving beetles, net flux occurs only because of changes in population density, and the flux should be in the opposite direction of increasing population gradient. This gives

$$\vec{\phi}_P = -\mu\nabla P(x, y, t).$$

Here the parameter μ is the constant of proportionality.

Now we can return to the balance law, (6). The total flux into Ω will be the integral of the flux vectors

around the boundary of the domain. This gives an expression

$$\frac{d}{dt} N = \int_{\partial\Omega} \vec{\phi} \cdot \vec{n} ds + \int_{\Omega} f dx dy.$$

Here \vec{n} is the unit normal vector to the boundary of Ω , $\partial\Omega$. Using the Divergence Theorem on the integral around the boundary gives

$$\frac{d}{dt} N = - \int_{\Omega} \nabla \cdot \vec{\phi} dx dy + \int_{\Omega} f dx dy.$$

Writing this expression in terms of only one integration,

$$\int_{\Omega} \left[\frac{\partial P}{\partial t} + \nabla \cdot \vec{\phi} - f \right] dx dy = 0.$$

Since Ω is completely arbitrary, the integrand must be zero, giving a spatio-temporal evolution equation for P ,

$$\frac{\partial}{\partial t} P = -\nabla \cdot \{ [k\nabla C + v(A_0 - A)\nabla A] P - \mu\nabla P \} + f(A, P, x, y, t). \quad (7)$$

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, the source should be the number of living, nesting beetles, Q . The losses will be due to diffusion through the canopy and chemical decomposition. These effects lead to a linear diffusion equation for A ,

$$\frac{\partial}{\partial t} A = b_1 \nabla^2 A + a_1 Q - \delta_1 A. \quad (8)$$

For host volatiles, which we track with the concentration C , the source is an unknown function of time, $g(t)$. Again, we expect some loss due to chemical decomposition, giving an equation similar to that for A ,

$$\frac{\partial}{\partial t} C = b_2 \nabla^2 C - \delta_2 C + g(t). \quad (9)$$

These two equations, along with (20), provide a complete description for the spatially-varying components of the MPB/host system.

2.4. THE GLOBAL MODEL

We can now define the entire system for the seven dependent variables P , Q , R , S , H , A , C .

First we note that the source/sink function for P in (7) is

$$f = -\omega_1 P - r_1 P(1 + \sigma A) + \gamma(x, y, t),$$

where γ is an arbitrary emergence distribution. This gives the complete equation for P ,

$$\frac{\partial}{\partial t} P = -\nabla \cdot \{ [k\nabla C + v(A_0 - A)\nabla A] P - \mu\nabla P \} - \omega_1 P - r_1 P(1 + \sigma A) + \gamma(x, y, t). \quad (10)$$

The other spatially dynamic variables are the chemical concentrations, which satisfy diffusion equations,

$$\frac{\partial}{\partial t} A = b_1 \nabla^2 A + a_1 Q - \delta_1 A, \quad (11)$$

$$\frac{\partial}{\partial t} C = b_2 \nabla^2 C + g(t) - \delta_2 C \quad (12)$$

Here $g(t)$ is a source of primary chemical attraction. The variables Q , R , S and H depend on space parametrically, and satisfy the equations,

$$\frac{\partial}{\partial t} Q = -\omega_2 Q + r_1 P(1 + \sigma A) - \beta_1 r_3 QR, \quad (13)$$

$$\frac{\partial}{\partial t} R = [r_2(R_0 - R) - r_3 H] R, \quad (14)$$

$$S = r_3 H R, \quad (15)$$

$$\frac{\partial}{\partial t} H = r_1 P(1 + \sigma A) - r_4 H R. \quad (16)$$

Equations (10–16) are a complete spatio-temporal description of the dependent variables controlling the behavior of MPB attacking host pines. A complete list of parameters is included in Table 1.

We will discuss the properties of this model in future work. Since the model involves nonlinear partial differential equations, one of which has anti-diffusive properties, even numerical approaches are difficult. Moreover, data on spatial distributions of MPB are difficult to procure. What data exists on MPB attacks is typically local, taken at individual locations. Consequently, it is very difficult to verify or falsify the model based on existing data; the equations above are predicting spatial behavior which has not been sufficiently measured, though its effects have been observed. What is needed is a rational way to derive from these equations a purely local temporal model, say on the scale of a single tree, which nonetheless reflects the global behavior of spatial redistribution and mass attack. Deriving such a model is the subject of the next section.

TABLE 1

The list of parameters appearing in the global PDE model for MPB redistribution

Parameter	Description
κ	A measure of the beetles' perception of and attraction to weakened pines
ν	Attractiveness of pheromones
μ	Diffusivity of flying beetle population due to randomness
A_0	Critical concentration at which pheromone becomes repulsive
a_1	Rate of pheromone creation by burrowing beetles
b_1	Rate of pheromone diffusion
δ_1	Loss rate of pheromone
$g(t)$	Rate of kairomone creation (not constant)
b_2	Rate of kairomone diffusion
δ_2	Loss rate of kairomone
R_0	Local peak resin capacity
σ	Rate of directed infestation
r_1	Rate of sampling infestation
r_2	Rate of resin replenishment
r_3	Rate of resin outflow through burrows
r_4	Rate of resin crystallization
ω_1	Death rate of airborne beetles
ω_2	Death rate of nesting beetles
β	Rate at which trees' natural defenses kill nesting beetles
$\gamma(t)$	Emergence rate of new populations of airborne beetles (not constant)

3. Rational Local Equations

3.1. PROJECTION ONTO SPATIAL MODES

To produce a local set of equations reflecting global redistribution we must “parametrize” spatial behavior in a local way, that make requirements about the temporal evolution of parameters in a spatial description of variables. To do this, we must choose a parametrized spatial form for the variables, then allow the parameters to vary temporally in a way consistent with the governing PDE. We will assume that the variables are Gaussian in space. Letting l denote the distance from the focus tree,

$$P = \frac{2p(t)}{w_p(t)} e^{-l^2/w_p(t)}$$

$$A = \frac{2a(t)}{w_a(t)} e^{-l^2/w_a(t)}$$

$$C = \frac{2c(t)}{w_c(t)} e^{-l^2/w_c(t)}$$

$$Q = \frac{2q(t)}{w} e^{-l^2/w}$$

$$R = \frac{2r(t)}{w} e^{-l^2/w}$$

$$H = \frac{2h(t)}{w} e^{-l^2/w}$$

$$S = r_3 RH.$$

This will not provide an exact solution of the PDE, but will reflect the character of the PDE behavior. The dependence of Gaussian parameters on time is explicit above. The number w is constant, representing the characteristic size of the tree of interest. The variables Q, R, H and S vary temporally only in size, reflecting the fact that their spatial scale is fixed.

For the diffusion of chemical concentrations, the Gaussian “ansatz” is exact: the radial diffusion equation maps Gaussians to Gaussians over time. On the other hand, the Gaussian “ansatz” for the flying MPB is extremely optimistic—solutions to the governing equations for P are surely not Gaussian. We can, however, understand this description of P in a statistical spirit: we are asking for a normal distribution in space to be fitted to the population, recognizing that this will force the Gaussian parameters to evolve with time.

To determine how the Gaussian parameters vary in time, we will integrate equations (10–12) over space. We illustrate this procedure on (11). Noting that

$$\int_0^\infty 2 \frac{M}{\lambda} e^{-l^2/\lambda} dl = M,$$

and that

$$\int_0^\infty 2 \frac{M}{\lambda} e^{-l^2/\lambda} P dl = M\lambda,$$

integrating (11) over space gives

$$\begin{aligned}\dot{a} &= \frac{d}{dt} \int_0^\infty A l dl = \int_0^\infty \left[b_1 \frac{1}{l} \frac{\partial}{\partial l} (lA_l) + a_1 Q - \delta_1 A \right] l dl \\ &= a_1 q - \delta_1 a.\end{aligned}$$

Performing the same integration with an additional l^β in the integrand gives

$$\begin{aligned}\frac{d}{dt} a w_a &= \frac{d}{dt} \int_0^\infty A l^\beta dl \\ &= \int_0^\infty \left[b_1 \frac{1}{l} \frac{\partial}{\partial l} (lA_l) + a_1 Q - \delta_1 A \right] l^\beta N dl \\ &= (4b_1 - \delta_1) a w_a + a_1 q w.\end{aligned}$$

These two equations may be simplified to give a system of two differential equations for the pheromone parameters $a(t)$ and $w_a(t)$,

$$\dot{a} = a_1 q - \delta_1 a, \quad (17)$$

and

$$\dot{w}_a = 4b_1 + a_1 q \frac{w - w_a}{a}. \quad (18)$$

Equations for $c(t)$ and $w_c(t)$ are derived similarly, treating g as a delta function in space for the purposes of integration

$$\dot{c} = g - \delta_2 c, \quad (19)$$

and

$$\dot{w}_c = 4b_2 - g \frac{w_c}{c}. \quad (20)$$

Transforming the purely local eqns (13, 14, 16) is much simpler, since these equations already track variables whose dependence on space is implicit. Although these equations describe how densities vary in time, the normalizing area factor for a single lodgepole pine ($\sim w$) is constant for these variables. This implies that essentially the same equations hold for the number of nesting MPB, $q(t)$, the number of entrance holes, $h(t)$, and resin capacity, $r(t)$. The only trouble is that some of the forcing terms depend on the rate of infestation, which in turn depends on the spatially-varying variables P and A . To overcome this difficulty we introduce the concept of a ‘‘radius of engagement’’, ρ . This is the radius about the tree within which a flying MPB actively perceives and

engages the tree of interest. The number of flying MPB infesting the tree at any given time will then be

$$\begin{aligned}I &= \int_0^\rho r_1 P (1 + \sigma A) l dl \\ &= r_1 p (1 - e^{-\rho^2/w_p}) \left[1 + 2 \frac{\sigma a}{w_a + w_p} (1 - e^{-\rho^2/w_a}) \right].\end{aligned}$$

The governing equations for the purely local variables become

$$\dot{q} = I - \omega_2 q - \beta_1 r_3 q r, \quad (21)$$

$$\dot{h} = I - r_4 h r, \quad (22)$$

and

$$\dot{r} = r[r_2(R_0 - r) - r_3 h]. \quad (23)$$

The last and most serious stumbling block is projecting the equation for flying MPB (10) into a local framework. All of the terms involving dependent variables can be integrated as above, but the term γ having to do with the background emergence of MPB in the forest will become unbounded in the integral. To overcome this, we examine the flux of the background MPB generated by the local versions of A and C . The flux of background beetles through a circle of radius L is

$$\phi(L) = -2\pi L \gamma \left[\kappa \frac{\partial C}{\partial l} + v(A_0 - A) \frac{\partial A}{\partial l} \right].$$

The total flux of background MPB into the local framework (normalized by a factor of 2π) is given by the integral

$$\int_0^\infty \phi(l) dl = 2\gamma(t) \left[\kappa c + v a \left(A_0 - \frac{a}{w_a} \right) \right],$$

when this integral is positive. Hence, we can define the forcing, F , due to flux of background MPB into the local framework as

$$F = \max \left\{ 2\gamma(t) \left[\kappa c + v a \left(A_0 - \frac{a}{w_a} \right) \right], 0 \right\}.$$

With this approach to connect the general emergence of flying MPB with forcing for the number of local beetles, we can now proceed to apply the integrations

$$\int_0^\infty (\cdot) dl \text{ and } \int_0^\infty (\cdot) l^\beta dl$$

to (10). This results in ordinary differential equations for $p(t)$ and $w_p(t)$,

$$\dot{p} = F - I - \omega_1 p, \quad (24)$$

and

$$\begin{aligned} \dot{w}_p = & 4\mu + \frac{w_p}{p} F + 2\sigma r_1 \frac{aw_p^2}{(w_a + w_p)^2} - 8\kappa \frac{cw_p}{(w_c + w_p)^2} \\ & - 8\nu aw_p \frac{A_0 w_a (w_a + 2w_p)^2 - 2a(w_a + w_p)^2}{w_a (w_a + w_p)^2 (w_a + 2w_p)^2}. \end{aligned} \quad (25)$$

Equations (17–25) define our local model of MPB mass attack on a particular focus tree.

3.2. PARAMETER APPROXIMATION

The parameter space for the local equations is large (twenty-one dimensional). Although some research has been directed at understanding spatial implications of bark beetle chemical ecology, values for most of the parameters in our local model have not been explicitly measured. We therefore use published information to establish orders of magnitude for unknown parameter values based on known quantities. We assume no dispersal effect due to wind, and microorganism-induced changes in host physiology are inherent in relationships described below. The basic timescale we have chosen is the beetle-flight-hour (fh) of which there are approximately five per day. Area is measured in hectares (1 hec = 10⁴ m²). We have contemplated general, non-dimensionalization, and undertake it in a paper currently in preparation. However, we have found that although non-dimensionalization gives the modeling effort fewer degrees of freedom, it also reduces our ability to directly interpret model responses. Consequently, we have left all parameters (save resin capacity, for which no reasonable dimensions currently exist), dimensional in what follows. At the very least, this has helped us understand the functions of the parameters we vary below.

The first focus of the parametrization effort is the tree’s defensive response. We have chosen to non-dimensionalize the tree’s resin capacity, r , using $r = \hat{r}R_0$. The equations for hole dynamics and resin capacity can then be written

$$\frac{d}{dt} \hat{r} = [r_2 R_0 (1 - \hat{r}) - r_3 h] r,$$

and

$$\frac{d}{dt} h = I - r_4 R_0 h \hat{r}.$$

Measured rates of resin replenishment seem to indicate that a tree’s resin capacity recovers on a

2-day, or 10 fh scale (Nebeker *et al.*, 1995). Therefore

$$r_2 R_0 \simeq 0.1 \text{ fh}^{-1}.$$

If we assume that crystallization of resin occurs approximately twice as rapidly,

$$r_4 \simeq 0.2 \text{ fh}^{-1}.$$

We obtain the rate of resin outflow, r_3 , indirectly. Although the critical density of attack varies among trees and seasons (Raffa & Berryman, 1983), for the purposes of this modelling endeavor we assume that a general attack rate of 500 MPB over a 5-day period is critical for overwhelming a healthy tree’s defenses (Berryman, 1978; Wood, 1972). This translates into an infestation rate of $I = 20 \text{ fh}^{-1}$. The two differential equations above can be written in the form

$$\frac{d}{dt} \left[\hat{r} - \frac{r_3}{r_4 R_0} h \right] = r_2 R_0 (1 - \hat{r}) \hat{r} - \frac{r_3}{r_4 R_0} I.$$

If I is the critical cut-off at which a tree’s defenses are overwhelmed, then below this attack rate a tree survives. Parsing this mathematically, the l.h.s. of the above equation must be zero or less at this attack density. Noting that $(1 - \hat{r}) \hat{r} \leq \frac{1}{4}$ gives

$$\frac{r_3}{r_4} I \simeq \frac{1}{4} r_2 R_0.$$

Solving for r_3 gives

$$r_3 \simeq 0.00025 R_0.$$

We have chosen an arbitrary reference scale R_0 for convenience; the defensive responses are all scaled relative to the units of R_0 .

For purposes of estimating the attack rates of the flying MPB, we assume that 5%/fh of the flying population randomly lands and samples trees, giving

$$r_1 \simeq -\ln(0.95) \text{ fh}^{-1}.$$

We estimate that the attack rate in the presence of attracting pheromones is on the order of five times or more greater, giving

$$\sigma A_0 \simeq 5,$$

which will become definite when A_0 is determined. The rate of beetle pitch-out is a function of resin flow (Raffa & Berryman, 1983b) such that

$$\beta r_3 R_0 = \frac{24}{5} \text{ MPB-fh}^{-1},$$

meaning that resin flowing through a burrow pitches the occupying beetle out at a rate of 1 per real hour, where 24/5 translates beetle flight hours to real hours.

The diffusion equations for pheromones and kairomones are parametrized using information in (Geiszler *et al.*, 1980). From this chemical plume data, we estimate

$$b_1 = 50 \text{ hec} - \text{fh}^{-1}.$$

The loss rate of pheromone due to vertical diffusion can be estimated by choosing an eigen-function which decays vertically on the scale of the canopy, say 10 meters. This gives a loss rate due to diffusion of

$$\delta_1 \simeq \frac{b_1}{100 \text{ m}^2} \frac{10^4 \text{ m}^2}{\text{hec}} = 500 \text{ fh}^{-1}.$$

Borden *et al.* (1986) estimated that female MPB emit trans-verbenol at an average rate of 10 ng fh⁻¹. We change this to a rate of concentration emission by averaging over the area of emission, $w \simeq 1 \times 10^{-5}$ hec. Changing seconds to flight hours, and converting to tens of micro-grams of pheromone (tmg) gives

$$a_1 \simeq 25 \frac{\text{tmg}}{\text{MPB-fh-hec}}.$$

We assume the rates of loss and diffusion of kairomone concentration to be a similar magnitude to the loss of pheromone. However, based on production rates of α -pinene oxidation products (Hunt *et al.*, 1989), we assume the rate of kairomone production in the absence of beetles to be an order of magnitude smaller. Currently, the only effect of kairomones in our model is in the initial attraction of MPB to a focus tree.

Next we parametrize the equations for the flying MPB. We assume the rate of death for the flying population of MPB to be 5% per day, giving

$$\omega_1 = -0.2 \ln(0.95) \text{fh}^{-1}.$$

The rate of death of nesting MPB we take to be zero on the timescale of this model. Turchin & Theony (1993) estimated a parameter for the southern pine beetle (*Dendroctonus frontalis*) which is related to the ratio of diffusion rate (μ) and loss rate of the population ($r_1 + \omega_1$). Using our estimates for the loss rates and Turchin & Theony's estimate for the southern pine beetle parameter, we find

$$\mu \simeq 1 \text{ hec} - \text{fh}^{-1}.$$

It remains to estimate the flux parameters for kairomone and pheromone response (κ and ν). We assume that pheromone response is on the order of

ten times more powerful than kairomone response, giving

$$A_0 \kappa = 0.1 \nu.$$

Geiszler *et al.* (1980) suggest that MPB are responsive to concentrations of 0.003 ng m⁻³. We presume that this means they are sensitive to gradients in concentration on the order of 0.003 ng m⁻⁴. We assume a directed flight velocity for flying MPB of 5 km per hour, and a vertical air column of 3 meters. We may then write

$$\begin{aligned} \nu A_0 &\simeq \frac{\text{m}^4}{0.003 \text{ ng}} \frac{10^4 \text{ ng}}{\text{tmg}} \frac{5 \times 10^3 \text{ m}}{\text{fh}} \\ &\times \frac{1 \text{ hec}^2}{10^8 \text{ m}^4} \frac{1}{3 \text{ m}} \simeq 50 \frac{\text{hec}^2}{\text{tmg-fh}}. \end{aligned}$$

From Geiszler *et al.* (1980) we estimate that the rate of pheromone production that occurred at "switch-over" is 40 tmg-fh⁻¹. Taking into account the diffusivity gives

$$A_0 \simeq 40 \frac{\text{tmg}}{\text{fh}} \frac{\text{fh}}{50 \text{ hec}} = 0.8 \frac{\text{tmg}}{\text{hec}}.$$

As a consequence, this gives

$$\nu \simeq 60 \frac{\text{hec}^3}{\text{tmg}^2 - \text{fh}}.$$

4. Qualitative Behavior of the Model

4.1. COMPARISON WITH OBSERVATION

The number of attacks necessary to kill a lodgepole pine has been estimated between 11.5 and 29.5 attacks per square meter (Cole, 1962; Reid, 1963; Raffa & Berryman, 1979; Klein *et al.*, 1978). Based on these values, for an average size lodgepole pine, approximately 500 total attacks would be required for a successful infestation. For our model to achieve this density many parameters were fine tuned from the values in the previous section. Although these parameters are slightly different, they are of the same order of magnitude as in the previous section. We did not tune rate parameters, and as we will note below the correspondence between the timescales over which attack and saturation are surprisingly good. For what may seem to be a very complicated model, the qualitative dynamics are very simple: a mass attack is either successful and the focus tree is rendered defenseless, or the tree successfully defends itself from attack. A successful attack is characterized by two stages. In the first stage the spatial scale of the population of responding beetles decreases as randomly distributed flying MPB orient themselves

TABLE 2

Parametric values for numerical simulation and units. Units involving resin are measured relative to R_0 .

Parameter	Value	Units	Parameter	Value	Units
a_1	20	tmg hec ⁻¹ fh ⁻¹ MPB ⁻¹	$g(t)$	—	tmg hec ⁻¹ fh ⁻¹
b_1	50	hec fh ⁻¹	b_2	0	hec fh ⁻¹
δ_1	1000	fh ⁻¹	δ_2	0.1	fh ⁻¹
A_0	3	tmg hec ⁻¹	v	100	hec ³ tmg ⁻² fh ⁻¹
μ	0.3	hec fh ⁻¹	κ	10	hec ² tmg ⁻¹ fh ⁻¹
ω_1	0.0103	fh ⁻¹	ω_2	0	fh ⁻¹
σ	10	hec tmg ⁻¹	β	1.92×10^4	MPB R_0^{-1}
r_1	0.0513	fh ⁻¹	r_2	0.1	R_0^{-1} fh ⁻¹
r_3	2.5×10^{-4}	fh ⁻¹	r_4	0.1	R_0^{-1} fh ⁻¹
R_0	1	R_0	ρ	2	hec ^{1/2}
w	0.1	hec	$\gamma(t)$	—	MPB hec ⁻¹ fh ⁻¹

on the focus tree and attack. We refer to this as “nonlinear self-focussing” since the mechanism of focussing involves nonlinear spatial feedback: the more beetles that attack the focus tree, the more pheromone is emitted, leading to more beetle attacks. The second stage of an effective attack is the creation of an “epidiotic wave” of repulsed beetles as pheromone concentrations grow too large. This is termed as “switching” (Geiszler & Gara, 1978; Geiszler *et al.*, 1980; McCambridge, 1967). In our model this phase is characterized by linear growth in the scale of the cloud of reacting MPB (see Fig. 7).

To illustrate our model’s depiction of a successful attack, we chose the parameter values as in Table 2. For an emergence curve we used

$$\gamma = 10 \left[\tan h \left(\frac{t - 25}{10} \right) - \tan h \left(\frac{t - 75}{10} \right) \right].$$

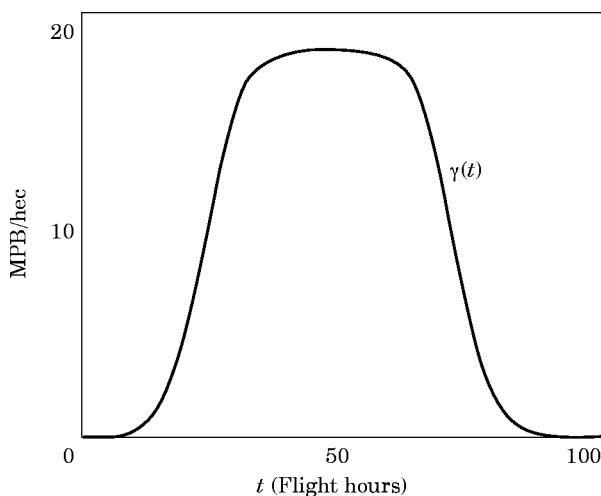


FIG. 1. Emergence curve, $\gamma(t)$, in beetles/hectare against flight hours. The entire emergence occurs over a period of 28 days.

The structure of the emergence curve is depicted in Fig. 1. The time variable t , is measured in flight hours, so that the emergence curve peaks and declines over a period of 20 days. We have chosen relatively small parameter values for the diffusion and creation of kairomones so that kairomone concentrations serve only as a primary attractant, but do not influence the development of mass attack. As a pre-attack source of kairomones, we specified

$$g(t) = 0.1 \exp \left[- \frac{t}{10} \right].$$

The behavior of the total population of MPB reacting to the single tree is illustrated in Fig. 2. The reaction of the flying MPB has two phases: an initial attack phase during which the population of MPB respond by moving toward the focus tree. In the second stage, all MPB which have not made

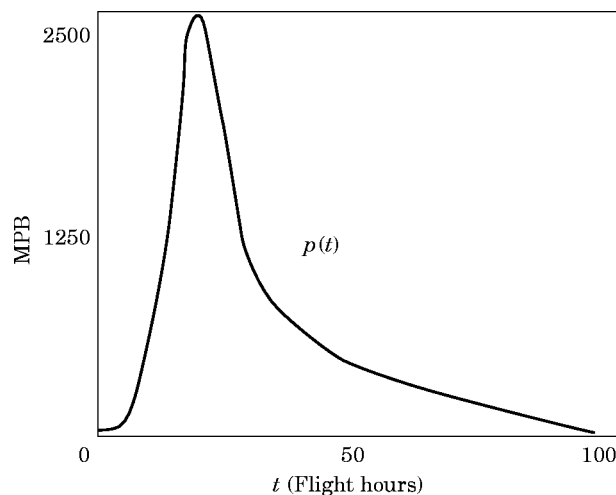


FIG. 2. Total number of beetles, $p(t)$, responding to a single tree under attack as a function of flight hours. See Raffa & Berryman (1983) for empirical curves of similar shape.

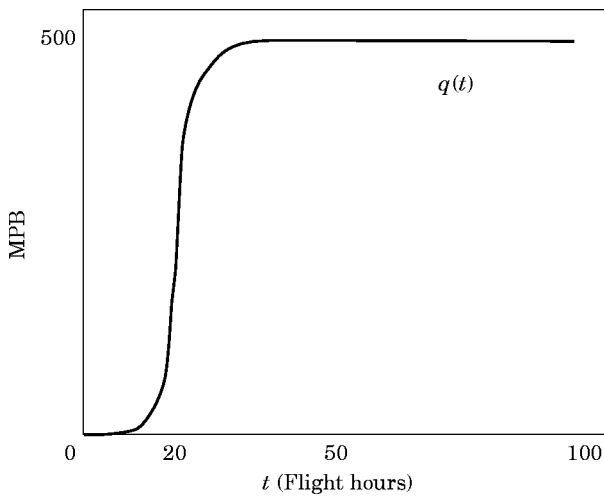


FIG. 3. Number of MPB, $q(t)$, nesting in the focus tree as a function of flight hours.

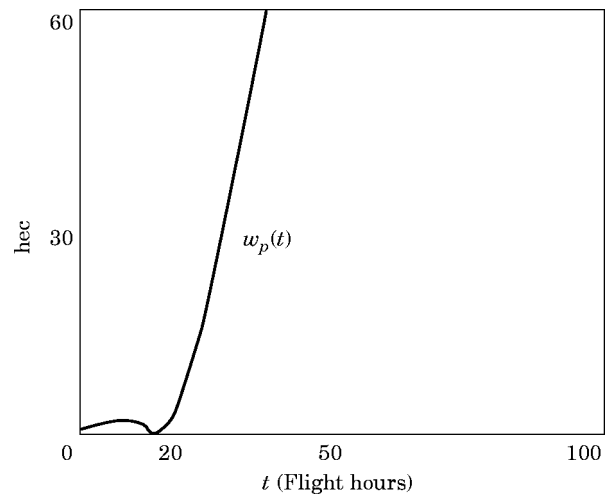


FIG. 5. Area scale w_p , of the cloud of attacking beetles, measured in hectares and plotted against number of flight hours.

successful attacks are repelled by high concentrations of pheromones at the focus tree (see Fig. 5). The behavior of the nesting population is depicted in Fig. 3. The population of beetles resident in the focus tree levels off at approximately 500 in this simulation of a successful attack. At 20 flight hours the population curve has an inflection point caused by the discontinuity in the flux function, which at this point has hit zero as the net effect of the pheromone suite become anti-aggregative at the focus tree. This is also the time at which the tree has been rendered effectively defenseless. Figure 4 illustrates the focus tree's resin capacity, which has become nearly zero at 50 flight hours.

The data in Fig. 3 can be compared with data on the cumulative number of successful attacks published by Geiszler *et al.* (1980). In their observations,

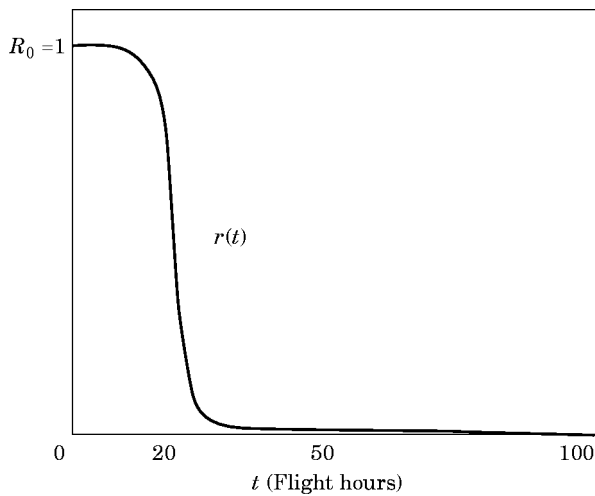


FIG. 4. Resin capacity of tree as a function of flight hours.

an attack on a single focus tree saturated with on the order of 120 nesting beetles in 2 m of bole, or around 500 in the whole tree. The number of attacks increased from zero to the saturation value in 9 days, or 45 flight hours. The correspondence between these numbers and Fig. 3 is striking. The parameter values in Table 2 were chosen to deliver a similar number of nesting MPB, but the rate parameters were estimated independently, which makes it unlikely that the correspondence in rates of attack is accidental. This comparison is only a qualitative but is heuristic nonetheless.

The difference between the two phases of attack behavior are made clear in Fig. 5. Here the cloud size w_p , of flying MPB responding to attacks at the focus tree is plotted against flight hours. In the initial, attack phase (from 0 to 20 flight hours) the scale over which beetles attack first increases (as the size of the pheromone cloud grows) and then decreases to nearly zero (as the nonlinear self-focussing occurs). In the second, epidietic phase of the attack, flying MPB are repulsed from the focus tree by the anti-aggregating pheromone suite (plotted in Fig. 6). The spatial scale of the involved MPB grows linearly, reflecting the existence of a "wave" of repulsed MPB leaving the vicinity of the focus tree.

4.2. CRITICAL BEHAVIOR IN PARAMETER SPACE

The parameter space is large and complex, and a sensitivity analysis of these equations in parameter space is more appropriately the subject of a thesis in applied mathematics than of the current paper. However, it is possible to illustrate how some of the most important parameters affect the behavior of

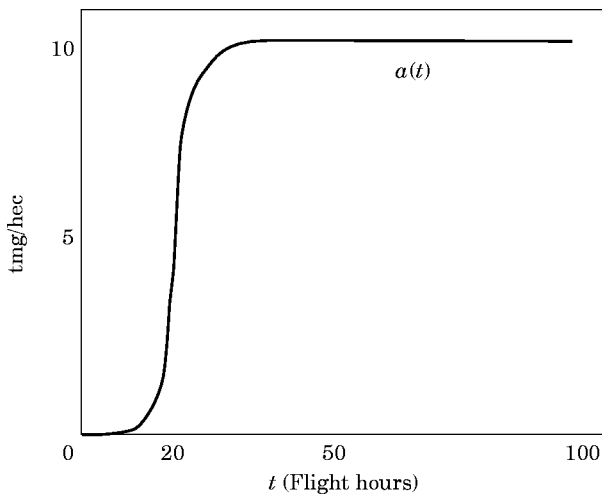


FIG. 6. Pheromone concentration at tree, $a(t)$, measured in tmg/hectare, as a function of flight hours.

solutions. The three parameters we have chosen to study here are:

- (a) β , which controls the effectiveness of resin pitch-out as a defense mechanism,
- (b) A_0 , which controls the epidietic effects of the pheromone suite, and
- (c) δ_1 , which controls how rapidly the pheromone concentration decays through canopy losses or chemical decomposition.

In this section we will study how varying these parameters changes the model's prediction of the final number of successful attacks on the focus tree.

In Fig. 7 the behavior of MPB populations attacking several trees with different β are plotted simultaneously as a function of time. As the trees' capacity to pitch-out incoming beetles increases, the

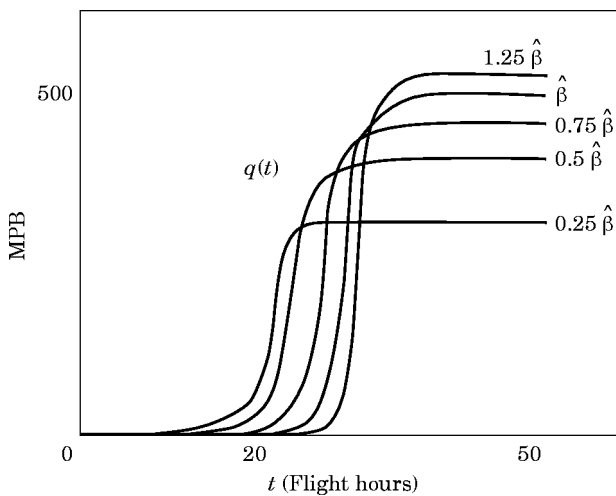


FIG. 7. Population/time plots for six different values of tree defensive ability, $\beta = 0.25\hat{\beta}$ to $1.25\hat{\beta}$, $\hat{\beta} = 24(5R_0r_3)^{-1}$.

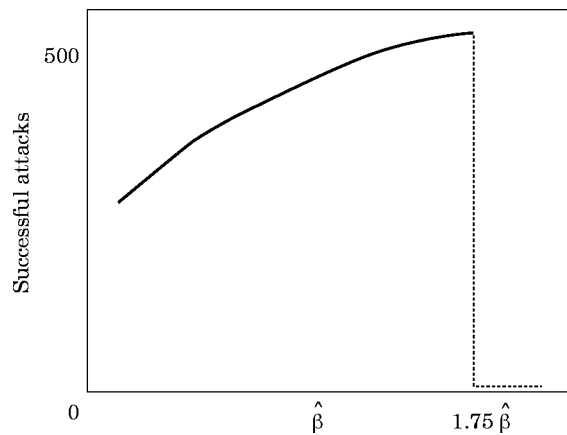


FIG. 8. Number of successful attacks as a function of β .

time needed for MPB to successfully attack and nest in the tree also increases. The final number of successful attacks on a single tree proved to be an increasing function of β in this parameter regime (Fig. 8). This result agrees with the field determinations of Raffa & Berryman (1983b). As the tree's resin defense system increases (e.g. a vigorous, healthy tree), the number of attacks necessary for overwhelming the tree also increases. The net result: if the tree defended itself more effectively, more beetles arrived to overwhelm it. At much higher levels of β , the tree was able to defend itself successfully and the number of successful attacks fell to zero.

In Fig. 9 the behavior of MPB populations attacking several trees as a function of time are plotted simultaneously for different A_0 . A_0 is the critical concentration at which the pheromone suite becomes repelling. As we expected, as A_0 increased, more attacks occurred on a given tree before switching. Notice the bifurcation which occurs for small values of A_0 (Fig. 10). From the transition at

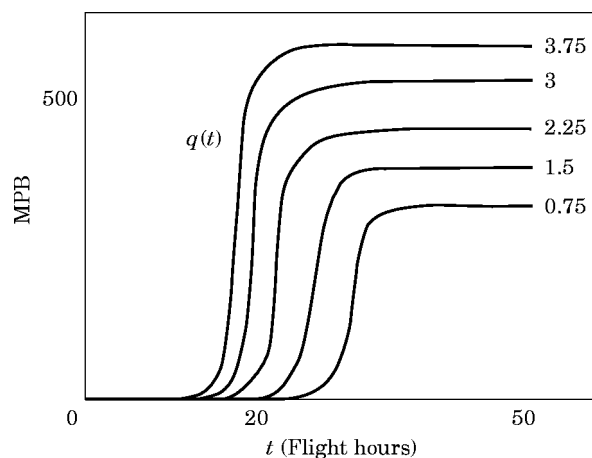


FIG. 9. Temporal behavior of the infesting population as a function of A_0 for parameter values between 0.75 and 3.75.

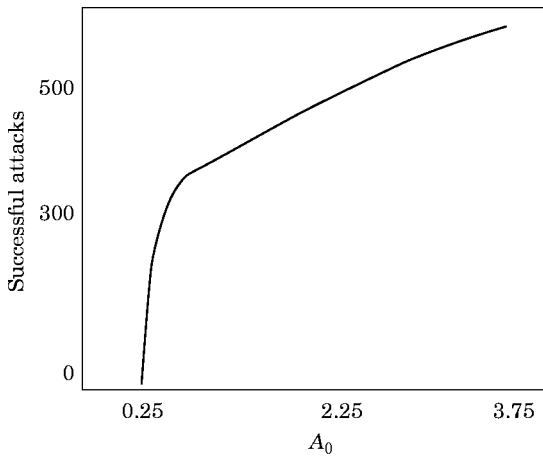


FIG. 10. Net number of successful attacks against A_0 .

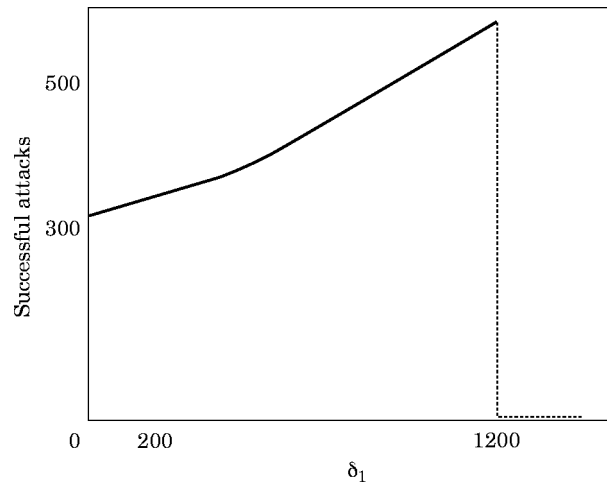


FIG. 12. Total number of successful attacks as a function of δ_1 .

$A_0 \approx 0.2$, the population of nesting MPB grows approximately linearly with the threshold for repulsion. This was more or less in concord with our expectations; A_0 is directly related to the amount of pheromone produced when beetles “switch” from a self-focussing attack to an epidetic wave of dispersal.

In Fig. 11 the behavior of several infesting populations as a function of time are plotted simultaneously for different δ_1 . In Fig. 12 we plot the final number of successful attacks against the parameter δ_1 . As the rate of loss of pheromone is increased, the net number of successful attacks increases until δ_1 approaches 1200. This may seem to be counter-intuitive, but increasing the rate of loss of pheromone delays the time at which the pheromone concentration approaches anti-aggregative levels, thus allowing a tighter focus of attacking MPB. As δ_1 passes 1200, the loss rate is so high that the pheromone cloud never grows large enough to initialize a mass attack. Consequently, a large-magni-

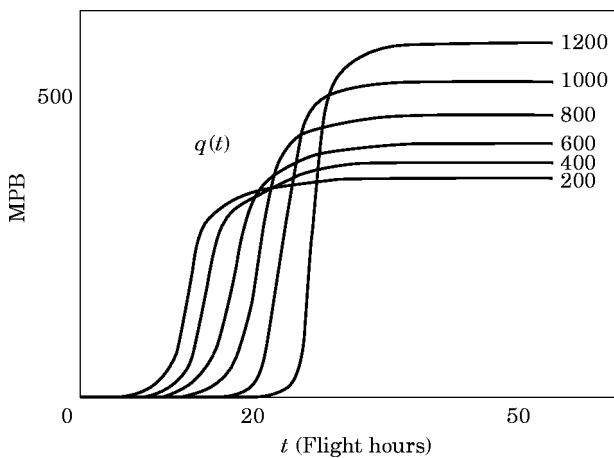


FIG. 11. Temporal attack structure as a function of δ_1 between 200 and 1200.

tude change in asymptotic behavior, reminiscent of a first-order phase transition, occurs at large values of δ_1 .

4.3. COMPARISON WITH THE GLOBAL MODEL

To illustrate the pros and cons of the local projection we have undertaken a comparison of predictions in the local equations with statistics derived from simulation of the global PDE in radial coordinates. The PDE simulation was initialized with parameters as in Table 2, and initial conditions of spatial Gaussians with exact correspondence to the local projection: Gaussians with amplitude and width parameters set to match the initial conditions of the local ODE model. The PDE solution technique was a second-order Runge–Kutta predictor corrector, with second-order centered discretization in space. Since the chemical timescale are so much faster than the MPB timescales, the implementation was designed to allow the time step of the chemicals to be an integer fraction of the total time step (generally chosen to be ten, based on the order of magnitude differences in diffusive scales). Even so, the extreme stiffness of the equations required time steps on the order of 10^{-5} , making numerical solution of the governing PDE extremely costly in time. We are currently testing other methods of solution which should prove more efficient. The solution difficulty for the PDE at this point illustrates the entire reason why a strategy for projection onto lower-dimensional systems is so important.

In Figs 13 and 14 statistics from the partial differential equation solutions (dashed lines) are plotted against predictions from the local model (solid lines). In Fig. 13 the raw number of MPB in the simulation area is computed through radial inte-

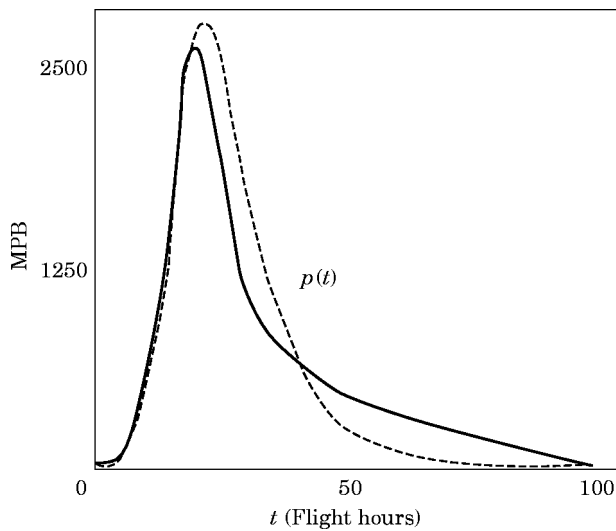


FIG. 13. Comparison of number of beetles responding to the focus tree in the local ODE projection (solid) and the global PDE model (dashed).

gration, and compared with the function $p(t)$ computed for the local model. The agreement is very good up to and including the successful attack on the focus tree (at $r = 0$), and becomes much less exact for later times. In part this is because the Gaussian ansatz is least appropriate for the flying MPB in the repulsion stage of an attack, which difference will be more apparent in Fig. 14. More importantly, there are no individual trees in the PDE model; the forest is a contiguous lump of biomass, like algae. Thus, when the beetles are being repelled from one site, they are being focused at another, which accounts for the continued increase of MPB beyond focusing in the PDE model. Later on, the apparent decrease in the

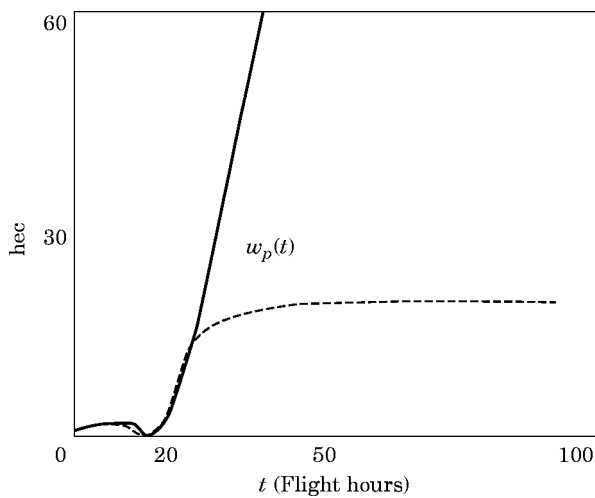


FIG. 14. Comparison of area scale, $w_p(t)$, of attacking MPB cloud responding to the focus tree in the local ODE projection (solid) and the global PDE model (dashed).

number of flying MPB is due to the same effect. In the local model there is only one nesting site to serve as a sink for flying MPB, whereas in the PDE model there is a contiguous bio-mass of attackable forest absorbing available flying MPB. Consequently, at longer times there are more “trees” available to draw down on beetle emergence, making the net number of flying MPB lower in the PDE model at times larger than forty.

The comparison of widths in Fig. 14 illustrates a separate problem with the projection onto Gaussian models. The dashed curve in Fig. 14 is calculated from evaluating the integral

$$\int_0^\infty P(r, t)r^3 dr,$$

using $P(r, t)$ from the PDE simulation. During the focusing phase of the attack, the agreement between the calculated and projected widths is good. However, during the repulsive phase of the attack the agreement is not even qualitatively correct beyond time 25 or so. In fact, in the PDE simulations the attacks saturated in a distinct “spot” of constant area. This is exactly what should happen according to the model; there are finitely many beetles attacking the trees, and consequently a finite source in the chemical equations. In two dimensions, concentration diffusion from a finite source results in an asymptotically stable concentration profile of constant size. Since the MPB are chemotactic, this implies that the MPB should end up in a ring of constant width, centered more or less about the $A = A_0$ isocline, and with numbers decreasing to zero inside the ring. The only way that the Gaussian ansatz can resolve the zero beetles at the focus is for the number of MPB to go to zero. Then for the projection to resolve a profile with a mean at some distance from zero, the width must increase without bound. This explains the disagreement between the two graphs for long time; the Gaussian ansatz is simply a bad description of the epidietic wave of beetles repulsed from a successful infestation. On the positive side, it is an accurate description of the attraction and mass attack phase of the interaction.

5. Conclusion

In this paper we have presented one approach to moving from a complicated, infinite dimensional system to a relatively uncomplicated, finite dimensional system. The global MPB redistribution processes described by nonlinear reaction-diffusion PDE on a multi-kilometer scale were projected on

local spatial modes representing spatial movements of the population centered at a single focus tree. Even though these local modes are not solutions to the PDE as a whole, they have proven remarkably descriptive of published observations of the behavior of attacking MPB populations at the individual tree level. In addition to providing an effective modeling environment to address ecological questions regarding MPB community structure and function, three objectives motivated this work: connecting local data with global parameter estimation, improving computational efficacy, and assisting the collaboration of our research team. The effect of the model on these issues is assessed below.

5.1. PARAMETER ESTIMATION

Parameter estimation is always a challenge in development of credible ecological models (Logan, 1994). This difficulty is further compounded with spatial models. Direct observations of beetle responses to pheromones and/or kairomones on the scale of a stand or forest is not possible. As a result, almost all field experimental data deal with the local or point analysis (individual tree) of beetle response to pheromones. While data from field experiments are influenced by the flux of beetles from the background, the global population responsible for these fluxes is unknown and unmeasurable. The local projection model we describe here represents the individual, tree-level consequences that result from some arbitrary background population, which is analogous to the typical field situation. Because the local projection model more nearly represents field experiments, it is easier to interpret empirical results for parameter estimation by the use of this model. For example, in the descriptive runs above (Figs 1–3) we chose parameter values partially in order to replicate local observations of single-tree dynamics by Geiszler *et al.* (1980). This would have been impossible without a “local” formulation of the model. Now that parameters have been estimated from the local projection model, they can be used directly in the global model. Additionally, because of the greater similarity between the local projection model and field experiments, it is easier to compare published results to the local projection model. Using the technology of the local model, we were able to successfully estimate parameters and produce results in qualitative agreement with observational data.

5.2. COMPUTATIONAL DIFFICULTY

At least some of the reason for the paucity of spatial models in ecological applications is due to the mathematical and computational difficulty associ-

ated with partial differential equation models. Solution procedures for PDEs are substantially more difficult than for ODEs, and closed form solutions are unlikely for most meaningful ecological models. Although there is a rich theory for numerical solution of PDEs, these solutions tend to be computationally demanding. Numerical solutions to the global model require at least work-station level computing power, computational capabilities that are beyond the ecological component of our collaborative team. Computational intractability is particularly problematic during model formulation. It is perhaps tenable in management applications (for example in forest planning or other management related activities) for a model run to take hours, or even days. Such delays during model development, when a multiplicity of runs are required, are intolerable.

In contrast to the intractability of the global model, the local projection model is easily coded in an application language such as Mathematica. In fact, the projection formalism all but requires a symbolic-computational approach. Programing in a symbolic language allows for convenient modification of model structure as well as all the output (i.e. graphics) power of a commercial application. Since the local projection model was derived directly from the global model, insights gained through gaming with the convenient local projection model can be incorporated immediately into the global model. This is not to imply that the local projection model replaces the global model. The two model formulations are philosophically and procedurally quite different, and each has its particular strengths and weaknesses. However, by providing a computationally simple version of the ecological interaction, the local projection model facilitated rapid development of both model representations.

5.3. A VEHICLE FOR COLLABORATION

The combined mathematical and empirical difficulty of considering the explicit spatial dynamics of MPB has provided significant motivation for collaborative research. Either the mathematical or the empirical aspects of MPB spatial dynamics, by themselves are difficult problems. The most efficient way to make significant progress is through an effective collaboration between applied mathematicians and MPB ecologists. Unfortunately, the language of PDEs are esoteric, and model equations couched in these terms are opaque to most field ecologists (Holmes *et al.*, 1994; Logan, 1994). The global model derived in Section 2 requires several hours for one run on a computational mainframe. The result was that the mathematician on the team

independently gamed and experimented with the model, and then met with the ecologists to demonstrate the resulting model behavior. At these meetings, the ecologists attempted to evaluate model dynamics and make suggestions regarding representation of model interactions, parameter values etc., but were unable to implement these suggestions on their own to establish their utility. While we were able to make progress, everyone felt that the pace was slower than if we were all able to participate equally in basic model formulation. We expect that our experience is not unique, and that similar problems are common impediments to effective collaborative research.

Formulation and implementation of the local projection model has done much to facilitate effective collaboration for our team. The model has been formulated as a Mathematica Notebook (Wolfram, 1991) with either the options of reconstructing a projection from first principles (i.e. symbolically deriving the local from the global model) or simply changing parameters for the local model. Either option runs in a reasonable amount of time on a mid-range 486 PC, and it is always possible to background a model run and proceed with word-processing or other applications while the model is running. Notebooks can be exchanged independent of operating system and computer. Since the model is coded in a higher level language/application like Mathematica, particular portions of the model can be extracted for more in-depth exploration or development. Functional representations can be modified and/or completely changed, then reinserted into the model. In short, the local model has gone a long way toward allowing equal contribution from all research team members. It has focused our independent efforts as well.

It may seem that our approach to the local modeling effort was long-winded. However, there is no modeling technique we know of which is built to include spatial redistribution and focusing in a finite-dimensional model. The natural language to speak about such phenomena is the mathematical language of partial differential equations. However, many observations about spatially dispersing systems are of a "local" nature; attacks on a particular host/prey by members of a spatially extended population of parasites/predators spring to mind. We have considered only the mass attack of mountain pine beetles on individual pine trees, but similar approaches to clouds of biting flies, swarms of bees, and schools of fish may be equally interesting. The technique of "local projection" which we have presented here is a natural way to address such

questions. This approach makes the leap from esoteric PDE models to more readily accessible ODE models for localizing/focusing phenomena in natural systems.

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