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PARAMETER ESTIMATION OF THE MOUNTAIN
PINE BEETLE-HOST TREE SYSTEM

by

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of the requirements for the degree

of

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in

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Approved:

Thesis Advisor

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Chapter 1

Introduction

1.1 Literature Review

The spatial redistribution of organisms in an ecosystem is often a complex process. Many ecosystems exhibit spatial complexity on a broad range of scales, driven by the physical environment and biotic interactions [1]. As different species aggregate and disperse in spatially complex ways, even an initially uniform environment will soon evolve spatial heterogeneity.

There are a variety of factors that drive the spatial dynamics of a population, including defense against predators, improved success as predators, and enhanced reproductive success. Also, spatial complexity often arises from dispersal and aggregation. When an organism is itself responsible for chemical, auditory, visual or other cues which lead to aggregation, nonlinear feedback occurs, creating self-organized groups of individuals (self-focusing). Self-dissipation also plays an important role in many ecosystems' dynamics. It is the interaction between self-focusing and self-dissipating forces that leads to the complex spatial reorganization of populations of organisms.

Spatial dynamics typically play a central role in the community dynamics of highly mobile insects [2] such as the mountain pine beetle (MPB) [3]. The spatial dynamics of the MPB/pine tree host system has long been the subject of research because of its ecological and economic impact. As an aggressive bark beetle (one that kills its host), eruptions of this species are impressive events resulting in intensive and extensive outbreaks with serious economic and ecological consequences. It is clear that disturbances, such as MPB outbreaks, may be central to maintaining the structure, function and health of western forests. For many bark beetle species, including MPB, self-focusing and self-dissipating aspects of the species' chemical ecology are integral components affecting population dispersal and aggregation. Many models have been constructed [4, 5, 6, 7, 8, 2] to describe bark beetle dispersion dynamics. In 1996,

Powell *et al.* [9] built upon these to develop a large-scale (e.g. forest-sized) reaction-diffusion partial differential equation (PDE) model of the spatial interaction between MPB and its host trees, including critical components of the species' chemical ecologies.

The spatial dynamics of beetle populations have been of particular interest in characterizing and modeling both endemic and epidemic population levels. Self-focusing and self-dissipating mechanisms play a particularly important role for small predators that attack dangerous prey which are, at the same time, easily over-exploited. To overcome a tree's defenses, hundreds of beetles must coordinate their attack [10, 11, 12, 13]. However, once a tree has been successfully overcome, the phloem layer in which MPB nest is easily over-crowded.

To facilitate a mass attack and subsequent repulsion, a chemical communication system has evolved [14, 15, 16]. This system relies on attractive and repulsive pheromones to coordinate aggregation [17, 18, 19, 20, 21] and anti-aggregation [22, 23, 15, 24, 25]. As a population organizes according to these forces the dispersal pattern can become very complex. Understanding the spatial dynamics is crucial to the modeling of the interaction between MPB and host trees. The reaction-diffusion PDE, or *global*, model of Powell *et al.* has proved to be too complicated for easy ecological use. A *local* projection based upon a Gaussian *ansatz* captures both aggregation and dispersal in a single system of ordinary differential equations (ODEs), which has facilitated experimentation and parametrization.

1.2 Mountain Pine Beetle Life History

To effectively model the MPB/host system we must have a clear understanding of the beetles' life history and how beetles and trees interact. MPB larvae overwinter in the phloem tissue of trees. As they reach maturity, in late summer, they disperse through the forest in search of new trees in which to nest and breed. Once a female beetle has found a suitable host tree it will begin drilling a hole through the outer layer of bark to reach the phloem tissue. Remaining in the phloem layer, the beetle turns and begins boring a gallery up the trunk of the tree. As beetles bore through the phloem tissue, they interrupt the transport of high-energy compounds produced by the tree during photosynthesis.

Pine tree hosts do not passively submit to MPB attacks; they have evolved physiological mechanisms to resist beetle attacks [26, 27, 28, 29, 30]. When a beetle bores into a tree, the tree responds by flooding the gallery with resin which contains compounds toxic to the beetle. In addition to the toxic properties resin also serves as a physical barrier to MPB. The beetle is either forced out of the attack hole by the viscous resin or encased by it as it crystallizes.

In order for MPB to complete their galleries and successfully nest, the tree's resin defenses must first be exhausted. If MPB manage to successfully overcome a tree and lay eggs, these eggs will develop into larvae. As these larvae develop

they move horizontally through the phloem layer, feeding on its energy-rich sugars, interrupting even more of the tree's nutrient transport. It is this girdling effect that eventually kills the tree. In this stage of development, MPB arrest and typically overwinter as larvae. As spring temperatures warm, the larvae recommence development [31, 32, 33]. Once fully developed, a mass emergence is initiated by appropriate environmental conditions. MPB emerge from the tree as mature adults in search of a new host in which to continue the cycle. It is this redistribution during the search for new hosts that we attempt to model.

1.3 Behavior of the Pine Beetle/Host Tree System

The danger to a single beetle attacking a tree is great. The resin resources of a tree are large compared to the amount required to pitch out one beetle; in a one-on-one battle, a healthy tree will win. As with many systems in which a small predator attacks a large dangerous prey, the tree has the advantage in that it can repel many attacks before being overcome.

The strategy, then, for the beetles is to coordinate their attacks so that, together, they can exhaust the tree's resin supply. Synchrony must play a crucial role if such a mass attack is to be successful [34]. Many beetles in a population must emerge at the same time and focus their attacks on a single tree weak enough to be overcome. To coordinate such attacks, MPB have evolved a communication system based on beetle-produced chemical pheromones (see above) and tree-produced chemical kairomones [22]. This communication system enables MPB to focus their attacks to a common host tree.

As beetles emerge, they follow kairomone and pheromone cues which direct them in their flight [35, 36, 37, 38]. Kairomones may play a more dominant role in initiation of a mass-attack by signaling a tree as weakened by disease or other stresses [39, 40, 41]. At low population densities, attacking MPB selectively attack these trees. Visual [42, 43], auditory and tactile cues likely play a role in attack initiation. Once it lands and begins boring into a tree, a beetle emits pheromones which attract more beetles. These new beetles emit even more pheromone, strengthening their effect. This nonlinear self-focusing has the effect of attracting large numbers of beetles to a single tree. In defense, the tree floods attack holes with resin, depleting its reserves. If the beetles successfully coordinate their attack, the tree will quickly exhaust its resin supply and will not be able to repel further attacks.

This type of self-focusing will attract many beetles, often more than can optimally infest a single tree. If too many beetles infest one tree, they begin competing with one another for limited nesting space resulting in mortality from within-tree competition. To avoid intraspecific competition due to over-population the pheromone communication system also includes an anti-

aggregation mechanism. Once a certain stage is reached in the attack, different pheromones begin to play the dominant role. These pheromones have the effect of repelling new attacks from a tree.

Some of the specific chemicals involved in the MPB communication system are known. Once an attack has been initiated, a major constituent of the resin of *Pinus* spp., α -pinene, is converted by attacking female beetles into *trans*-verbenol [22]. This is often used as an aggregation pheromone attracting both sexes. At higher concentrations of *trans*-verbenol, higher proportions of males are attracted. Males produce *cis*-brevicomin, which at low concentrations primarily attracts females [17]. Attacking males also release verbenone, which, at high concentrations, inhibits the landing of additional beetles. Once the concentration of verbenone sufficiently exceeds the concentration of aggregating pheromones, flying beetles in the area switch their attacks to nearby host trees.

In this manner beetle populations manage to survive from year to year at endemic levels, killing only a few trees. At endemic levels, only weaker trees can be successfully attacked. As population numbers grow, more vigorous, and subsequently more nutritional, trees can be overcome. When populations grow large enough, an outbreak results, in which populations can kill large numbers of healthy pines.

Experiments have been designed [44] to help facilitate the study the aggregation and dispersal of MPB. To observe beetle attack behavior Bentz *et al.* [44] organized plots of about 450 square meters. To ensure MPB activity in a plot they attached a chemical lure to the tree in the center of the plot which drew MPB to the area. Once a mass attack had begun on the center tree, baits were removed and they recorded how the beetles would completely overcome the center tree, then switch the mass attack to a nearby tree. To track MPB behavior, daily counts were made of new attacks in designated sections of each lodgepole within the plot. This allowed creation of a temporal and spatial picture of beetle activity in the area.

In this paper, I describe the global model and its meaning. Also, the assumptions and steps used to create the local projection are given. Many parameter values can be estimated by referencing literature. Once a local model has been constructed we can use our experimental data to determine values for remaining parameters.

1.4 Global Model

To understand the behavior of the pine beetle/host tree system, Powell *et al.* [9] constructed a model which accounts for the effects of the populations size of flying beetles and nesting beetles, the health of a forest, and the pheromone and kairomone concentrations in a forest.

The following variables describe densities and depend on spatial location, x , y , and time, t :

- $P(x, y, t)$ - population of flying MPB.
 $Q(x, y, t)$ - population of (alive) nesting MPB.
 $A(x, y, t)$ - concentration of volatiles released by beetles; pheromones.
 $C(x, y, t)$ - concentration of volatiles released by attacked trees; kairomones.
 $S(x, y, t)$ - resin outflow.
 $R(x, y, t)$ - resin capacity (related to phloem thickness and size of tree).
 $H(x, y, t)$ - number of entrance holes bored by attacking MPB.

With these variables they constructed the model. By neglecting spatial redistribution, the number of flying MPB decreases proportionally to the death rate, $\omega_1 P$ and the number of beetles who land and attempt to nest in a tree, $r_1 \frac{R}{R_0} P$. The term $r_1 P$ captures the rate at which MPB land to attack hosts. R_0 is the rest resin capacity of the tree, proportional to the surface area of the bole. Consequently, the fraction $\frac{R}{R_0}$ measures the uninfested portion of the bole. This gives a dynamic equation for changes in flying MPB density:

$$\dot{P} = -\omega_1 P - r_1 \frac{R}{R_0} P + \gamma.$$

The term γ captures the emergence rate of flying MPB.

The nesting population, Q , grows proportionally to $r_1 P$. Nesting MPB die at some rate, $\omega_2 Q$. Finally, beetles may be killed by the natural defense mechanisms of the host, resin out-flow. The population of nesting MPB should decrease in proportion to the resin out-flow through occupied burrows, $\beta_1 S \frac{Q}{H}$. This gives an equation for Q ,

$$\dot{Q} = -\omega_2 Q + r_1 \frac{R}{R_0} P - \beta_1 S \frac{Q}{H}. \quad (1.1)$$

The rate of increase in the number of holes drilled is precisely equal to the number of MPB who have attempted to nest. On the other hand, resin crystallizes after flowing through burrows, slowly closing the hole. This means that the 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,

$$S = r_3 H R.$$

A rate equation for H is given by

$$\dot{H} = r_1 \frac{R}{R_0} P - r_4 r_3 H R. \quad (1.2)$$

It remains to be determined how the local resin capacity and amount of resin outflow vary with time. Let R_0 be the constitutive resin level of the tree. When $R = 0$ the tree has no capacity to replenish its reservoir, so that the

rate of change of the resin capacity should be proportional to $R(R - R_0)$. Resin capacity is depleted proportionally to the number of entrance holes and the available amount of resin which can flow out through the holes. These two processes give

$$\dot{R} = [r_2(R_0 - R) - r_3H]R. \quad (1.3)$$

This model for the tree defensive response is essentially that proposed by Berryman et. al. [5], with the difference in interpretation that the R used here describes the total resin capacity of the attacked tree, whereas the Berryman defensive variable is the resin available to flood a single nest gallery. One advantage of this interpretation is that the resin capacity is proportional, in part, to the surface area of the host bole, which is convenient for analyzing rate of attack and the effect of resin exudation on nesting MPB. Otherwise, the host-MPB model above differs from Berryman et. al. by including host recovery (via the variable H) and an explicit mechanism for relating the number of attacks on a host to MPB population densities.

This set of equations reflects the temporal behavior without spatial redistribution. One mechanism for understanding spatial redistribution is to consider mass balances in some arbitrary two-dimensional spatial domain, Ω [45, 46, 47]. The total number of beetles in that domain is

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

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 a simple law,

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

The source and sink terms are described above. For brevity these terms are denoted as $F(P, A, x, y, t)$, so that

$$\text{Source Terms} - \text{Sink Terms} = \iint_{\Omega} F \, dx \, dy.$$

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

Denote the flux vector by $\vec{\phi}$. There are three basic components to the flux function, reflecting the beetles' recognition of potential hosts, their response to pheromones, and the degree of randomness in their behavior. This allows for an interplay between random and nonrandom movement, as in [48]. Thus,

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

where

- $\vec{\phi}_C$ is flux along gradients of $C(x, t)$ due to chemotactic recognition of potential hosts,

$$\vec{\phi}_C = \kappa P \nabla C.$$

- $\vec{\phi}_A$ 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, repulsive in larger concentrations, giving

$$\vec{\phi}_A = \nu P \frac{A_0 - A}{A_0 - A/A_3} \nabla A.$$

- $\vec{\phi}_P$ 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

$$\vec{\phi}_P = -\mu \nabla P.$$

Returning to the balance law, the total flux into Ω will be the integral of the flux vectors around the boundary of the domain. This gives the expression

$$\frac{d}{dt} N = \iint_{\partial\Omega} \vec{\phi} \cdot \vec{n} \, ds + \iint_{\Omega} F \, dx \, dy = \iint_{\Omega} [F - \nabla \cdot \vec{\phi}] \, dx \, dy.$$

Here \vec{n} is the unit normal vector to the boundary, $\partial\Omega$, of Ω , and the Divergence Theorem is used for the latter equality. Writing this expression in terms of only one integration,

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

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

$$\frac{\partial}{\partial t} P = -\nabla \cdot \{[\kappa \nabla C + \nu \nabla f(A)] P - \mu \nabla P\} - \omega_1 P - r_1 \frac{R}{R_0} P + \gamma, \quad (1.4)$$

where

$$f(A) = A_3 A_0 \left\{ (A_3 + 1) \ln \left[1 + \frac{A}{A_3 A_0} \right] - \frac{A}{A_0} \right\}.$$

This equation and its derivation are similar to equations for environmentally-induced movement in [49, 50, 51, 52].

Powell *et al.* 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 advection through the canopy. These effects give a linear diffusion equation for A ,

$$\frac{\partial}{\partial t} A = b_1 \nabla^2 A + a_1 Q - \delta_1 A. \quad (1.5)$$

For host kairomones, C , the source is resin outflow. Again, some loss is expected due to chemical decomposition, giving an equation similar to that for A .

$$\frac{\partial}{\partial t} C = b_2 \nabla^2 C + a_2 S - \delta_2 C. \quad (1.6)$$

Equations (1.1 - 1.6) are a complete spatio-temporal description of the dependent variables controlling the behavior of MPB/pine relationship.

Chapter 2

Methods

2.1 Objectives and Experimental Design

The global model describing MPB/host tree system behavior is complex and involves many parameters describing various physical quantities or rates. To understand better what these parameter values should be, a local projection of the global model has been taken which will allow direct comparison of physical data and model predictions. Below is an explanation of the basis for the localization of the model and the values used for estimated parameter values. Also, the technique used to fit values for the most troublesome parameters is described and the results reported. Providing support for non-fitted parameter values and for parameter values obtained using field data will help clarify our choices and justify parameter use in the global model. The global model has great potential for not only understanding system behavior, but also prediction and management.

To reach these goals Bentz *et al.* [44] designed experiments which focus on the aggregation and dispersal of MPB. Initiating an MPB mass attack on one tree then allowing beetle pheromones to drive system dynamics provides an area where we can track daily attacks on neighboring trees. It is possible to create a picture of how MPB attacks vary temporally and spatially using these daily attack counts.

2.2 Localization of the Global Model

The global model has been constructed taking into account factors such as numbers of flying and nesting beetles, vigor of a tree, and pheromone and kairomone concentrations. This model, describing dynamics on a forest-sized scale, has proved difficult for ecological use. This is because variables describing an entire forest are spatially and temporally extended. For example, the model vari-

able representing the population of nesting beetles. Q , describes the density of nesting beetles as a continuum throughout the forest, rather than the number of beetles nesting in a single tree. Directly measuring this type of number is difficult, making parameter estimation impractical.

Localizing the global model will convert variables from densities to numbers at a point, for example, numbers of beetles in a single tree. These types of numbers are more easily obtained from field studies. This will allow use of the observational data to approximate parameter values which best match the model to observed system dynamics.

Powell *et al.* [9] assume that the relationship between global state variables (densities) and local variables (numbers at a point) is Gaussian in space for all of the time-centered variables (A , C , H , Q and R). The response of the population, P , will be approached with a steady-state description used in [53].

Integrating the global model is a difficult proposition, particularly considering that the parameters are unknown and existing data is temporally extended at a single spatial location. This section will investigate the consequences of the global model at a single spatial location using a local modelling technique initiated in [9]. The idea is to use the integrals

$$\int_0^{\infty} (\cdot) dt \quad \text{and} \quad \int_0^{\infty} (\cdot) t^3 dt$$

to 'project' the equations (1.4 - 1.6) onto ODE for the evolution of Gaussian parameters. Equivalently, this may be viewed as an analytic calculation of the zeroth and second moments of the profile, which are then used to parametrize a Gaussian with the same moments. This will not be satisfactory for P , which becomes multimodal due to nonlinear self-focusing/defocusing. In what follows we will resolve this difficulty by using the leading eigenfunction for P to replace (1.4), thus achieving an adiabatic response for flying MPB density.

2.2.1 Projection onto Spatial Modes

To produce a local set of equations reflecting global redistribution Powell *et al.* [9] *parametrize* spatial behavior in a local way, that is, determine requirements about the temporal evolution of parameters in a spatial description of variables. To do this, They choose a parametrized spatial form for the variables, then allow the parameters to vary temporally in a way consistent with the governing PDE. This spatial description of variables could take the form of a cone or a cylinder. However, they assume that the variables are Gaussian in space. Statistically, this shape best describes a quantity which is localized at a point and drops off quickly as you move outward. A Gaussian form describes the pheromone variable, A , particularly well since the pheromone molecules obey random diffusion laws and are lost to the environment as they move outward.

Letting ℓ denote the distance from the focus tree,

$$\begin{aligned} A &= 2 \frac{a(t)}{w_a(t)} e^{-\ell^2/w_a(t)}, \\ Q &= 2 \frac{q(t)}{w} e^{-\ell^2/w}, \\ R_0 &= 2 \frac{r_0(t)}{w} e^{-\ell^2/w}, \\ H &= 2 \frac{h(t)}{w} e^{-\ell^2/w}. \end{aligned}$$

Since the local model deals mainly with the behavior of an already initiated attack, they largely neglect the effects of tree-produced attractants, C . The experimental design of Bentz *et al.* [44] employs baited trees to initiate attacks; mimicking, then removing effects of host kairomones. Neglecting C leaves A , Q , R_0 , H and P with which to construct a local model.

These local variables 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. To localize the variable P (1.4) it is replaced with its leading eigenfunction, which maintains the desired characteristic PDE behavior;

$$P = \frac{\gamma_0}{r_1 + w_1} \exp \left[\frac{\nu}{\mu} A_3 A_0 \left((A_3 + 1) \ln \left[1 + \left(\frac{A}{A_3 A_0} \right) \right] - \frac{A}{A_0} \right) \right]. \quad (2.1)$$

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, if a Gaussian *ansatz* were used for the flying MPB, not only would it be extremely optimistic, it would fail to capture the repulsive wave following successful infestation, which has already been discussed.

To determine how the Gaussian parameters vary in time, we will integrate (1.5) over space. Noting that

$$\int_0^\infty 2 \frac{M}{\lambda} e^{-\frac{\ell^2}{\lambda}} \ell \, d\ell = M,$$

and that

$$\int_0^\infty 2 \frac{M}{\lambda} e^{-\frac{\ell^2}{\lambda}} \ell^3 \, d\ell = M\lambda,$$

integrating (1.5) over space gives

$$\dot{a} = \frac{d}{dt} \int_0^\infty A \ell \, d\ell = \int_0^\infty \left[b_1 \frac{1}{\ell} \frac{\partial}{\partial \ell} (\ell A_\ell) + a_1 Q - \delta_1 A \right] \ell \, d\ell$$

$$= a_1 q - \delta_1 a.$$

Performing the same integration with an additional ℓ^2 in the integrand gives

$$\begin{aligned} \frac{d}{dt}(aw_a) &= \frac{d}{dt} \int_0^\infty A \ell^3 d\ell = \int_0^\infty \left[b_1 \frac{1}{\ell} \frac{\partial}{\partial \ell} (\ell A_\ell) + a_1 Q - \delta_1 A \right] \ell^3 d\ell \\ &= (4b_1 - \delta_1)aw_a + a_1 qw. \end{aligned}$$

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

$$\dot{a} = a_1 q - \delta_1 a,$$

and

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

2.2.2 A Local Model for Infestation

Powell *et al.* replace the nonlinear redistribution equation (2.1) with the quasi-steady response. Next, they determine how to convert this response function, which gives population density as a function of chemical forcing, into a number of flying MPB available locally to infest the focus tree, which is referred to as I .

Leaving I undetermined, the final system of ODEs is:

$$\dot{a} = a_1 q - \delta_1 a, \quad (2.2)$$

$$\dot{w}_a = 4b_1 + a_1 q \frac{w - w_a}{a}, \quad (2.3)$$

$$\dot{q} = r_1 \frac{r}{r_0} I - \beta \frac{r_3}{w} q r, \quad (2.4)$$

$$\dot{h} = r_1 \frac{r}{r_0} I - \frac{r_3}{w} r_4 h r, \quad (2.5)$$

$$\dot{r} = r \left[\frac{r_2}{w} (r_0 - r) - \frac{r_3}{w} h \right]. \quad (2.6)$$

The number of infesting MPB, I , is taken to be proportional to the number of flying MPB in the steady-state solution, evaluated at the location of the host tree,

$$I = 2\pi \int_0^{r_c} P r dr \approx \frac{\pi \gamma_0 r_c^2}{r_1 + \omega_1} \exp \left[\frac{\nu}{\mu} A_3 A_0 \left((A_3 + 1) \ln \left[1 + \left(\frac{A}{A_3 A_0} \right) \right] - \frac{A}{A_0} \right) \right].$$

The constant r_c is a 'radius of engagement,' or conversion factor transforming the density of flying MPB into the number of MPB attacking the focus tree. It may be thought of as the distance at which an individual MPB can sight

and orient on a particular tree. The approximation of the integral is based on a cylindrical approximation to the volume under P when $r_c^2 \ll 1$ hec. Letting $c = \frac{\pi r_c^2}{r_1 + a_1}$ we have

$$I = cr_e^2 \exp \left[\frac{\nu}{\mu} A_3 A_0 \left((A_3 + 1) \ln \left[1 + \left(\frac{A}{A_3 A_0} \right) \right] - \frac{A}{A_0} \right) \right]. \quad (2.7)$$

It is important to note that if we assume that the chemical profile reaches equilibrium rapidly, the variable describing the pheromone cloud, A , can be written in terms of the number of nesting beetles, q ,

$$A = \frac{2a_1 q}{4b_1 + w\delta_1} \exp \left[-\frac{\delta_1 l^2}{4b_1 + w\delta_1} \right].$$

As will be discussed below, this is a valid assumption because δ_1 is large. If we want to know the value of this variable at the location of the tree we can evaluate it at $l = 0$ and obtain

$$A = \frac{2a_1 q}{4b_1 + w\delta_1}.$$

So the infestation function given in terms of beetle population, assuming A is at equilibrium and P is quasi-steady, is

$$I = cr_e^2 \exp \left[\frac{\nu}{\mu} A_3 A_0 \left((A_3 + 1) \ln \left[1 + \left(\frac{2a_1 q}{(4b_1 + w\delta_1) A_3 A_0} \right) \right] - \frac{2a_1 q}{(4b_1 + w\delta_1) A_0} \right) \right]. \quad (2.8)$$

Lists of variable and parameter definitions used in the local projection model are presented in Table 2.1 and Table 2.2. Even though the model is very complex, involving seven global variables, six local variables, and more than twenty parameters, there is a balance of complexity maintained by the number of ecological degrees of freedom of the system. Compared to the complexity of the system, the model is reasonable.

2.3 Non-fitted Parameter Values

Before using the local model for parameter estimation, values were chosen using literature and knowledge of the biological systems involved, for parameters not being fitted. Because of the lack of understanding and previous study, three of the most difficult parameters to estimate are A_0 , ν and c . Assigning values to the other model parameters, I use a least-squared fitting method to obtain approximate values for the final three parameters. In this section are brief explanations for non-fitted parameter estimates. See Table 2.3 for a summary of non-fitted parameter values.

Model Variable Definitions	
Variable	Definition
A	Global model variable describing pheromone concentrations
C	Global model variable describing kairomone concentrations
H	Global model variable describing attack hole density
P	Global model variable describing flying beetle density
Q	Global model variable describing nesting beetle density
R	Global model variable describing the vigor of forest trees
S	Global model variable describing resin outflow
a	Local model variable describing the number of pheromone molecules at a particular site
h	Local model variable describing number of attack holes in a single tree
I	Equation describing number of beetles available locally to infest a tree
q	Local model variable describing population of nesting beetles at a particular site
r	Local model variable describing current vigor (resin capacity) of a tree
w_a	Local model variable describing the spread of a pheromone cloud

Table 2.1: A list of variables appearing in the global and local models for MPB redistribution.

2.3.1 A_3 — Saturation Parameter for Pheromones

In an early version of the model [9] the flux due to beetles' attraction to and repulsion from the suite of pheromones, A , was modeled as

$$\Phi = \nu P(A_0 - A)\nabla A,$$

where P is the population of flying beetles [9, 53]. This model did not work well for large values of A . It had the effect of not only repelling beetles from a tree, but also from the entire area. To better fit empirical evidence, A_3 , a parameter describing the maximum saturation concentration of pheromones, was added. This has the effect that, once pheromone concentrations reach a certain value, no higher concentration will increase the repulsive effect. The new model for chemotaxis is

$$\Phi = \nu P \frac{A_0 - A}{A_0 + A/A_3} \nabla A.$$

This flux function has the effect of attracting beetles for small A and repelling beetles for large A , parametrized by A_3 for $A > A_0$. We have chosen a value for A_3 that, for small A , will behave much like the earlier model and still allow the saturating effect to restrain the repulsion as A grows large. A value of $A_3 = 1$ was chosen, which has the effect that, as A gets large, the flux is approximately

$$\Phi = -\nu P \nabla A, \quad (2.9)$$

and as A gets small the flux is approximately

$$\Phi = \nu P \nabla A, \quad (2.10)$$

Parameter Definitions and Units		
Parameter	Definition	Units
A_0	Critical concentration at which pheromones become repulsive	$\mu\text{g hec}^{-1}$
A_3	Saturation parameter for pheromones	—
a_1	Rate of pheromone production by nesting beetles	$\mu\text{g fh}^{-1} \text{HMPB}^{-1}$
a_2	Rate of resin exudation by host tree	$\mu\text{g fh}^{-1}$
β	Mortality rate of beetles due to resin outflow	$\text{hec}^{-1} R_0^{-1}$
b_1	Rate of pheromone diffusion	hec fh^{-1}
b_2	Rate of kairomone diffusion	hec fh^{-1}
c	Scaling constant to describe MPB background emergence far from a tree	HMPB hec^{-1}
δ_1	Loss rate of pheromones	fh^{-1}
δ_2	Loss rate of kairomones	fh^{-1}
ℓ	Distance from the focus tree	$\text{hec}^{\frac{1}{2}}$
μ	Diffusivity of flying beetles due to random movement	hec fh^{-1}
ν	Strength of directed MPB motion due to pheromone gradients	$\text{hec}^2 \mu\text{g}^{-1} \text{fh}^{-1}$
r_0	Rest resin capacity of a healthy tree	$\text{hec } R_0$
r_1	Rate of landing and conversion from flying to nesting beetles	fh^{-1}
r_2/w	Rate of resin replenishment	$\text{hec}^{-1} \text{fh}^{-1} R_0^{-1}$
r_3/w	Rate of resin outflow through holes bored by beetles	fh^{-1}
r_4	Rate of resin crystallization (tree recovery)	$\text{hec}^{-1} R_0^{-1}$
r_ϵ	Conversion factor for transforming the density of flying MPB into the number of MPB attacks; or 'radius of engagement'	$\text{hec}^{\frac{1}{2}}$
σ	Parameter describing the openness of a stand of trees	
w	Parameter representing the characteristic size of a tree	hec

Table 2.2: A list of parameters appearing in the global and local models for MPB redistribution.

so that neither peak repulsion nor attraction depend directly on the magnitude of λ , but only on its gradient. The fact that 2.9 and 2.10 are equal but opposite agrees well with the logic that the maximum speed of beetles leaving an area should equal the maximum speed of their arrival.

2.3.2 a_1 — Rate of Pheromone Production

Estimating the emission rate of the pheromone trans-verbenol by a female MPB at about 20ng fl^{-1} [54], gives

$$a_1 = 2\mu\text{g fl}^{-1} \text{HMPB}^{-1}.$$

2.3.3 β — Mortality Rate of Beetles Due to Tree Defenses

I estimate β indirectly by assuming that a general attack rate of 500 MPB over a 5-day period is just barely sufficient for overwhelming a healthy tree's defenses [55, 56]. Estimating there to be 5 flight hours in a day, this translates into an infestation rate of 0.20 HMPB per flight hour. Using this in (2.4) in place of the infestation term should correspond to $\dot{q} = 0$ giving

$$0 \frac{\text{HMPB}}{\text{fl}} = 0.2 \frac{\text{HMPB}}{\text{fl}} - \beta \frac{r_3}{w} q r. \quad (2.11)$$

At this point the tree should be able to replenish its resin reserves at the same rate as they are being depleted by attacking beetles, thus no net change should be seen. From the steady state of (2.6) we have $r = r_0 - \frac{r_3}{r_2} h$. Assuming the number of attack holes to be approximately equal to the number of attacking female beetles and replace r in (2.11) results in

$$0.2 \frac{\text{HMPB}}{\text{fl}} = \beta \frac{r_3}{w} r_0 q \left(1 - \frac{r_3}{r_0 r_2} q \right). \quad (2.12)$$

In this form, the resin capacity of a tree is a function of numbers of nesting beetles, $f(q) = q \left(1 - \frac{r_3}{r_0 r_2} q \right)$. This quadratic has zeros at $q = 0$ and $q = r_0 r_2 / r_3$, and has the form of a parabola (Figure 2.1) with its maximum half way between the zeros, meaning that the maximum response of the tree will be when $q = r_0 r_2 / 2 r_3$. Using this value in (2.12) we have

$$0.2 \frac{\text{HMPB}}{\text{fl}} = \frac{\beta r_2}{4w}$$

where r_0 has been replaced with its value, 1 hec R_0 . This equation will be one of four used to solve for the related parameters β , r_2 , r_3 , and r_4 (Section 2.3.10). Unit analysis reveals the units of β to be $\text{hec}^{-1} R_0^{-1}$.

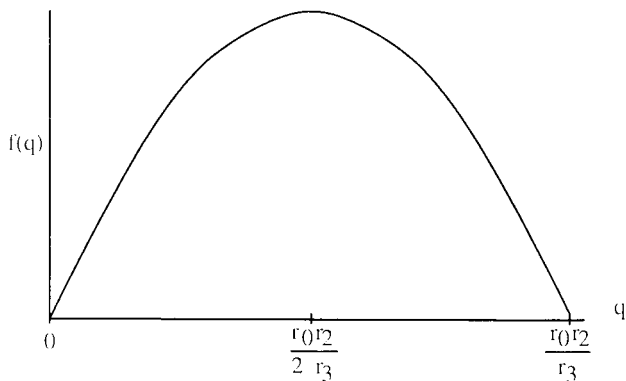


Figure 2.1: The resin capacity of a tree as a function of numbers of attacking beetles.

2.3.4 b_1 — Rate of Pheromone Diffusion

δ_1 — Loss Rate of Pheromone

The self-modifying spatial behavior of the system is mediated by the pheromone plume produced by nesting MPB. One model for the diffusion of the pheromone plume produced by q nesting MPB at the origin would be

$$A_t - uA_x = b_1 A_{yy} + b_2 A_{xx} - \delta_1 A + a_1 q \delta(x, y). \quad (2.13)$$

where u is the average wind speed, which is assumed to be directed along the x axis in the positive direction. Also, by assuming, based on observations of smoke plumes, that the diffusion in the direction of the wind itself is small ($b_2 \simeq 0$). The parameter a_1 is known to be approximately $2\mu\text{g fl}^{-1} \text{HMPB}^{-1}$. To determine the remaining parameters, b_1 and δ_1 we rely on dimensional arguments. Let ξ be the average separation between hosts (~ 3 meters) in an open-canopy stand. We estimate the scale of losses to satisfy

$$\xi^2 \simeq \frac{b_1}{\delta_1}.$$

so that characteristic losses occur on a tree-to-tree scale in open-stand conditions. The rate of chemical mixing due to turbulence we relate to the advection generated by solution via method of steepest descents. Solving these two expressions for b_1 and δ_1 gives

$$b_1 = \frac{u\xi}{2} \quad \text{and} \quad \delta_1 = \frac{u}{2\xi}.$$

As the canopy of a stand becomes more closed the air below the canopy becomes more isolated from the air above. While for a particular choice of u this should not change the rate of horizontal diffusion, it will influence the rate of loss through the canopy. The descriptions of b_1 and δ_1 may be augmented with a scaling factor, σ , reflecting the degree of closure of the canopy ($\sigma = 1$ means open stand conditions, $\sigma = 0$ means solid canopy). Choosing an average wind speed of $u = 0.6$ m/s and an average spatial scale of loss of $\xi = 3$ m gives $b_1 = 0.324/\sigma$ hec fl $^{-1}$ and $\delta_1 = 360\sigma$ fl $^{-1}$.

2.3.5 μ — Diffusivity of Flying Beetles Due to Random Redistribution

Turchin and Theony [2] estimate a parameter for the southern pine beetle which is related to the ratio of diffusion rate (μ) and loss rate of the population ($r_1 + w_1$). Their model of diffusion with removal (due to landing and background death) in polar coordinates is

$$\frac{\partial u}{\partial t} = D \left(\frac{\partial^2 u}{\partial r^2} + \frac{1}{r} \frac{\partial u}{\partial r} \right) - \delta u. \quad (2.14)$$

Here u is the density distribution of beetles as a function of one temporal (t) and two spatial (x, y) coordinates. The two parameters are D , the diffusion rate, and δ , the rate at which beetles are lost from the dispersing population. Assuming that their capture rate was proportional to the instantaneous density of insects at a point, they write $c(r, t) = \alpha u(r, t)$ where α , the constant of proportionality is the capture efficiency of the traps. Cumulative captures over the entire course of the study can be written

$$C(r) \equiv \int_0^{\infty} c(r, t) dt = \alpha \int_0^{\infty} u(r, t) dt. \quad (2.15)$$

The well known solution [57] of (2.14) can be substituted into (2.15) and integrated over time giving

$$C(r) = \frac{\alpha N_0}{2\pi D} K_0 \left(\sqrt{\frac{\delta}{Dr}} \right)$$

where N_0 is the initial number of dispersing beetles and K_0 is a modified Bessel function. This can be approximated by

$$C(r) \approx Ar^{-\frac{1}{2}} \exp[-r/B]$$

where $A \equiv (\alpha N_0)/(\sqrt{8\pi r} \sqrt{D^3 \delta})$ and $B \equiv \sqrt{D/\delta}$. Fitting this to field data, Turchin and Theony obtained estimates of A and B . Their estimates of B (ranging from 0.19 to 4.8 hec $^{\frac{1}{2}}$) are most relevant here.

In the Powell *et al.* model, the diffusion rate, μ , is analogous to Turchin and Theony's D and flying beetle loss due to landing and death (1.1); our $r_1 + \omega_1$ is analogous to their δ . This gives

$$B = \sqrt{\frac{\mu}{r_1 + \omega_1}}.$$

With $B = 2.4 \text{ hcc}^{\frac{1}{2}}$, $\omega_1 = 0.014 \text{ fh}^{-1}$, and $r_1 = 0.16 \text{ fh}^{-1}$ we can solve for μ :

$$\mu = 1.00 \frac{\text{hcc}}{\text{fh}}.$$

2.3.6 r_0 — Resin Capacity of a Healthy Tree

This parameter describes the health or vigor of a lodgepole of 10 inch diameter at breast height under no environmental stress and can be related to the volume of resin in a tree. This parameter can be non-dimensionalized by scaling all measures of resin capacity to the health of a healthy, unstressed tree. Units of resin capacity should describe a volume. To simplify unit analysis this can be denoted by units of $[wR_0]$, where R_0 , a global parameter, describes volume of resin per area, so that

$$r_0 = 1 \text{ hcc } R_0.$$

2.3.7 r_1 — Rate of Landing and Conversion from Flying to Nesting Beetles

To estimate the attack rate of flying MPB, based upon anecdotal evidence, I assume that 15% of the flying beetles randomly land and attack trees per flight hour. At any time, t , the population of flying beetles can be written

$$P_t = -r_1 P.$$

The solution to this is

$$P = P_0 e^{-r_1 t}.$$

At time $t = 1 \text{ fh}$ the population should only have decreased by 15%, leaving 85% of the original population. Substituting these in the solution gives

$$0.85P_0 = P_0 e^{-r_1}.$$

Solving for r_1 gives

$$\begin{aligned} r_1 &= -\ln(0.85) \text{ fh}^{-1} \\ &= 0.16 \text{ fh}^{-1}. \end{aligned}$$

2.3.8 r_2 — Rate of Resin Replenishment

Since global model variables describe densities rather than numbers at a point, the parameters r_2 and r_3 must also describe rates involving densities. To use them in the local model they must be converted to rates involving numbers. This can be accomplished by dividing by w , the characteristic size of a tree (Section 2.3.12). To avoid introducing a new parameter we will simply use the ratios r_2/w and r_3/w . From personal communication [58] r_2 should be approximately equal to $r_3 r_4$, meaning that the rate at which a tree can replenish its resin reserves should be about equal to the rate at which it flows out and crystallizes. This will be the second of a system of equations involving β , r_2 , r_3 , and r_4 .

2.3.9 r_3 — Rate of Resin Outflow Through Attack Holes

To estimate r_3 we consider equation (2.6). This equation has steady states at $r = 0$ and $r = r_0 - \frac{r_3}{r_2}h$. The solution of interest is

$$r = r_0 - \frac{r_3}{r_2}h.$$

Observing that there should be a value for h which is sufficient to deplete the constitutive resin capacity of the tree, I estimate this value to be about 2 HMPB [10, 11, 12, 13]. So, when $r = 0$, $h = 2$, with $r_0 = 1$, we have

$$\frac{r_3}{r_2} = 0.5 \text{ nec } R_0.$$

This is the third equation in the β , r_2 , r_3 , r_4 system.

2.3.10 r_4 — Rate of Resin Crystallization

It takes one to two days (5 to 10 fh) for resin to crystallize. Recalling (2.5) and taking there to be no continued infestation of an initially attacked, healthy tree ($r = r_0 = 1$), we have

$$\dot{h} = -\frac{r_3}{w}r_4h.$$

The solution to this differential equation is (recalling that h is dependent upon time)

$$h = h_0 \exp\left(-\frac{r_3}{w}r_4\Delta t\right).$$

Assuming that after two days the number of holes left unfilled by resin should be nearly zero, we can say that this should be approximately equal to $h = h_0 \exp(-1)$. Comparing these two equations gives the relationship,

$$1 = 10 \frac{r_3}{w}r_4,$$

which gives an estimate of

$$\frac{r_3}{w}r_4 = 0.1 \text{ hec}^{-1} \text{ fh}^{-1} R_0^{-1}.$$

This equation completes the system involving β , r_2 , r_3 , and r_4 .

$$\begin{aligned} 0.2 &= \frac{\beta r_2}{4w}, \\ r_2 &= r_3 r_4, \\ \frac{r_3}{r_2} &= 0.5, \\ \frac{r_3}{w}r_4 &= 0.1. \end{aligned}$$

Solving this system results in

$$\begin{aligned} \beta &= 8 \text{ hec}^{-1} R_0^{-1}, \\ \frac{r_2}{w} &= 0.1 \text{ hec}^{-1} \text{ fh}^{-1} R_0^{-1}, \\ \frac{r_3}{w} &= 0.05 \text{ fh}^{-1}, \\ r_4 &= 2 \text{ hec}^{-1} R_0^{-1}. \end{aligned}$$

2.3.11 r_e — Radius of Engagement

This describes the maximum distance away from a tree a flying beetle can be and still be visually attracted to it. It acts as a conversion factor for transforming the density of flying MPB into the number of MPB attacking a tree. Assume

$$r_e = 2 \text{ m},$$

equivalently, in units of hectares

$$r_e = 0.02 \text{ hec}^{\frac{1}{2}}.$$

2.3.12 w — Constant Number Describing the Characteristic Size of a Tree

This parameter is descriptive of the size of a tree being attacked. It is important to note that this is not the basal area of a tree but more a description of the micro-climate of a tree. I have chosen an average size of three square meters cross sectional area. In hectares this is

$$w = 0.003 \text{ hec}.$$

Non-fitted Parameter Values	
Parameter	Value
A_3	1
a_1	$2\mu g \text{ fh}^{-1} \text{ HMPB}^{-1}$
b_1	$0.324/\sigma \text{ hec fh}^{-1}$
β	$8 R_0^{-1}$
δ_1	$360\sigma \text{ fh}^{-1}$
μ	1 hec fh^{-1}
r_0	$1 \text{ hec } R_0$
r_1	0.16 fh^{-1}
r_2/w	$0.1 \text{ fh}^{-1} R_0^{-1}$
r_3/w	0.02 fh^{-1}
r_4	$5 R_0^{-1}$
r_e	$0.02 \text{ hec}^{\frac{1}{2}}$
σ	0 - 1
w	0.003 hec

Table 2.3: A list of parameter values estimated using literature and knowledge of the systems involved.

2.4 The Study Areas and Data Collection

I have used several data sets from the summers of 1995, 1996 and 1997. The 1995 data were collected from a plot in a lodgepole pine stand in the Gold Creek drainage of the Sawtooth National Recreation Area (SNRA), Idaho. On August 6, 1995, a mountain pine beetle pheromone tree bait was placed on a single tree and left on for 24 hours. All trees within a radial distance of 10m from the focus tree were monitored for beetle attacks until August 18. Attacks were recorded on individual trees from the ground up to six feet twice a day. In the fitting procedures I used only data from trees that were successfully attacked. A graphical example of these attack series is seen in Figure 2.2. The attack series on this particular tree exhibits the behavior the model is designed to capture, a single peak representing beetle mass attack, with a fast initial attack time and a slightly less abrupt cessation of attack.

The 1996 data were collected in a similar manner. Two plots near St. Charles, Idaho were monitored from July 29 through August 13. Two focus trees were artificially baited to initiate attacks, with the baits being removed once attacks had begun. All pine trees within a radial distance of 40 feet from the focus tree were monitored. Attacks were counted twice daily on a section of the bole from two to five feet from the base of the tree.

In 1997, three plots in the Williams Creek drainage of the SNRA were mon-

itored between August 6 to August 18. The plot radius from the focus trees were 40 feet and counts were made twice daily between two and five feet from the base of the tree. Two plots near St. Charles, Idaho were monitored in a similar manner from August 2 to August 17.

Figure 2.3 depicts an attack series that does not conform to the expected model behavior. These data, from the summer of 1997, show several peaks with interspersed days of no beetle activity. I believe this is due to temperatures too low for MPB activity.

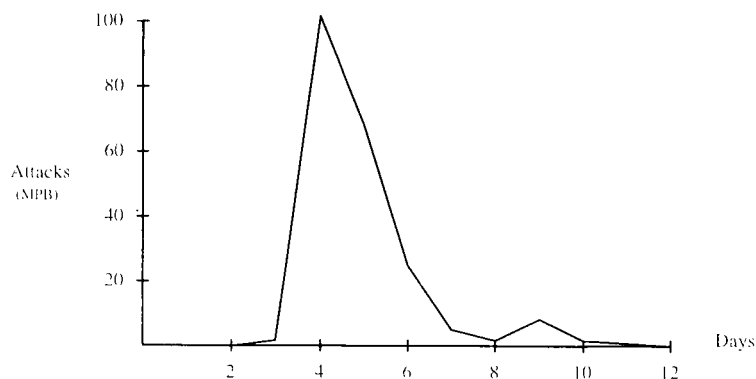


Figure 2.2: An example of MPB attack series on a single tree. Tree number 7 from the 1995 data.

2.5 Fitting the Model to the Data

The collected data reflect the rate of attack by MPB on single trees. This corresponds to the term appearing in (2.4) and (2.5):

$$r_1 \frac{r}{r_0} I.$$

I use this to estimate A_0 , ν and c , which are embedded in the infestation function, I . By extracting the infestation term and replacing it with the experimental data I created a stepwise model that will back-calculate the number of beetles infesting a tree at any given time step based upon the number of new attacks observed that day. Then, noting that the infestation function, I , is ultimately dependent upon the number of nesting beetles, I used the calculated number of infesting beetles to obtain predictions from the infestation function of

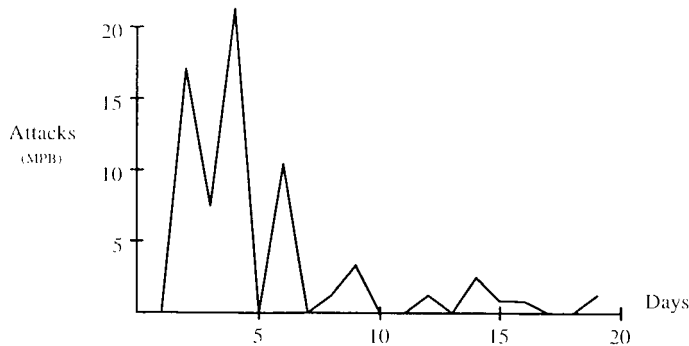


Figure 2.3: An example of MPB attack series on a single tree. Tree number 2 from the 1997 data.

how many new attacks to expect at the next time step. Essentially, this creates two sets of ordered pairs consisting of the current number of nesting beetles and the number of new attacks at the next time step. Fitting these two data sets will allowed me to estimate A_0 , ν and c . Although this method cannot validate the model, it can show an internal consistency. That is, given reasonable estimates for tree parameters, we can find consistent parameter values for both movement and aggregation.

The ordered pairs will be as follows, where A_n represents observed new attacks at each time step, n .

$$\{q_n, A_n\} \text{ vs. } \left\{q_n, r_1 \frac{r_n}{r_0} I(q_n)\right\}.$$

To flatten the more sensitive infestation function we can rewrite these pairs using a logarithmic transform,

$$\left\{q_n, \ln\left(\frac{A_n r_0}{r_1 r_n}\right)\right\} \text{ vs. } \{q_n, \ln(I(q_n))\}.$$

To create these ordered pairs and use the data in the parametrization of the local model I first constructed a stepwise model that allows for back-calculation of the number of beetles infesting a tree at any given time step based upon the number of new attacks observed that day. Some simplifying assumptions about the physical characteristics of the system are required.

2.5.1 Simplifying Assumptions and the Stepwise Model

From (2.4), the term describing the number of beetles infesting a tree is

$$r_1 \frac{r}{r_0} I.$$

From (2.6), assuming that r does not equal zero (the case where the tree is dead) and that, on our time scale, the change in tree vigor, r' , is small, we can estimate r to be

$$r = r_0 - \frac{r_3}{r_2} h. \quad (2.16)$$

In (2.5), if we take r_4 , the rate of resin crystallization, to be slow compared to beetle activity, the $r_3 r_4 r h$ term is negligible and

$$\dot{h} = r_1 \frac{r}{r_0} I.$$

The right-hand side of this equation is the part of the model that corresponds to the observational data, the number of attacks per time on a particular tree. We replace this part of the model with our observational values and define the following stepwise terms based on the preceding assumptions.

$$\begin{aligned} h_n &= \text{the sum of attacks observed from time 1 to } n \\ &= \sum_{i=1}^n A_i. \\ r_n &= \text{the initial health of a tree - resin loss due to attack holes} \\ &= r_0 - \frac{r_3}{r_2} h_n, \\ \dot{q}_n &= \text{rate of new attacks - beetles killed or pitched out by tree defenses} \\ &= \frac{A_n}{\Delta t} - \beta r_3 q_n r_n. \end{aligned}$$

In the last equation I assume that A_n and r_n are constant at a given time step. For Δt we can use one time step, $n-1$ to n , which corresponds to an initial condition for q_n given by q_{n-1} . The solution for the differential equation of \dot{q}_n is

$$q_n = \frac{A_n}{\beta r_3 r_n \Delta t} [1 - \exp(-\beta r_3 r_n \Delta t)] + q_{n-1} \exp(-\beta r_3 r_n \Delta t).$$

With this stepwise model I use the number of attack holes currently in a tree and estimate the number of nesting beetles at the previous time step.

2.5.2 Fitting Techniques

The goal is to fit the model prediction,

$$\{q_n, \ln(I(q_n))\},$$

to the data.

$$\left\{ q_n, \ln \left(\frac{A_n r_n}{r_1 r_n} \right) \right\},$$

by choosing values for A_0 , ν and c , which are embedded in I . I use a least-squares regression method to fit model predictions to the observed data. Specifically, I used *Mathematica's* `NonlinearRegress` routine [59] which performs their LevenbergMarquardt method, gradually shifting the search from steepest descent to quadratic minimization.

Instead of creating one large set from the observed data and fitting the model to every tree simultaneously I dealt with one tree at a time and repeated the fitting procedure several times. This was necessary since the apparent background density of MPB (related to c) could potentially be different for each tree. In addition, separate fitting procedures, to some extent, provides independent validation of the model – if the shape parameters change radically from tree to tree it would suggest that the model is invalid. Since the parameter estimates agree reasonably well, it lends validation to the model.

Chapter 3

Results

3.1 Estimation of A_0 , ν and c by Non-linear Regression

Tables 3.1, 3.2 and 3.3 provide a summary of the results of the fitting procedure applied to successfully attacked trees and the average values for A_0 , ν , and c . For simplicity, in these results I have chosen $\sigma = 0.5$ (Section 2.3.4) for all plots, meaning that all plots are half way between completely open and completely closed. The correlation coefficient of the fit, r^2 , is a measure of how good the fit is; $r^2 = 1$ means the function predicts the data perfectly. The correlation coefficient describes the fit of all three parameters simultaneously, not a partial correlation of each parameter individually.

Although years 1996 and 1997 have lower correlation coefficients than 1995, the estimates from these years remain in the neighborhood of the 1995 estimates. The most extreme estimated values for A_0 and ν differ by a factor of about ten, with most estimates being much more consistent. The estimates for c vary by four orders of magnitude. More variation is expected in c since it is related to background emergence of beetles, which will vary from site to site.

Figures 3.1 and 3.2 show how well the fitting procedure matches the step-wise model predictions. The dotted lines represent model predictions with the current number of attacking beetles on the x-axis and the predicted number of new attacks at the next time step on the y-axis. The solid lines show model predictions using fitted values of A_0 , ν and c . Figure 3.1 represents the same attack series shown in Figure 2.2. The model captures system behavior very nicely, with $r^2 = 0.92$. Figure 3.2 is based upon the attack series seen in Figure 2.3. In this case the model does a poor job of capturing system behavior.

1995 Fitted Parameter Estimates				
Tree	A_0	ν	c	r^2
1	2.5	14.0	455	0.41
2	7.8	4.6	637	0.75
3	4.1	10.2	95	0.55
4	5.4	5.7	821	0.71
5	7.7	4.7	999	0.91
6	3.6	9.0	2238	0.50
7	4.0	8.3	1929	0.92
8	3.7	7.8	636	0.86
Average	4.8	8.0	976	0.70

Table 3.1: Parameter estimates using 1995 data.

1996 Fitted Parameter Estimates				
Tree	A_0	ν	c	r^2
1	2.7	11.2	600	0.35
2	2.0	14.8	162	0.31
3	2.1	10.3	910	0.31
4	5.3	5.4	312	0.37
5	3.6	4.5	1962	0.41
6	4.1	7.0	904	0.66
Average	3.3	8.9	808	0.40

Table 3.2: Parameter estimates using 1996 data.

1997 Fitted Parameter Estimates				
Tree	A_0	ν	c	r^2
1	6.9	5.0	1651	0.22
2	3.8	4.1	1500	0.02
3	5.0	7.9	2.8	0.07
4	4.7	8.6	1769	0.51
5	3.3	8.7	892	0.42
6	3.6	7.1	2089	0.25
7	9.7	2.8	5109	0.21
8	11.4	3.1	98	0.08
9	7.9	3.2	2248	0.20
10	8.7	3.2	2412	0.90
11	8.1	3.0	2056	0.25
12	10.7	2.5	1950	0.25
13	6.0	3.2	4253	0.39
14	3.1	5.2	2410	0.21
15	6.5	3.3	11401	0.09
16	3.0	11.0	1050	0.48
17	5.9	3.2	3825	0.25
18	10.6	3.9	0.9	0.02
19	3.5	10.3	75	0.86
20	7.6	3.3	5023	0.19
21	20.9	1.3	2523	0.44
22	21.2	1.2	4795	0.24
Average	7.8	4.8	2597	0.30

Table 3.3: Parameter estimates using 1997 data.

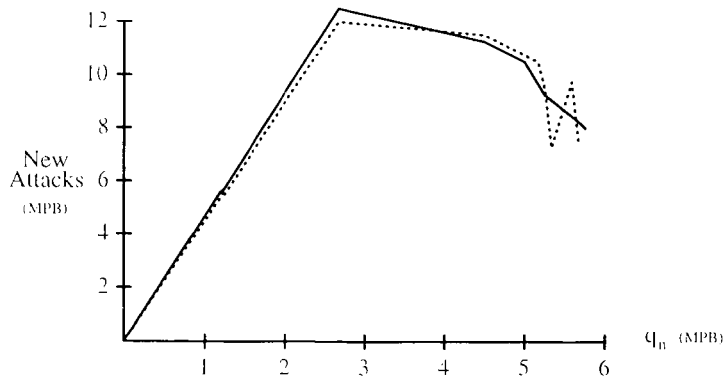


Figure 3.1: Stepwise model prediction (dotted) and model prediction (solid) using fitted parameter values. Tree number 7 from the 1995 data.

3.2 Difficulties of the Model and the Fitting Procedure

The results of our parameter estimation procedures are encouraging. We have obtained reasonable and consistent estimates for A_0 , ν and c . Although these estimates give confidence in the modeling effort, there are some difficult points worth considering.

One difficulty occurred when the stepwise model occasionally predicted negative values for the current resin capacity of a tree and the number of beetles expected to infest a tree. To compensate for this problem I used the second branch of the adiabatic solution set for r , $r = 0$, from

$$r = \max \left[r_0 - \frac{r_3}{r_2} h, 0 \right].$$

Also, difficulties with the 1996 and 1997 data point to a shortcoming of the model. As with many insects and plants, MPB and tree activity are closely tied to temperature. Optimal temperatures produce the greatest beetle and tree activity. Colder or warmer temperatures lead to lower rates of activity, not necessarily to the same degree in MPB and a host tree. The model has no mechanisms to account for this temperature dependence. This means that it is assumed the temperature remains reasonably constant from one day to the next and that temperatures are always conducive to full beetle and tree activity. This assumption worked well in the 1995 experiments. However, during the collection of the 1996 and 1997 data, temperatures fluctuated widely and often became

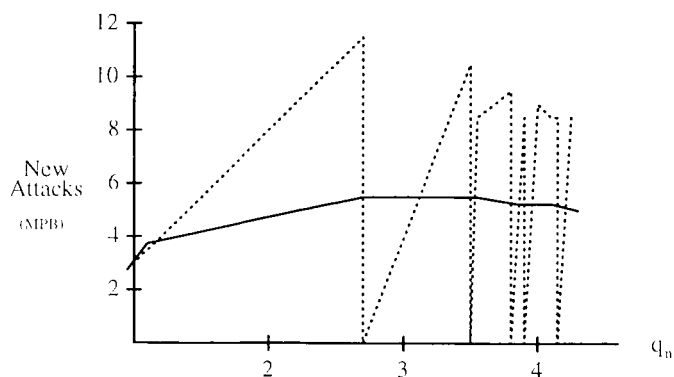


Figure 3.2: Stepwise model prediction (dotted) and model prediction (solid) using fitted parameter values. Tree number 2 from the 1997 data.

very cold. This would, essentially, reduce or eliminate the true number of hours in a day available for activity. In the data, this is seen as a day with fewer attacks being observed. Five flight hours are still counted as having passed. Inspection of the St. Charles data reveals several suspicious drops in beetle activity. This messiness may be due, in part, to lower temperatures. The fitting procedure was able to converge upon physically real parameter estimates for only a few of the trees' data series. Unfortunately, temperature data for our sites is not available.

In an effort to compensate, at least in part, for the temperature fluctuations I attempted to identify and remove data points that were likely collected on days when beetle activity was less than optimal. This did not improve the fit. Without records of daily temperatures it is difficult to guess which *low-activity* days are due to low temperature and which are due to other causes. Also, a low-activity data point should not necessarily be eliminated from the data series. Logically, it should be viewed as a fraction of the optimal activity and merely needs to be weighted differently. However, in such an effort, determining how much to increase or weight any given data point would be difficult. Because of the difficulty and ineffectiveness of these attempts, I have left the data unmodified.

To include temperature terms in the model is possible. However, it would necessitate the introduction of many new parameters and increase the complexity of the fitting procedures and other modeling efforts. Since temperature changes do not affect tree and beetle activity to the same degree separate parameters would have to be included for both. Keeping in view that, for now, a simpler, less accurate model may be much more useful than a complex, precise model,

temperature dependence may be saved for a later version.

3.3 Dimensional Analysis: The Buckingham Pi Theorem

A dimensional analysis of the model can provide an important understanding of what exactly the fitting procedure is accomplishing. Making use of the Buckingham Pi theorem, [60] which states that if there is a physical law that gives a relation among a certain number of physical quantities, then there is an equivalent law that can be expressed as a relation among certain dimensionless quantities, π_1, π_2, \dots , hence the name. In the Powell *et al.* model we see that there are at least two non-dimensional combinations. From equation (2.7),

$$\pi_1 = \frac{\nu}{\mu} A_0$$

and

$$\pi_2 = \frac{a_1 q}{A_0 (A b_1 + w \delta_1)}.$$

In the fitting procedure I chose values for most parameters and fit for A_0 , ν and c . In reality, the procedure fits for the non-dimensional combinations involving these three parameters. By assigning values for a_1 , b_1 , δ_1 , μ and w , we obtain values for A_0 , ν and c . So we can see how changes in any of the parameters affect the values of the others. For example, if $\frac{\nu}{\mu} A_0$ equals a constant then as you increase ν , μ must increase proportionally to maintain the equality. This is true of both π_1 and π_2 .

Knowing that it is π_1 and π_2 which were fit for saves time and work. For example, if further experiments were to give a better estimate of b_1 , I would not need to re-estimate the value of A_0 , I could simply need to adjust it in such a way as to keep the value of π_2 the same.

3.4 Sensitivity Analysis

Our confidence in the values used for model parameters varies. Some parameters are more easily and reliably estimated from previous research, literature and knowledge of the systems involved. Other parameters' estimates, however, are less reliable. It will be helpful to know how sensitive the fitting procedure is to model parameters. If variation in parameters causes large changes in the estimates of A_0 , ν and c , the confidence in the fitted parameter values can only be as strong as the confidence in the estimated parameter values. However, if the estimates of A_0 , ν and c are resistant to change due to variation in the other parameters this may suggest that either the fitting procedure does not depend heavily on these parameters or that the fitted values are good estimates and not easily affected by incorrect parameter choices.

Sensitivity Analysis Summary		
Parameter	Perturbation (%)	r^2 Response (%)
β	+10	+0.07
β	-10	-0.07
r_2	+10	-0.26
r_2	-10	-1.73
r_3	+10	-1.88
r_3	-10	-0.49
σ	+200 (to 1)	< +0.001
σ	-98 (to 0.01)	-61.40

Table 3.4: Sensitivity of fitting procedure to small variations in parameter values.

In order to determine how sensitive the fitting procedure is to the choices of estimated parameter values, I performed a simple sensitivity analysis by increasing and decreasing values by, usually, ten percent. To measure the response of the model I tracked the correlation coefficient, r^2 , of the fitted parameters. During my work with the model it has been apparent that some parameters are more influential than others. I have chosen to investigate four of the most influential: β , r_2 , r_3 and σ . Table 3.4 shows varied parameters, the perturbations and the response of the model.

These are interesting results. It appears that the model is fairly insensitive to β , the parameter describing mortality rate of beetles to a tree's resin defenses. The parameters r_2 and r_3 have more of an influence, but mainly with perturbations in certain directions. With a decrease in r_2 or an increase in r_3 there seems to more of an effect than with an increase or decrease, respectively. To understand this we recall (2.16). The fraction r_3/r_2 increases with a drop in r_2 or an increase in r_3 . This suggests that the model is sensitive to the value of the fraction rather than the individual values of r_2 or r_3 , which appear separately in other places in the model.

By performing similar analysis with the other parameters I found that the fitting procedure is most sensitive to r_3/r_2 . This is an interesting point and may reveal something important about the assumptions I have made to obtain these estimates. In Section 2.3.9 I assume that it requires about two hundred beetles to deplete the resin capacity of a healthy tree. Since changes in this number make the model much less able to predict system behavior it suggests that this is a critical assumption. Also, this suggests that there is a specific number of attacks which overcome a tree's defenses and that this is less than the number of beetles that can nest in a tree before it is maximally colonized.

The parameter σ also has an interesting effect. An increase to $\sigma = 1$ only

increases r^2 slightly, while a decrease to $\sigma = 0.01$ (describing a completely closed stand of trees) lowers the r^2 value substantially. With σ near zero, b_1 would be very large, corresponding to a fast diffusion rate of beetle pheromones and δ_1 would be very small, corresponding to a low loss rate of pheromone molecules out of the canopy. This suggests that the dynamics of the system may be very different depending on whether a forest is open or closed.

From these results and similar analysis of the other parameters, we see that the model is robust in relation to most parameters. However, small changes in a few parameters greatly decreases the accuracy of the fitting procedure.

3.5 Directions for Continued Work

With a good understanding of which parameters are the most influential and important to estimate very accurately, experiments aimed at obtaining more precise estimates can be planned. Also, experiments to overcome some of the apparent shortcomings of the model will help refine the model. These may include experiments to track background emergence of beetles, which would give better estimates of c and might additionally be used as an indicator of temperature effects on beetle activity. Other experiments may focus on beetle activity once they have arrived in an attacked area or have landed on an attacked tree.

In addition to new experimental design, the inclusion of temperature or weather influences in the model is likely to enable the model to match system behavior much more closely. These environmental factors affect system behavior in many ways, two of the most important being MPB development and emergence and tree health.

Chapter 4

Conclusion

In an effort to better understand and describe the behavior of the MPB/Host Tree system a global model that mimics the complex spatial dynamics of MPB movement was created. Finding the global model difficult to parametrize and work with, a local projection which allowed the use of observational data to make estimates of three of the parameters was made. Using a least-squares fitting method I estimated values for A_0 , ν and c by fitting model predictions based on the infestation function to analogous predictions based on observational numbers.

The localization can be considered analogous to system behavior at a single tree. Using empirical data of numbers of MPB attacks on a single tree I have compared true system behavior with behavior predicted by the local model. Leaving three model parameters free, I used a least-squares fitting procedure to make estimates of their values. Repeating this procedure with data collected from many trees allowed me to compare and average many estimated values.

The parameter values obtained using the local projection model can be applied to the global model. The global model now more accurately describes and predicts system behavior on a forest-sized scale. Although the results suggest parameter estimates to be reasonably reliable, continued research is necessary to obtain a better understanding and, ultimately, control of the MPB/pine tree host system. Such continued work may include new experimental designs and model modifications which focus on current shortcomings.

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