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Dynamics of a single species natural forest in the presence of a disease

Peter J. McCauley

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DYNAMICS OF A SINGLE SPECIES
NATURAL FOREST
IN THE PRESENCE OF A DISEASE

By

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Dynamics of a single species natural forest in the presence of a disease

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Forests are very dynamic, yet they can exhibit behavior in predictable patterns. When an infectious agent is introduced in a forest site these patterns are typically affected and the evolutionary course of the site is altered. We seek to explore these events and how the forest adjusts.

In this paper we develop a mathematical model to characterize these patterns and effects of disease on a forest site. The model is developed for a natural forest (i.e. no artificial planting of trees and/or harvesting/thinning) with a single species of tree and a single pathogenic component. The model consists of a set of integro-differential equations. Under certain assumptions we reduce it to a corresponding set of ordinary differential equations.

A perturbation in the forest system may evolve into a steady state or lead to oscillatory behavior. With a better understanding of these events, forest management decisions can be more effective at realizing a healthy and productive forest system.
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Chapter 1

Introduction

The dynamics of a forest are dependent on the available resources within the site, whereas the health of a forest is due to the success of seeds to sprout into a new generation of trees. Resources, such as water, minerals and sunlight are necessary for the survival of a tree, and are continually being consumed by adult trees. Though a forest site may have plenty of resources to support already existing adult tree growth, it may not have enough open space for seedlings to grow. Open space is necessary for seedlings to sprout and is created when adult trees die. A forest site may, as well, have an over abundance of open space caused by fire, wind or some other natural event. These sites generally seek equilibrium through growth, mortality and the introduction of new seedlings. A forest site is in equilibrium when it has a steady state age distribution of trees and seedlings. When growth exceeds mortality a forest can become saturated with adult trees for extended periods. Over time this can lead to large oscillations in tree count and forest volume.

With the introduction of disease in the forest site, yet another dynamic is created. As trees age, they may become infected with disease. This process, can result in an infected tree dying rapidly, leaving more available space for seedlings. Infected trees may, as well, have stunted growth and linger on for years fighting the disease they carry, while spreading it to the remaining uninfected forest. Though disease is generally considered to be undesirable for a forest, it is an effective tool to control over-growth or saturation of a forest site, and it plays an important role for rehabilitation of forest systems.

For this paper we will consider a forest of one tree species and one type of disease. We only address a "natural" forest in which no artificial planting of trees and no harvesting/thinning takes place. The trees will be randomly distributed throughout the site, leaving any open space evenly spread across the remaining area. Competition for this space will take place between trees and seedlings and will depend on the tree species and type of disease. Space may be a measure of canopy size, average tree height, or total basal area and is considered to be proportional to
resources consumed by the forest. An initial distribution of diseased trees will be introduced in the originally healthy system. The system, after this disturbance of disease, will seek regrowth through the introduction of new uninfected seedlings. We are interested in the response of the system to these disturbances (steady state or oscillatory). We will consider in this paper a mathematical model that describes these phenomena.
Chapter 2

Infectious diseases in a forest

In this section we discuss the major components of tree pathology and how they will be used to model an infected forest.

Trees undergo many types of stress during their adult life. From abiotic forms such as pollution and mineral deficiencies to biotic, such as viruses, mammals and insects. It is very natural to expect that a tree undergoes stress from multiple sources at the same time. It is also found that the interaction of different forms of stress affect how others manifest themselves [4]. We are interested in modeling a forest that has a single disturbance by a single biotic agent.

An infectious disease is defined as a biotic pathogen that establishes a food relationship with the host. The life cycle of a disease can be described by a sequence of events. The first event of the cycle is the transfer of a pathogen to a portal of entry in a host tree. The portal could be cracks in the outer bark, buds or any other wounds that create an opening in the surface layer of the tree. The time required for a specific disease to pass through a portal, is called the infection period. Once the inoculum enters the trees vascular system, the tree will generally show symptoms of disease. The time for these symptoms to occur, is referred to as the incubation period. For the disease to spread, the pathogen must produce inoculum and leave the host via a portal of exit. This is the latent period. Propagules are formed and the disease can then be transported by a variety of methods (such as wind, water, birds or insects) to infect other hosts.

The success of the pathogen to infect the forest is related to pathogen virulence, a favorable environment, and host susceptibility [1]. In general, a pathogen that interacts with the host for an extended period of time infects more tissue and spreads more disease.
Figure 2.0.1: This figure shows a relationship between the three general requirements for disease to successfully propagate in a forest.

Figure 2.0.1 shows a simple relationship between these three components known as the disease triangle. The area inside the triangle is related to the amount of disease in the forest, while the length of any one side is related to the contribution of that component. From this representation we see that when any one of the components is decreased to zero the disease disappears.

As the infected tree passes through the incubation period it begins to show signs of infection. These symptoms can be divided into three main categories: necrotic, hypoplastic and hyperplastic [8]. Necrotic symptoms result in complete cessation of function and most often leads to an accelerated death. Hypoplastic is an underdevelopment of function and in adult trees can remain active for many years without killing the tree. Hyperplastic symptoms are an acceleration of function.

After this brief summary of the major components of tree pathology we will formulate a mathematical model that represents a diseased forest.
Chapter 3

Integro-Partial Differential Equations model

In this chapter, we derive a set of integro-differential equations that models a diseased forest. The equations will describe the time-age dynamics of uninfected and infected trees in the forest, as well as, seedlings.

3.1 Integro-Partial Differential Equations (IPDE) formulation

In this section we state the assumptions and formulate the mathematical model. We consider for this model a forest site with one tree species, one disease and enough nutrients to support a forest with maximum coverage. We make assumptions as follows:

- The disease has a food source relationship with the host tree.
- The host tree is always susceptible to infection by the disease.
- Diseased trees can infect only during their life span.
- As an infected tree ages and subsequently dies, it will no longer carry disease. In this way, when all of the diseased trees have died, the disease has also been removed from the system.
- The environment is always favorable for pathogen growth.
- The method of transport of propagules to infect other hosts is random across the current age distribution of trees in the forest site.
- A forest site will have a minimum number of seedlings present at all times.
- Trees always have enough nutrients to continue growth.
Some other assumptions, such as on the character of resource consumption by the trees, will be added as particular model equations are introduced.

With these assumptions, we can formulate a specific model that describes the dynamics of such a forest. For this model we will consider the characteristic time domain,

\[ 0 \leq t \leq T, \quad (3.1.1) \]

and age distribution of trees in the following range:

\[ 0 \leq a \leq a_{max}. \quad (3.1.2) \]

We introduce the differentiable functions \( U(t,a) \) and \( W(t,a) \), measured in trees per unit age, that represent the age density of uninfected and infected trees in the forest site at the instant of time \( t \), respectively. In this way, for example, the total number of uninfected trees in the forest site between ages \( a_1 \) and \( a_2 \) is found by \( \int_{a_1}^{a_2} U(t,a) \, da \).

For this model we consider two distinct ways a tree can die out of the forest. One way corresponds to natural or non-infectious single events. These may include lighting strike, flood or deterioration due to a natural aging process. All these decay processes are characterized by a death rate constant \( \mu \). We may consider this to be a natural thinning process, which is responsible for a non-diseased forest site having few older trees. The other way corresponds to trees removed by infectious disease, with characteristic death rate constant \( \gamma \). Uninfected trees can become infected by disease at a rate proportional to the volume \( V_w(t) \) of infected trees, that establishes the amount of disease in the forest. We use the Law of Mass Action, where the rate of change of the uninfected and infected trees in the forest is considered to be proportional to the number of trees in the forest. The dynamics of a forest with disease can be generalized by the "reaction" equations:

\[
\begin{align*}
U & \xrightarrow{\mu} \text{die} \\
U & \xrightarrow{\beta V_w} W \\
W & \xrightarrow{\gamma} \text{die}
\end{align*}
\]

The proportionality constant \( \beta \) may represent the susceptibility of the host to disease or the virulence of the pathogen, where an increase in \( \beta \) suggests a more favorable condition for disease propagation. Once a tree is infected it dies at the rate proportional to \( \gamma \), corresponding to the specific manifestation of symptoms caused by a disease. Symptoms that are necrotic in nature correspond to a greater \( \gamma \) compared to those that are hypoplastic. As trees die and space in
the forest becomes available, new seedlings $S(t)$ are introduced. These seedlings have ample nutrients to survive and their number is dependent on the available space in the forest $K(V(t))$, which we introduce as the seedling carrying capacity. A mathematical model describing these dynamics can be written as a system of integro-partial differential equations,

$$\frac{\partial U(t,a)}{\partial t} + \frac{\partial U(t,a)}{\partial a} = -\mu U(t,a) - \beta V_w(t)U(t,a), \quad (3.1.4)$$

$$\frac{\partial W(t,a)}{\partial t} + \frac{\partial W(t,a)}{\partial a} = -\gamma W(t,a) + \beta V_w(t)U(t,a), \quad (3.1.5)$$

with initial conditions,

$$\int_0^{a_{\text{max}}} U(t,a)\delta(a)\,da = U(t,0) = S(t), \quad (3.1.6)$$

$$U(0,a) = \Phi(a), \quad (3.1.7)$$

$$W(t,0) = 0, \quad (3.1.8)$$

$$W(0,a) = \Psi(a). \quad (3.1.9)$$

Functions $\Phi(a)$ and $\Psi(a)$ describe the initial age distribution of uninfected and infected trees in the forest, respectively. In (3.1.6) the Dirac delta function is used to describe the seedling function $S(t)$ which represents the total seedling count at time $t$. In (3.1.4) and (3.1.5), the function $V_w(t)$ represents the size of the infected forest as a function of time. We also introduce $V_u(t)$, the size of the uninfected forest as a function of time. They are obtained via integration over all tree ages in the forest and take the form,

$$V_u(t) = \int_0^{a_{\text{max}}} U(t,a)B_u(a)\,da, \quad (3.1.10)$$

$$V_w(t) = \int_0^{a_{\text{max}}} W(t,a)B_w(a)\,da. \quad (3.1.11)$$

In equations (3.1.10) and (3.1.11), $B_u(a)$ and $B_w(a)$, are continuous functions, suitably defined to represent the amount of resources an infected or uninfected tree of age $a$, respectively, consumes. The quantity $V_w(t)$, since it can be interpreted as the physical space taken by a tree in the site, also characterizes the total amount of disease present in the forest at time $t$. Because a seedling consumes virtually no resources in the forest, we let

$$B_u(0) = B_w(0) = 0. \quad (3.1.12)$$

Let us introduce the function $V(t)$:
\[ V(t) = V_u(t) + V_w(t). \] (3.1.13)

The function \( V(t) \) is directly proportional to the total resources consumed by the trees in the forest site at time \( t \). This quantity may be associated either with canopy size, or tree height, or total tree basal area. At time \( t = 0 \), the resources consumed by the forest are defined as

\[
V_u(0) = \int_0^{a_{\text{max}}} U(0, a) B_u(a) \, da = \int_0^{a_{\text{max}}} \Phi(a) B_u(a) \, da = V_u^0,
\] (3.1.14)

\[
V_w(0) = \int_0^{a_{\text{max}}} W(0, a) B_w(a) \, da = \int_0^{a_{\text{max}}} \Psi(a) B_w(a) \, da = V_w^0.
\] (3.1.15)

To model the seedling population, we use a logistic equation with time dependent seedling carrying capacity \( K(V(t)) \):

\[
\frac{dS(t)}{dt} = \sigma S(t) \left( 1 - \frac{S(t)}{K(V(t))} \right),
\] (3.1.16)

The parameter \( \sigma \) is the seedling reestablishment rate and initial conditions for (3.1.16) are

\[ S(0) = U(0, 0) = \Phi(0) = S^0 \] (3.1.17)

The seedling carrying capacity \( K(V(t)) \) is represented by

\[ K(V(t)) = \max(S_{\text{min}}, S_{\text{max}} - \lambda V(t)), \] (3.1.18)

with initial value,

\[ K(V(0)) = \max(S_{\text{min}}, S_{\text{max}} - \lambda V(0)) = K^0. \] (3.1.19)

The maximum seedling carrying capacity of the forest occurs when there are no adult trees in the forest:

\[ K(0) = S_{\text{max}}. \] (3.1.20)

The value \( 0 < S_{\text{min}} \ll S_{\text{max}} \), represents a minimum number of seedlings in the forest site at any time \( t \) (background seedling "noise"). From (3.1.18) we determine a critical value of the forest volume exists for which
When the forest reaches this particular volume, the seedling carrying capacity of the forest $K = S_{\text{min}}$. Recall, that we have assumed, that even in a forest site completely filled with adult trees, a few seedlings will be able to grow. The value $S_{\text{max}}$ is the maximum seedling count that could survive on a site with no adult trees. The parameter $\lambda$ (measured in units of trees per unit volume) reflects the extent of competition between seedlings and adult trees for available space. An increase in $\lambda$ coincides with a forest where adult trees successfully compete for a larger portion of the remaining resources. This will decrease the seedling count at time $t$. A forest with total volume greater than the critical volume (3.1.21) will have the seedling carrying capacity equal to $S_{\text{min}}$. This situation arises when a forest becomes saturated with adult trees. Seedling count will be reduced to this minimum value until the forest volume returns to a state with the volume that is below the critical forest volume. When this occurs seedling count will slowly increase filling the open space with trees. The slow reestablishment of seedlings from this minimum state occurs because seedlings are more vulnerable when they are few in numbers, where a large percentage are easily killed by animals, wind or heavy rain. As there numbers increase the ability for new seedlings to sprout is affected more by competition with adult trees for resources.

### 3.2 Rescaled model

In this section we define units of nonrescaled variables from the previous section, introduce rescaled variables and derive a new form of equations (3.1.4) - (3.1.21). Primary quantities used are time (T) with units in years, length (L) with units in feet, and trees (M). We define units of unrescaled variables as follows.

\[ [t] = T, \quad [a] = T, \quad (3.2.1) \]

\[ [U] = MT^{-1}, \quad [W] = MT^{-1}, \quad (3.2.2) \]

\[ [\mu] = T^{-1}, \quad [\gamma] = T^{-1}. \quad (3.2.3) \]

\[ [V] = [V_u] = [V_w] = L^2, \quad [B_u] = [B_w] = L^2 M^{-1}, \quad (3.2.4) \]

\[ [S] = M, \quad [\Phi] = MT^{-1}, \quad [\Psi] = MT^{-1}, \quad [K] = M. \quad (3.2.5) \]
\[ [\beta] = L^{-2} T^{-1}, \quad [\sigma] = T^{-1}, \quad [\lambda] = ML^{-2}, \]  

(3.2.6)

In the formulations above we have chosen \( L^2 \) as a measure of forest volume as it relates to tree basal area. Rescaling is performed using characteristic time and age:

\[ \theta = \mu t, \quad \alpha = \mu \tau. \]  

(3.2.7)

Remaining variables are rescaled as follows.

\[ u(\theta, \alpha) = \frac{U(\frac{\theta}{\mu}, \frac{\alpha}{\mu})}{\mu S_{\text{max}}}, \quad w(\theta, \alpha) = \frac{W(\frac{\theta}{\mu}, \frac{\alpha}{\mu})}{\mu S_{\text{max}}}. \]  

(3.2.8)

\[ s(\theta) = \frac{S(\frac{\theta}{\mu})}{S_{\text{max}}}, \quad s_{\text{min}} = \frac{S_{\text{min}}}{S_{\text{max}}}. \]  

(3.2.9)

\[ b_u(\alpha) = \frac{B_u(\frac{\alpha}{\mu})}{B_{\text{max}}}, \quad b_w(\alpha) = \frac{B_w(\frac{\alpha}{\mu})}{B_{\text{max}}}. \]  

(3.2.10)

\[ \psi(\alpha) = \frac{\Psi(\frac{\alpha}{\mu})}{\mu S_{\text{max}}}, \quad \phi(\alpha) = \frac{\Phi(\frac{\alpha}{\mu})}{\mu S_{\text{max}}}. \]  

(3.2.11)

\[ \nu_u(\theta) = \frac{V_u(\frac{\theta}{\mu})}{S_{\text{max}} B_{\text{max}}}, \quad \nu_w(\theta) = \frac{V_w(\frac{\theta}{\mu})}{S_{\text{max}} B_{\text{max}}}, \quad \nu(\theta) = \frac{V(\frac{\theta}{\mu})}{S_{\text{max}} B_{\text{max}}}. \]  

(3.2.12)

\[ k(\nu(\theta)) = \frac{K(\frac{V(\frac{\theta}{\mu})}{S_{\text{max}}})}{S_{\text{max}}} = \max(s_{\text{min}}, 1 - \lambda B_{\text{max}} \nu(\theta)). \]  

(3.2.13)

The quantity \( B_{\text{max}} \) represents the maximum resources used by a tree in the forest site and is equal to the maximum value of the functions \( B_u(\alpha) \) and \( B_w(\alpha) \) for \( \alpha \in [0, \alpha_{\text{max}}] \). Substituting (3.2.7) - (3.2.13) into equations (3.1.4) - (3.1.21) and introducing the parameters \( \rho \) and \( \eta \), where \( \rho \) has units \( [\rho] = T^{-1} \) and \( \eta \) is dimensionless:

\[ \rho = \beta S_{\text{max}} B_{\text{max}}, \quad \eta = \lambda B_{\text{max}}. \]  

(3.2.14)

we arrive at the rescaled set of equations

\[ \frac{\partial u(\theta, \alpha)}{\partial \theta} + \frac{\partial u(\theta, \alpha)}{\partial \alpha} = -u(\theta, \alpha) - \frac{\rho}{\mu} \nu_w(\theta) u(\theta, \alpha). \]  

(3.2.15)

\[ \frac{\partial w(\theta, \alpha)}{\partial \theta} + \frac{\partial w(\theta, \alpha)}{\partial \alpha} = -\frac{\gamma}{\mu} w(\theta, \alpha) + \frac{\rho}{\mu} \nu_w(\theta) u(\theta, \alpha). \]  

(3.2.16)

10
with rescaled initial conditions:

\[
\int_0^{\mu_{\text{max}}} u(\theta, \alpha) \delta(\alpha) d\alpha = u(\theta, 0) = s(\theta),
\]
\[
u(0, \alpha) = \phi(\alpha),
\]
\[
w(\theta, 0) = 0,
\]
\[
w(0, \alpha) = \psi(\alpha).
\]

The total forest volume is rescaled:

\[
v(\theta) = v_u(\theta) + v_w(\theta),
\]

where,

\[
v_u(\theta) = \int_0^{\mu_{\text{max}}} u(\theta, \alpha) b_u(\alpha) d\alpha,
\]
\[
v_w(\theta) = \int_0^{\mu_{\text{max}}} w(\theta, \alpha) b_w(\alpha) d\alpha,
\]

with initial values,

\[
b_u(0) = b_w(0) = 0,
\]
\[
v_u(0) = \int_0^{\mu_{\text{max}}} \psi(\alpha) b_u(\alpha) d\alpha = v_u^0,
\]
\[
v_w(0) = \int_0^{\mu_{\text{max}}} \phi(\alpha) b_w(\alpha) d\alpha = v_w^0.
\]

The seedling carrying capacity becomes

\[
k(v(\theta)) = \max(s_{\text{min}}, 1 - \eta v(\theta)),
\]

with initial value that satisfies

\[
k(0) = \max(s_{\text{min}}, 1 - \eta v(0)) = k^0,
\]

where \(k^0\) is the initial seedling carrying capacity, and

\[
k(0) = 1.
\]

Here \(k(0)\) is the maximum seedling carrying capacity of the forest rescaled to unity, and \(0 < s_{\text{min}} \ll 1\) is the rescaled minimum seedling count. The rescaled critical forest volume is,
\[ v(\theta) = \frac{1 - s_{min}}{\eta} \approx \frac{1}{\eta} \]  

(3.2.30)

The rescaled seedling equation (3.1.16) with substitution from (3.2.27) and using (3.2.21) becomes,

\[ \frac{ds(\theta)}{d\theta} = \frac{\sigma s(\theta)}{\mu} \left( 1 - \frac{s(\theta)}{\max(s_{min}, 1 - \eta(v_w(\theta) + v_a(\theta)))} \right), \]  

(3.2.31)

with initial conditions

\[ s(0) = u(0, 0) = \phi(0) = s^0. \]  

(3.2.32)

The non-dimensionalized statement of the problem consists of equations (3.2.15), (3.2.16), (3.2.22), (3.2.23) and (3.2.31), with conditions (3.2.17)-(3.2.20), (3.2.25), (3.2.26), and (3.2.32). We now introduce a numerical method to approximate the solution.

### 3.3 Examples of the IPDE system

In this section we present results of numerical computations (based on the algorithm introduced in the Appendix A.1) for two particular examples of the IPDE model.

#### 3.3.1 Example 1 (linear resource consumption, low initial forest volume and tree count, with few infected trees)

In this example we consider a forest site with linear resource consumption, low initial forest volume and tree count. There are infected trees in this site. Figures 3.3.1-3.3.6 show the behavior of the site, while a discussion of the results follows at the end of this section. We list the parameters and initial values below, and along the right hand side of each Figure.
Domain:
\[ \theta \in [0, 7] \]  
\[ \alpha \in [0, 7] \]  
Initial Values:
\[ u(0, \alpha) = 0.05 \exp(-3\alpha) \] (initial uninfected trees)  
\[ w(0, \alpha) = 0.05\alpha \exp(-4\alpha) \] (initial infected trees)  
\[ s(0) = u(0, 0) \] (initial seedling count)  
Resource Consumption:
\[ b_u(\alpha) = 0.1\alpha \] (size of uninfected trees of age \( \alpha \))  
\[ b_w(\alpha) = 0.05\alpha \] (size of infected trees of age \( \alpha \))  
Parameters:
\[ \mu = 0.05 \] (constant proportional to death rate of uninfected trees)  
\[ \gamma = 0.1 \] (constant proportional to death rate of infected trees)  
\[ \rho = 10 \] (pathogen virulence)  
\[ \eta = 10 \] (competition between seedlings and adult trees)  
\[ \sigma = 1 \] (constant proportional to seedling reestablishment) 

Figure 3.3.1: This plot shows the evolution of the total trees age distribution on the forest site. The site has very few infected trees at initial instant of time. The system tends to a steady state.
Figure 3.3.2: This plot shows the evolution of the infected trees age distribution. The parameters are the same as Figure in 3.3.1.

Figure 3.3.3: This plot shows the initial distribution of trees. Notice that there is only a small number of young trees that are infected at the initial instant of time.
Figure 3.3.4: This plot shows the evolution of the total volume of trees. The parameters are the same as Figure in 3.3.1.

Figure 3.3.5: This plot shows the evolution of the total number of trees and seedlings. The parameters are the same as Figure in 3.3.1.
The Example 1 site, whose behavior is shown in Figures 3.3.1-3.3.6, responds quickly to the large open space in the forest. At initial instant of time a small amplitude distribution of young infected trees is present on the site. Both uninfected and infected trees exhibit linear resource consumption, $b_u(\alpha) = .1\alpha$ and $b_v(\alpha) = .05\alpha$, respectively. In this case the pathogen virulence is $\rho = 10$. The death rate constants of infected and uninfected trees are, $\gamma = .1$ and $\mu = .05$, respectively. Though they are few in numbers at the initial time, the infected trees are successful at spreading their disease to other uninfected trees. The site evolves to a steady state, where a substantial part of the forest distribution is now infected with disease. This particular example will be revisited in Chapter 4 for further analysis.

Our next example will show the effect of increasing the values of parameters $\rho$ and $\eta$ on behavior of the system. This particular change will correspond to a highly infectious pathogen. Competition between seedlings and adult trees for resources will also be much higher. By increasing the competitiveness between trees and seedlings, we are describing a forest site where seedlings have a very difficult time sprouting even though there may be available space.

### 3.3.2 Example 2 (linear resource consumption, low initial forest volume and tree count, with few infected trees)

In this example we consider a forest site with linear resource consumption, low initial forest volume and tree count. Parameters and initial values are the same as in Example 1 except for
\( p = 40 \) and \( \eta = 80 \). Figures 3.3.7-3.3.12 show the behavior of the site while a discussion of the results follows at the end of this section.

Domain:
\[
\begin{align*}
\theta & \in [0, 15] \quad \text{(time)} \\
\alpha & \in [0, 7] \quad \text{(age)}
\end{align*}
\]

Initial Values:
\[
\begin{align*}
u(0, \alpha) &= 0.05 \exp(-3\alpha) \quad \text{(initial uninfected trees)} \\
w(0, \alpha) &= 0.05 \alpha \exp(-4\alpha) \quad \text{(initial infected trees)} \\
s(0) &= u(0, 0) \quad \text{(initial seedling count)}
\end{align*}
\]

Resource Consumption:
\[
\begin{align*}
b_u(\alpha) &= 0.1\alpha \quad \text{(size of uninfected trees of age} \ \alpha) \\
b_w(\alpha) &= .05\alpha \quad \text{(size of infected trees of age} \ \alpha)
\end{align*}
\]

Parameters:
\[
\begin{align*}
\mu &= .05 \quad \text{(constant proportional to death rate of uninfected trees)} \\
\gamma &= .1 \quad \text{(constant proportional to death rate of infected trees)} \\
p &= 40 \quad \text{(pathogen virulence)} \\
\eta &= 80 \quad \text{(competition between seedlings and adult trees)} \\
\sigma &= 1 \quad \text{(constant proportional to seedling reestablishment)}
\end{align*}
\]

The Example 2 site, where behavior is shown in Figures 3.3.7-3.3.12, is quite different compared to the site from Example 1. At the initial instant of time there is again a very small amplitude distribution of young infected trees in the site. However, in this case the pathogen virulence and competition for resources between trees and seedlings rates are significantly higher, \( p = 40 \) and \( \eta = 80 \), respectively. The infected trees are successful at spreading their disease to other uninfected trees, but in a much different way than before. As new seedlings are sprouted and the forest begins to age, the forest site quickly becomes saturated with adult trees. This results in a minimum carrying capacity \( S_{\text{min}} \) for the seedlings. The time interval corresponding to such is depicted in Figure 3.3.12; it is the interval between the points \( A \) and \( B \). Point \( B \) depicts the moment when the critical forest volume is reached, and the seedling count begins to increase.
Figure 3.3.7: This plot shows the evolution of the total trees age distribution on the forest site. The site, as Example 1, has very few infected trees at initial instant of time. The system exhibits oscillatory behavior.

Figure 3.3.8: This plot shows the evolution of the infected trees. The parameters are the same as Figure in 3.3.7.
Figure 3.3.9: This plot shows the initial distribution of trees. There are only a small number of young trees that are infected.

Figure 3.3.10: This plot shows the evolution of the total volume of trees. The parameters are the same as Figure in 3.3.7.
Figure 3.3.11: This plot shows the evolution of the total number of trees and seedlings. The parameters are the same as Figure in 3.3.7.

Since we use a very small minimum seedling carrying capacity, $s_{min} = 1e-008$, the seedling count will increase very slowly. The slow reestablishment of seedlings from $s_{min}$ may occur because of the vulnerability of seedlings when they are few in numbers and is clearly shown by
reference to the point B in Figures 3.3.12 and 3.3.11. Notice also on Figure 3.3.11, the timing of the oscillations, between the infected forest and the total tree count. The difference in phase shift of these two oscillations may be related to the incubation or latent period of the disease. The greater the phase shift the slower the disease spreads throughout the forest. This site has developed a well defined oscillating pattern, for both uninfected and infected trees, as well as for seedlings.

As can be seen from these two examples our system shows both steady state and oscillatory behavior. We will next derive a system of ordinary differential equations that represent our model under certain assumptions. We will be interested in further exploring the effect of introducing an infectious agent on a forest site and the response of that site.
Chapter 4

Ordinary Differential Equations model

In this section, under certain conditions, we derive a set of first order ordinary differential equations that represent the model. The equations will describe the total volume of uninfected and infected trees in the forest, the total number of uninfected and infected trees, as well as, seedlings. This new formulation will be defined in the re-scaled time domain $\theta \in [0, \mu T] \equiv [0, T^*]$.

4.1 Ordinary Differential Equations (ODE) formulation

Multiplying (3.2.15) and (3.2.16) by $b_u(\alpha)$ and $b_w(\alpha)$, respectively, and integrating over $\alpha$ from 0 to $\mu a_{max}$, we obtain,

\[
\int_0^{\mu a_{max}} \frac{\partial u(\theta, \alpha)}{\partial \alpha} b_u(\alpha) d\alpha + \int_0^{\mu a_{max}} \frac{\partial u(\theta, \alpha)}{\partial \alpha} b_u(\alpha) d\alpha =
- \int_0^{\mu a_{max}} u(\theta, \alpha) b_u(\alpha) d\alpha - \frac{p}{\mu} v(\theta) \int_0^{\mu a_{max}} u(\theta, \alpha) b_u(\alpha) d\alpha,
\]

\[
\int_0^{\mu a_{max}} \frac{\partial w(\theta, \alpha)}{\partial \alpha} b_w(\alpha) d\alpha + \int_0^{\mu a_{max}} \frac{\partial w(\theta, \alpha)}{\partial \alpha} b_w(\alpha) d\alpha =
- \frac{\gamma}{\mu} \int_0^{\mu a_{max}} w(\theta, \alpha) b_w(\alpha) d\alpha + \frac{p}{\mu} v(\theta) \int_0^{\mu a_{max}} u(\theta, \alpha) b_w(\alpha) d\alpha.
\]

Since in (4.1.1) and (4.1.2), $b_u(\alpha)$ and $b_w(\alpha)$ are functions of $\alpha$ only, we can take the $\frac{\partial}{\partial \alpha}$ out of the integral. We can also notice that the second term on the LHS of the above equations can be written as,

\[
\int_0^{\mu a_{max}} \frac{\partial u(\theta, \alpha)}{\partial \alpha} b_u(\alpha) d\alpha = - \int_0^{\mu a_{max}} u(\theta, \alpha) \frac{d b_u(\alpha)}{d\alpha} d\alpha
- \left. u(\theta, \alpha) b_u(\alpha) \right|_{\alpha = 0}^{\alpha = \mu a_{max}},
\]
As the forest ages some of the trees die, leaving fewer and fewer older trees. The number of older trees remaining at some maximum age is, thus, very small. Let us use the following approximations:

\[ u(\theta, \mu_{\text{max}}) \approx 0, \]  

\[ w(\theta, \mu_{\text{max}}) \approx 0. \]

From these and (3.2.24) it follows that the last terms on the RHS of both (4.1.3) and (4.1.4) will vanish. The functions \( b_u(\alpha) \) and \( b_w(\alpha) \) can have many different forms (see examples in Figure 4.1.1), depending on the species of tree and type of disease. This figure shows three types of resource consumption vs tree age. Linear growth, occurring when trees increase the use of resources linearly with age throughout their life. Early growth, when a species of tree exhibits higher rate of increase consumption at a relative early age with rate saturation at older age. Max-growth corresponds to a species of tree that tends to use less resources after it has reached some maximum. For our model we will consider a linear growth, where the change in the amount of resources a tree consumes is constant as it ages:

\[ \frac{db_u(\alpha)}{d\alpha} = \kappa_u, \]  

\[ \frac{db_w(\alpha)}{d\alpha} = \kappa_w. \]

We can easily solve these equations, with conditions (3.2.24), where \( b_u(0) = 0 \), and \( b_w(0) = 0 \):

\[ b_u(\alpha) = \kappa_u \alpha, \]  

\[ b_w(\alpha) = \kappa_w \alpha. \]

The relation between the consumption of resources between uninfected and infected trees is

\[ b_w(\alpha) = \frac{\kappa_w}{\kappa_u} b_u(\alpha). \]
Let us introduce the new time dependent variables for the total number of uninfected and infected trees in the forest, $\tilde{n}(\theta)$ and $\tilde{w}(\theta)$, respectively:

$$\tilde{n}(\theta) = \int_0^{\mu \alpha_{\text{max}}} u(\theta, \alpha) d\alpha,$$

$$\tilde{w}(\theta) = \int_0^{\mu \alpha_{\text{max}}} w(\theta, \alpha) d\alpha.$$  \hfill (4.1.12)

$$\tilde{n}(0) = \int_0^{\mu \alpha_{\text{max}}} u(0, \alpha) d\alpha = \int_0^{\mu \alpha_{\text{max}}} \phi(\alpha) d\alpha = \tilde{n}^0,$$

$$\tilde{w}(0) = \int_0^{\mu \alpha_{\text{max}}} w(0, \alpha) d\alpha = \int_0^{\mu \alpha_{\text{max}}} \psi(\alpha) d\alpha = \tilde{w}^0.$$  \hfill (4.1.13)

Using these new variables and previously obtained relations from (3.2.22), (3.2.23) and (4.1.11), we can simplify (4.1.1) and (4.1.2) to obtain equations that involve the time rate of change of the volume of uninfected and infected trees:
\[\frac{d\nu_r(\theta)}{d\theta} = \kappa_u \tilde{u}(\theta) - \nu_r(\theta) - \frac{\rho}{\mu} \nu_r(\theta) \nu_u(\theta), \quad (4.1.16)\]

\[\frac{d\nu_r(\theta)}{d\theta} = \kappa_r \tilde{v}(\theta) - \frac{\gamma}{\mu} \nu_r(\theta) + \frac{\rho}{\mu} \kappa_u \nu_r(\theta) \nu_u(\theta). \quad (4.1.17)\]

A similar process can be used to derive equations for the total number of healthy and infected trees in the forest, \(\tilde{u}(\theta)\) and \(\tilde{v}(\theta)\). Integrating the equations (3.2.15) and (3.2.16), with respect to \(\alpha\), we obtain,

\[\frac{d\tilde{u}(\theta)}{d\theta} = s(\theta) - \tilde{u}(\theta) - \frac{\rho}{\mu} \nu_r(\theta) \tilde{u}(\theta). \quad (4.1.18)\]

\[\frac{d\tilde{v}(\theta)}{d\theta} = -\frac{\gamma}{\mu} \nu_r(\theta) + \frac{\rho}{\mu} \nu_r(\theta) \tilde{u}(\theta). \quad (4.1.19)\]

The seedling equation is,

\[\frac{d\tilde{s}(\theta)}{d\theta} = \sigma \tilde{s}(\theta) \left(1 - \frac{s(\theta)}{\max(s_{min}, 1 - \eta(\nu_r(\theta) + \nu_u(\theta)))}\right). \quad (4.1.20)\]

We now have a coupled set of five ODE's that describes the dynamics of a forest with both uninfected and infected trees. Initial conditions for this set are (3.2.25), (3.2.26), (3.2.32), (4.1.14) and (4.1.15).

### 4.1.1 A forest without disease

From (4.1.16), (4.1.17), (4.1.18), and (4.1.19), (4.1.20) we can easily obtain a model with no disease in the forest:

\[\frac{d\tilde{u}(\theta)}{d\theta} = \kappa_u \tilde{u}(\theta) - \nu_u(\theta), \quad (4.1.21)\]

\[\frac{d\tilde{u}(\theta)}{d\theta} = s(\theta) - \tilde{u}(\theta), \quad (4.1.22)\]

with seedling equation,

\[\frac{ds(\theta)}{d\theta} = \sigma s(\theta) \left(1 - \frac{s(\theta)}{\max(s_{min}, 1 - \eta(\nu_u(\theta) + \nu_u(\theta)))}\right), \quad (4.1.23)\]

and rescaled initial conditions (3.2.25), (3.2.32), and (4.1.14).

### 4.2 Steady states and stability analysis

In this section we investigate system of equations (4.1.16), (4.1.17), (4.1.18), (4.1.19) and (4.1.20) for the purpose of identification of steady states.
4.2.1 Steady States

We obtain the steady states of these equations by setting the LHS to zero:

\[ \ddot{u}^* = \nu_u \left( \frac{1 + \frac{\rho v_w^*}{\mu}}{\kappa_u} \right), \]  
\[ \ddot{w}^* = \nu_w \left( \frac{\gamma}{\mu \kappa_w} - \frac{\rho v_u^*}{\mu \kappa_u} \right), \]  
\[ 0 = s^* - \ddot{u}^* (1 + \frac{\rho}{\mu} v_w^*), \]  
\[ 0 = -\frac{\gamma}{\mu} \ddot{w}^* + \frac{\rho}{\mu} v_u^* \ddot{u}^*, \]  
\[ s^* = 1 - \eta (v_u^* + v_w^*). \]

In equation (4.2.5) we have dropped the max operator because seedling count is always positive and \( s_{\text{min}} \) is simply a special case of \( 1 - \eta (v_u^* + v_w^*) \). As well, we do not need to consider the case \( s^* = 0 \), since this is below the minimum carrying capacity of the forest. Substitution of (4.2.1), (4.2.2) and (4.2.5) into (4.2.3) and (4.2.4) gives the relations,

\[ 0 = 1 - \eta (v_u^* + v_w^*) - v_u^* \left( \frac{(1 + \frac{\rho v_w^*}{\mu})^2}{\kappa_u} \right), \]  
\[ 0 = -\frac{\gamma}{\mu} v_w^* \left( \frac{\gamma}{\mu \kappa_w} - \frac{\rho v_u^*}{\mu \kappa_u} \right) + \frac{\rho}{\mu} v_u^* v_w^* \frac{1 + \rho v_u^*}{\kappa_u} \]  
\[ (4.2.7) \]

We can see that one steady state occurs when \( v_w(0) = 0 \). We will refer to this steady state as \( SS_{\text{trivial}} \). By virtue of (4.2.1), (4.2.5), and (4.2.6) we find the trivial steady state to be

\[ SS_{\text{trivial}} \rightarrow \begin{cases} v_u^* = \frac{\kappa_u}{\kappa_u \eta + 1}, \\ v_w^* = 0, \\ \ddot{u}^* = \frac{1}{\kappa_u \eta + 1}, \\ \ddot{w}^* = 0, \\ s^* = \frac{1}{\kappa_u \eta + 1} \end{cases} \]

Additional steady state (non-trivial) can be found by analyzing (4.2.6) and (4.2.7) rewritten in the form:

\[ v_u^* = f_1(v_w^*) = \frac{(1 - \eta v_w^*) \kappa_u}{\kappa_u \eta + (1 + \frac{\rho v_u^*}{\mu})^2}, \]

\[ (4.2.9) \]
\[ v_\mu^* = f_2(v_w^*) = \frac{(x_\mu)^2}{\kappa_\mu \nu (1 + \frac{x_\mu}{\nu} + \frac{\nu}{\mu} v_w^*)}. \tag{4.2.10} \]

Figure 4.2.2: Equations (4.2.9) and (4.2.10) are graphed on two plots above for different parameter values. The parameter values for the upper plot are \( \rho = 10; \mu = 0.05; \gamma = 1; \eta = 10; \kappa_\mu = 0.1; \kappa_w = 0.05. \) For the lower plot we have changed only one parameter: \( \gamma = 0.1. \) This set of parameters coincides with Example 3 of Section 5.3.3. Note that the curves in the upper plot do not intersect (we only consider positive valued dependent variables), hence there exists only the trivial steady state (4.2.8). Notice the function \( f_1(v_w^*) \) intersects the \( v_\mu^* \) axis at \( r = 1/\eta \) and the function \( f_2(v_w^*) \) asymptotically approaches the \( v_\mu^* \) axis. The lower plot shows the case where a non-trivial steady state exists, corresponding to the intersection of \( f_1 \) and \( f_2. \)

From (4.2.9) and (4.2.10), we obtain the general condition for existence of a steady state with a non-trivial \( v_w^* \) and \( \bar{w}^* \):

\[ f_1(0) = \frac{\kappa_\mu}{\kappa_\mu \eta + 1} > \frac{(x_\mu)^2}{\kappa_w \mu (1 + \frac{x_\mu}{\mu} + \frac{\nu}{\mu} v_w^*)} = f_2(0), \tag{4.2.11} \]

which we can simplify to the inequality,

\[ \frac{\kappa_w \mu}{\kappa_\mu \eta + 1} > \frac{(x_\mu)^2}{1 + \frac{x_\mu}{\mu}}, \tag{4.2.12} \]

We will refer to this additional steady state as \( SS_{\text{nontrivial}}. \) If this steady state exists then \( v_w^* \) and \( v_\mu^* \) satisfy the inequalities,
The functions $f_1$ and $f_2$ are plotted in Figure 4.2 to illustrate this condition. For the lower plot we have changed only one parameter: $\gamma = .1$. Note that the curves in the upper plot do not intersect (we only consider positive valued dependent variables), hence there exists only the trivial steady state (4.2.8). The function $f_1$ intersects the $v_2^*$ axis at $r = 1/\eta$. The lower plot shows the case where a non-trivial steady state exists, corresponding to the intersection of $f_1$ and $f_2$. From (4.2.9) and (4.2.10) we obtain a quadratic equation and taking into account the inequality (4.2.12), we can derive the expression for non-trivial steady states:

\[ v^*_w = \frac{-d_2 + \sqrt{d_2^2 - 4d_1d_3}}{2d_1}, \]  
\[ v^*_u = \frac{(1 - \eta v^*_w)\kappa_u}{\kappa_u + (1 + \frac{\rho}{\mu}v^*_w)^2}, \]  
\[ \bar{u}^* = v^*_u \frac{(1 + \frac{\rho}{\mu}v^*_w)}{\kappa_u}, \]  
\[ \bar{w}^* = v^*_w \left( \frac{\gamma}{\mu \kappa_w} - \frac{\rho v^*_u}{\mu \kappa_w} \right), \]  
\[ s^* = 1 - \eta(v^*_u + v^*_w), \]

where

\[ d_1 = \left( \frac{\rho}{\mu} \right)^2 \left( \left( \frac{\gamma}{\mu} \right)^2 + \kappa_u \eta \right), \]  
\[ d_2 = 2 \left( \frac{\gamma}{\mu} \right)^2 \frac{\rho}{\mu} + \kappa_w \frac{\rho}{\mu} \left( \frac{\gamma}{\mu} \eta + \eta - \frac{\rho}{\mu} \right), \]  
\[ d_3 = \left( \frac{\gamma}{\mu} \right)^2 \left( 1 + \kappa_u \eta \right) - \kappa_w \frac{\rho}{\mu} \left( \frac{\gamma}{\mu} + 1 \right). \]

### 4.2.2 Stability

Stability of steady states is determined by the eigenvalues of the Jacobian matrix of the system evaluated at the steady state. We obtain the general form of the Jacobian:
Evaluating $J$ at the trivial steady state (4.2.8), we obtain,

$$J(\text{SS}_{\text{trivial}}) = \begin{bmatrix}
-1 & -\frac{p}{\mu} & 0 & 0 \\
0 & -\frac{q}{\mu} & 0 & 0 \\
0 & \frac{q}{\mu} & -1 & 0 \\
-\eta & -\eta & 0 & 0
\end{bmatrix}$$

(4.2.23)

To analyze (4.2.23), we will employ the Routh-Hurwitz criteria. Consider the general form of the characteristic equation for this $(5 \times 5)$ matrix, where the eigenvalues $\lambda_i \{i = 1, 2, 3, 4, 5\}$ must satisfy the equation,

$$\lambda^5 + a_1 \lambda^4 + a_2 \lambda^3 + a_3 \lambda^2 + a_4 \lambda + a_5 = 0.$$  (4.2.24)

The coefficients $a_1, a_2, a_3, a_4$ and $a_5$ are found by rigorous algebraic manipulation of

$$\det(J(\text{SS}_{\text{trivial}}) - \lambda I) = 0,$$

(4.2.25)

where $I$ is the identity matrix. We obtain the coefficients:

$$a_1 = 2 + \frac{\sigma}{\mu} + 2 \frac{\gamma}{\mu} - \frac{\kappa_w}{\kappa_u} \frac{p}{\mu},$$

$$a_2 = 1 + \frac{2 \sigma}{\mu} + \frac{\gamma}{\mu} \left(4 + \frac{2 \sigma}{\mu} + \frac{\gamma}{\mu}\right) - \frac{\kappa_w}{\kappa_u} \frac{p}{\mu} \left(3 + \frac{\sigma}{\mu} + \frac{\gamma}{\mu}\right),$$

$$a_3 = \frac{\sigma}{\mu} + \frac{\gamma}{\mu} \left(2 + \frac{4 \sigma}{\mu} + \frac{2 \gamma}{\mu} + \frac{\gamma \sigma}{\mu^2}\right) + \frac{\kappa_u \gamma}{\mu} - \frac{\kappa_w}{\kappa_u} \frac{p}{\mu} \left(3 + \frac{3 \sigma}{\mu} + \frac{\gamma \sigma}{\mu^2} + \frac{2 \gamma}{\mu^2} + \frac{\gamma \sigma}{\mu^2}\right),$$

$$a_4 = \frac{\gamma}{\mu} \left(\frac{2 \sigma}{\mu} + \frac{\gamma}{\mu} + \frac{2 \gamma \sigma}{\mu^2}\right) + \frac{2 \kappa_u \gamma}{\mu} - \frac{\kappa_w}{\kappa_u} \frac{p}{\mu} \left(1 + \frac{3 \sigma}{\mu} + \frac{\gamma}{\mu^2} + \frac{2 \gamma}{\mu^2} + \frac{\gamma \sigma}{\mu^2}\right),$$

$$a_5 = \frac{\gamma^2}{\mu^3} + \frac{\kappa_u \gamma}{\mu} - \frac{\kappa_w}{\kappa_u} \frac{p}{\mu} \left(\frac{\gamma}{\mu^2} + \frac{\sigma}{\mu} + \frac{\kappa_u \gamma}{\mu} + \frac{\kappa_w \gamma}{\mu^2}\right)$$

(4.2.26)

Routh-Hurwitz criteria states that, a system is stable if and only if the coefficients of (4.2.24) satisfy the conditions:
By the Routh-Hurwitz criteria, if the inequalities (4.2.27)-(4.2.31) hold, then all the eigenvalues of (4.2.23) will have negative real part, and the trivial steady state \((v^*, v_m^*, \tilde{u}^*, \tilde{n}^*, s^*)\) is stable.

### 4.2.3 Stability of steady state of a forest without disease

The stability of the steady state of the system of equations (4.1.21)-(4.1.23) is determined, as before, by finding the eigenvalues of the Jacobian matrix of the system evaluated at the steady state. The steady state for (4.1.21)-(4.1.23) is,

\[
\begin{align*}
(v^*_{\nu}, v^*_{m}, \tilde{u}^*, \tilde{n}^*, s^*)
\end{align*}
\]

We obtain the general form of the Jacobian,

\[
J = \begin{bmatrix}
-1 & \kappa & 0 \\
0 & -1 & 1 \\
-\eta \frac{\sigma}{\mu} & 0 & -\frac{\sigma}{\mu}
\end{bmatrix}
\] (4.2.33)

Using Routh-Hurwitz criteria we find the coefficients of the characteristic equation of (4.2.33):
Since all parameters are positive and by using (4.2.28), we find the steady state of this system is stable if the condition holds:

\[ 2 + 4 \frac{\sigma}{\mu} + 2 \left( \frac{\sigma}{\mu} \right)^2 > \frac{\kappa_u \eta \sigma}{\mu} \]  

(4.2.35)

From the inequality (4.2.35), we see that instability can occur by either increasing \( \eta \) or \( \kappa_u \), the competition for available resources between seedlings and adult trees and the resource consumption of uninfected trees, respectively. These cases will be shown in examples of Section 5.3.
Chapter 5

Singularly perturbed ODE models

In the previous section we developed an ODE model consisting of 5 equations that describes the dynamics of a forest site. In this chapter we introduce two singularly perturbed models that can be obtained from, (4.1.16), (4.1.17), (4.1.18), (4.1.19) and (4.1.20), when we make certain assumptions on the parameters.

5.1 Two singularly perturbed models

5.1.1 Case 1: Fast death rate of infected forest and fast reestablishment of seedling

Parameter \( \gamma / \mu \), the ratio between the death rates of infected and uninfected trees, enters equation (4.1.17), while parameter \( \sigma / \mu \), the ratio between the reestablishment rate of seedlings and the death rate of uninfected trees, enters (4.1.20). When a tree becomes infected by disease the expected life span of that tree is typically reduced. This reduction rate is clearly dependent on the specific disease. For example, consider white pine. When infected by white pine blister rust (Cronartium ribicola), the life expectancy of such a tree may be reduced to only a few years, while the uninfected tree may still have over a hundred years of healthy life. In this first case we consider diseases that substantially reduce life expectancy of an infected tree. We will also consider the seedling reestablishment rate coefficient \( \sigma \) to be large compared to the death rate coefficient of uninfected trees \( \mu \). To represent this first case we introduce the notation:

\[
\frac{\gamma}{\mu} = \frac{1}{\epsilon}, \quad (5.1.1)
\]

\[
\frac{\sigma}{\mu} = \frac{\xi}{\epsilon}, \quad (5.1.2)
\]

where \( 0 < \epsilon \ll 1 \) is a small parameter and \( \xi \) is a constant \( O(1) \). Substituting these into the rescaled equations (4.1.17), (4.1.19) and (4.1.20) we obtain equations corresponding to Case 1:
The rescaled initial conditions (3.2.25), (3.2.26), (3.2.32), (4.1.14) and (4.1.15) are the same.

5.1.2 Case 2: Fast reestablishment of seedlings

In this case we consider infected trees to die at a rate comparable to that of uninfected trees. For example, a silver maple infected with broadleaf mistletoe (Phoradendron macrophyllum) may live nearly as long as an uninfected tree when the disease is restricted to only a few branches. This type of disease could instead affect the resource consumption rate $\kappa_w$ of an infected tree, but does not substantially reduce the expected life of the tree. In our forest site, as before, we will consider the seedling reestablishment rate coefficient $\sigma$ to be large compared to death rate coefficient of uninfected trees. With these assumptions we form the relation

$$\frac{\sigma}{\mu} = \frac{1}{\varepsilon};$$

where $0 < \varepsilon \ll 1$ is a small parameter. Substituting (5.1.8) into the rescaled equation (4.1.20) we obtain the system corresponding to Case 2:

$$\frac{dv_u(\theta)}{d\theta} = \kappa_u \tilde{u}(\theta) - v_u(\theta) - \frac{\rho}{\mu} v_w(\theta) v_u(\theta),$$

$$\frac{dv_w(\theta)}{d\theta} = \kappa_w \tilde{w}(\theta) - v_w(\theta) - \frac{\gamma}{\mu} v_w(\theta) v_u(\theta) + \frac{\rho}{\mu} \kappa_w v_w(\theta) v_u(\theta),$$

$$\frac{d\tilde{u}(\theta)}{d\theta} = s(\theta) - \tilde{u}(\theta) - \frac{\rho}{\mu} v_w(\theta) \tilde{u}(\theta).$$
\[
\frac{d\bar{w}(\theta)}{d\theta} = -\frac{\gamma}{\mu} \bar{w}(\theta) + \frac{\rho}{\mu} v_w(\theta) \bar{w}(\theta),
\]
(5.1.12)

\[
\epsilon \frac{ds(\theta)}{d\theta} = s(\theta) \left( 1 - \frac{s(\theta)}{\max(s_{\min}, 1 - \eta(v_u(\theta) + v_w(\theta)))} \right),
\]
(5.1.13)

with rescaled initial conditions (3.2.25), (3.2.26), (3.2.32), (4.1.14) and (4.1.15).

5.2 Asymptotic approximations of the ODE models for cases 1 and 2

A method, introduced by Tikhonov in 1948, for finding approximate solutions for singularly perturbed differential equations (with small parameters multiplying derivative terms in some of the equations) will be used. Case 1 and Case 2 systems are of this type.

5.2.1 Motivation for the boundary function method

To utilize the method of Tikhonov we must show that the following conditions hold for our systems of ODE’s. (A complete outline of this procedure is found in Vasil’eva, Butuzov and Kalachev [9]). We consider our autonomous set of equations in the general form:

\[
\epsilon \frac{dz}{d\theta} = F(z,y,\epsilon), \quad \frac{dy}{d\theta} = f(z,y,\epsilon),
\]
(5.2.1)

\[
z(0) = z^0, \quad y(0) = y^0.
\]
(5.2.2)

Here \( \epsilon > 0, z, \) and \( y \) are vector functions of dimension \( M \) and \( m \), respectively. \( F(z,y,\epsilon), f(z,y,\epsilon) \) and their derivatives are continuous vector functions with respect to \( z \) and \( y \) in some domain \( \Omega = \{ \| z \| \leq a, \| y \| \leq a, 0 \leq t \leq T \} \). The so-called degenerate or reduced system corresponding to (5.2.1) has the form:

\[
0 = F(\bar{z},\bar{y},0),
\]
(5.2.3)

\[
\frac{d\bar{y}}{d\theta} = f(\bar{z},\bar{y},0).
\]
(5.2.4)

\[
\bar{y}(0) = y^0.
\]
(5.2.5)

To obtain it we have set \( \epsilon = 0 \) in (5.2.1). We state the requirements that must hold for this method of approximation to be valid.
1°. The reduced system (5.2.3), has an isolated root with respect to $z$: $z = \varphi(y), y \in D = \left\{ \| y \| \leq a, 0 \leq t \leq T \right\}$ and the system (5.2.4) with initial condition (5.2.5), has a unique solution corresponding to this root in the interval $0 \leq t \leq T$.

2°. The stationary point $\dot{z} = \varphi(y)$, of the associated system:

$$\frac{d\dot{z}}{d\tau} = F(\dot{z}, y, 0) \quad \tau > 0,$$

where $\tau$ is the stretched variable and $y$ is considered a parameter, must be asymptotically stable in the sense of Lyapunov, uniformly in $y \in D$ as $\tau \to \infty$.

3°. The solution of the associated system, with $y = y^0$, must exist for $\tau > 0$ and tend to the stationary point $\varphi(y^0)$ as $\tau \to \infty$.

4°. $F(z, y, \varepsilon)$ and $f(z, y)$ must be infinitely differentiable ($C^1$ for construction of the leading order approximation).

Let us check the above conditions for the Case 1 system. We start with showing that the requirement 1° is satisfied. The reduced system for (5.1.4), (5.1.6) and (5.1.7) is easily found and the root is obtained:

$$\begin{align*}
\bar{v}_w &= 0, \\
\bar{w} &= 0, \\
\bar{s} &= \max(s_{\text{min}}, 1 - \eta(\bar{v}_w)).
\end{align*}$$

Using this root in equations (5.1.3) and (5.1.5), we arrive at a set of two ODEs:

$$\begin{align*}
\frac{d\bar{v}_u}{d\theta} &= \kappa_u \bar{u} - \bar{v}_u, \\
\frac{d\bar{u}}{d\theta} &= \max(s_{\text{min}}, 1 - \eta \bar{v}_u) - \bar{u}.
\end{align*}$$

This system can easily be solved (see Section 5.2.4) to arrive at a unique solution for the interval $\theta \in [0, T^*]$.

To show that condition 2° is satisfied we form the associated system:

$$\frac{d}{d\tau} \begin{bmatrix} \dot{v}_w \\ \dot{w} \end{bmatrix} = \begin{bmatrix} -1 & 0 \\ 0 & -1 \end{bmatrix} \begin{bmatrix} \dot{v}_w \\ \dot{w} \end{bmatrix},$$

35
\[ \frac{d\hat{s}}{d\tau} = \xi \hat{s} \left( 1 - \frac{\hat{s}}{\max(s_{\text{min}}, 1 - \eta(v_0 + \hat{v}_w))} \right), \quad (5.2.13) \]

where we now have \( v_w \) entered as a parameter. The eigenvalues of the constant coefficient matrix in equation (5.2.12) are \( \lambda_{1,2} = -1 \). Therefore the stationary point \( \hat{v}_w = 0 \) and \( \hat{w} = 0 \) is asymptotically stable. We can solve (5.2.13) by separation of variables using \( \hat{v}_w = 0 \). Let us first introduce the constant \( C_1 \):

\[ C_1 = \frac{1}{\max(s_{\text{min}}, 1 - \eta(v_0))}. \quad (5.2.14) \]

By substitution we obtain the simplified form:

\[ \frac{d\hat{s}}{d\tau} = \xi \hat{s} - \xi C_1 \hat{s}^2. \quad (5.2.15) \]

We obtain the general form of the solution:

\[ \hat{s} = \frac{1}{C_1 - C_2 e^{-\xi \tau}}. \quad (5.2.16) \]

where \( C_2 \) is the constant of integration. This solution asymptotically approaches \( 1/C_1 \) as \( \tau \to \infty \). To satisfy \( \sum^0 \), we substitute, \( v_w = v_0^0 \) into (5.2.12), and (5.2.13) to arrive at,

\[ \frac{d\hat{v}_w}{d\tau} = -\hat{v}_w \quad \Rightarrow \quad \hat{v}_w = D_1 e^{-\tau}, \quad (5.2.17) \]

\[ \frac{d\hat{w}}{d\tau} = -\hat{w} \quad \Rightarrow \quad \hat{w} = D_2 e^{-\tau}, \quad (5.2.18) \]

\[ \frac{d\hat{s}}{d\tau} = \xi \hat{s} \left( 1 - \frac{\hat{s}}{\max(s_{\text{min}}, 1 - \eta(v_0^0 + D_1 e^{-\tau}))} \right), \quad (5.2.19) \]

The constants \( D_1 \) and \( D_2 \) are constants of integration. It is clear that as \( \tau \to \infty \) the solutions of (5.2.17) and (5.2.18) tend to the stationary points (5.2.7) and (5.2.8). Taking the derivative of the RHS of (5.2.19), with respect to \( \hat{s} \), evaluated at the steady state (5.2.9), we obtain

\[ \xi(1 - \frac{2 \max(s_{\text{min}}, 1 - \eta v_0^0)}{\max(s_{\text{min}}, 1 - \eta (v_0^0 + D_1 e^{-\tau}))}) \quad (5.2.20) \]

Clearly (5.2.20) is negative for \( \forall \tau > 0 \). Therefore, the solution of equation (5.2.19) tends to the steady state (5.2.9) as \( \tau \to \infty \).

Condition \( 4^0 \) is clearly held for \( C^1 \).

Let us now check the conditions \( 1^0, 4^0 \) for the Case 2 system. We start with showing that the requirement \( 1^0 \) is satisfied. The reduced equation for (5.1.13) is easily found and its root obtained:
\[ s = \max(s_{\min}, 1 - \eta(\bar{v}_u + \bar{v}_w)), \quad (5.2.21) \]

where \( \bar{v}_u, \bar{v}_w \in D = \{ \| \bar{v}_u \|, \| \bar{v}_w \| \leq \alpha, 0 \leq \theta \leq T^* \} \). The system (5.1.9)-(5.1.12) using this root, has a unique solution since the RHS's are continuous, bounded and has Lipschitz constant. For \( 2^0 \) we use the same method as our previous case and find the associated system:

\[ \frac{d\xi}{d\tau} = \xi \left( 1 - \frac{\xi}{\max(s_{\min}, 1 - \eta(\bar{v}_u + \bar{v}_w))} \right), \quad (5.2.22) \]

We introduce the constant \( C_1 \):

\[ C_1 = \frac{1}{\max(s_{\min}, 1 - \eta(\bar{v}_u + \bar{v}_w))}, \quad (5.2.23) \]

and by substitution we obtain the simplified form:

\[ \frac{d\xi}{d\tau} = \xi - C_1 \xi^2. \quad (5.2.24) \]

Equation (5.2.24) can easily be solved by separation of variables. We obtain the general form of the solution,

\[ \xi = \frac{1}{C_1 - C_2 e^{-\tau}}. \quad (5.2.25) \]

This solution asymptotically approaches \( \frac{1}{C_1} \) as \( \tau \to \infty \).

To check condition \( 3^0 \), we consider (5.2.25), with \( \bar{v}_u = v^0 \) and \( \bar{v}_w = v^0 \) as \( \tau \to \infty \):

\[ \xi = \frac{1}{C_1 - C_2 e^{-\tau}} \]

\[ = \frac{1}{C_1}, \]

\[ = \max(s_{\min}, 1 - \eta(\bar{v}^0_u + \bar{v}^0_w)). \quad (5.2.26) \]

The requirement \( 4^0 \) is clearly satisfied.

**5.2.2 Form of the asymptotic approximation**

In this section we introduce asymptotic approximation for \( v_u(\theta), v_w(\theta), \bar{v}(\theta), \bar{v}(\theta) \) and \( s(\theta) \) that is valid uniformly in the entire interval \( 0 \leq \theta \leq T^* \) and with accuracy to the order \( \varepsilon^0 \). We seek the approximate solution in the form:
\[ \nu_u(\theta, \varepsilon) = \tilde{\nu}_u(\theta, \varepsilon) + \Pi \nu_u(\tau, \varepsilon), \]
\[ \nu_w(\theta, \varepsilon) = \tilde{\nu}_w(\theta, \varepsilon) + \Pi \nu_w(\tau, \varepsilon), \]
\[ \tilde{\eta}(\theta, \varepsilon) = \tilde{\eta}(\theta, \varepsilon) + \Pi \tilde{\eta}(\tau, \varepsilon), \]
\[ \tilde{\omega}(\theta, \varepsilon) = \tilde{\omega}(\theta, \varepsilon) + \Pi \tilde{\omega}(\tau, \varepsilon), \]
\[ s(\theta, \varepsilon) = s(\theta, \varepsilon) + \Pi s(\tau, \varepsilon), \]

where we have for the regular part:

\[ \tilde{\nu}_u(\theta, \varepsilon) = \tilde{\nu}_{u,0}(\theta) + \varepsilon \tilde{\nu}_{u,1}(\theta) + \cdots + \varepsilon^n \tilde{\nu}_{u,n}(\theta) + \cdots, \]
\[ \tilde{\nu}_w(\theta, \varepsilon) = \tilde{\nu}_{w,0}(\theta) + \varepsilon \tilde{\nu}_{w,1}(\theta) + \cdots + \varepsilon^n \tilde{\nu}_{w,n}(\theta) + \cdots, \]
\[ \tilde{\eta}(\theta, \varepsilon) = \tilde{\eta}_{0}(\theta) + \varepsilon \tilde{\eta}_{1}(\theta) + \cdots + \varepsilon^n \tilde{\eta}_{n}(\theta) + \cdots, \]
\[ \tilde{\omega}(\theta, \varepsilon) = \tilde{\omega}_{0}(\theta) + \varepsilon \tilde{\omega}_{1}(\theta) + \cdots + \varepsilon^n \tilde{\omega}_{n}(\theta) + \cdots, \]
\[ s(\theta, \varepsilon) = s_{0}(\theta) + \varepsilon s_{1}(\theta) + \cdots + \varepsilon^n s_{n}(\theta) + \cdots, \]

and for the boundary layer part (using the stretched variable \( \tau = \theta / \varepsilon \)),

\[ \Pi \nu_u(\tau, \varepsilon) = \Pi_0 \nu_u(\tau) + \varepsilon \Pi_1 \nu_u(\tau) + \cdots + \varepsilon^n \Pi_n \nu_u(\tau) + \cdots, \]
\[ \Pi \nu_w(\tau, \varepsilon) = \Pi_0 \nu_w(\tau) + \varepsilon \Pi_1 \nu_w(\tau) + \cdots + \varepsilon^n \Pi_n \nu_w(\tau) + \cdots, \]
\[ \Pi \tilde{\eta}(\tau, \varepsilon) = \Pi_0 \tilde{\eta}(\tau) + \varepsilon \Pi_1 \tilde{\eta}(\tau) + \cdots + \varepsilon^n \Pi_n \tilde{\eta}(\tau) + \cdots, \]
\[ \Pi \tilde{\omega}(\tau, \varepsilon) = \Pi_0 \tilde{\omega}(\tau) + \varepsilon \Pi_1 \tilde{\omega}(\tau) + \cdots + \varepsilon^n \Pi_n \tilde{\omega}(\tau) + \cdots, \]
\[ \Pi s(\tau, \varepsilon) = \Pi_0 s(\tau) + \varepsilon \Pi_1 s(\tau) + \cdots + \varepsilon^n \Pi_n s(\tau) + \cdots. \]

### 5.2.3 Leading order approximation

In this section, we construct the zeroth order approximation of the solutions of the model Cases 1 and 2. Initial conditions for these approximations in the leading order approximation can be written as
\[
\begin{align*}
\tilde{v}_{u,0}(0) + \Pi_0 v_u(0) &= v_u^0, \\
\tilde{v}_{w,0}(0) + \Pi_0 v_w(0) &= v_w^0, \\
\tilde{u}_0(0) + \Pi_0 \tilde{u}(0) &= \tilde{u}_0^0, \\
\tilde{w}_0(0) + \Pi_0 \tilde{w}(0) &= \tilde{w}_0^0, \\
\delta_0(0) + \Pi_0 \delta(0) &= s_0^0. 
\end{align*}
\]

(5.2.29)

Additional conditions for the boundary functions in the leading order are

\[\Pi_0 v_u(\infty) = \Pi_0 v_w(\infty) = \Pi_0 \tilde{u}(\infty) = \Pi_0 \tilde{w}(\infty) = \Pi_0 \delta(\infty) = 0.\]  

(5.2.30)

### 5.2.4 Case 1 of Section 5.1.1

Substituting (5.2.27) and (5.2.28) into (5.1.3) - (5.1.7), and comparing like terms (multiplying zero power of \(\epsilon\)), we obtain problems for terms in the leading order approximation for regular and boundary functions for Case 1 (we also use leading order initial conditions (5.2.29), as well as (5.2.30)):

\[
\frac{d\tilde{v}_{u,0}(\theta)}{d\theta} = \kappa_u \tilde{u}_0(\theta) - \tilde{v}_{u,0}(\theta),
\]

(5.2.31)

\[
\frac{d\tilde{u}_0(\theta)}{d\theta} = \tilde{\delta}_0(\theta) - \tilde{u}_0(\theta).
\]

(5.2.32)

\[
\frac{d\Pi_0 v_w(\tau)}{d\tau} = -\Pi_0 v_w(\tau).
\]

(5.2.33)

\[
\frac{d\Pi_0 \tilde{w}(\tau)}{d\tau} = -\Pi_0 \tilde{w}(\tau),
\]

(5.2.34)

\[
\tilde{v}_{w,0}(\theta) = \tilde{\nu}_0(\theta) = \Pi_0 v_w(\tau) = \Pi_0 \tilde{w}(\tau) = 0.
\]

(5.2.35)

We can easily solve (5.2.33) and (5.2.34) with conditions (5.2.29) and (5.2.30) to obtain

\[
\Pi_0 v_w(\tau) = v_w^0 e^{-\tau},
\]

(5.2.36)

\[
\Pi_0 \tilde{w}(\tau) = \tilde{w}_0^0 e^{-\tau}.
\]

(5.2.37)
By virtue of (5.2.35) and (5.1.7), the zeroth order approximation for regular part of the seedling equation becomes,

\[ \bar{s}_0(\theta) = \max(s_{\text{min}}, 1 - \eta v_{u,0}(\theta)). \tag{5.2.38} \]

The boundary layer part of the seedling equation is found by expanding \( s_0(\theta) \) in the Taylor series about \( \theta = 0 \), and substitution from (5.2.36). We obtain the equation,

\[ \frac{d\Pi_0 s(\tau)}{d\tau} = \Pi_0 s(\tau) [G_1(\tau) - G_2(\tau)\Pi_0 s(\tau)], \tag{5.2.39} \]

where,

\[ G_1(\tau) = \xi \left( 1 - \frac{2 \max(s_{\text{min}}, 1 - \eta v_0^0)}{\max(s_{\text{min}}, 1 - \eta (v_0^0 + v_0^0 e^{-\tau}))} \right), \tag{5.2.40} \]
\[ G_2(\tau) = \frac{\xi}{\max(s_{\text{min}}, 1 - \eta (v_0^0 + v_0^0 e^{-\tau}))}. \tag{5.2.41} \]

with initial condition using (5.2.29):

\[ \Pi_0 s(0) = s^0 - \bar{s}_0(0). \tag{5.2.42} \]
\[ \Pi_0 s(0) = s^0 - \max(s_{\text{min}}, 1 - \eta v_0^0). \tag{5.2.43} \]

The additional condition (5.2.30), on \( \Pi_0 s \), must be satisfied as well.

**Lemma 5.2.4.1.** The trivial steady state solution to (5.2.39) is the stable steady state solution.

**Proof.** We find the steady state solution of (5.2.39) to be,

\[ \Pi_0 s = 0. \tag{5.2.44} \]

Linearizing near the steady state we obtain

\[ \frac{df}{d\Pi_0 s} = G_1(\tau) - 2G_2(\tau)\Pi_0 s. \tag{5.2.45} \]

Evaluating (5.2.45) at the steady state (5.2.44) and noting (5.2.40) is negative \( \forall \tau > 0 \), we conclude the trivial steady state (5.2.44) is stable. \( \square \)

**Lemma 5.2.4.2.** The initial condition (5.2.43) is in the domain of attraction of the trivial stable steady state of (5.2.39).
Proof. The RHS of (5.2.39) for any particular time $\tau = \tau^*$ has the form shown in Figure 5.2.1.

From Figure 5.2.1 we see that to prove the initial condition (5.2.43) is in the domain of attraction amounts to showing that the initial condition lies to the right of $G_1(\tau^*)/G_2(\tau^*) \forall \tau^* > 0$:

$$\frac{G_1(\tau^*)}{G_2(\tau^*)} < \Pi_{05}(0),$$  \hspace{1cm} (5.2.46)  

$$\xi \left(1 - \frac{2 \max(s_{\max}, s_{\min} - \eta \nu_0)}{\max(s_{\min}, s_{\min} - \eta (\nu_0 + \nu_0 e^{-\tau^*}))}\right) < s^0 - \max(s_{\min}, 1 - \eta \nu_0),$$  \hspace{1cm} (5.2.47)  

$$\max(s_{\min}, 1 - \eta (\nu_0 + \nu_0 e^{-\tau^*})) - \max(s_{\min}, 1 - \eta \nu_0) < s^0,$$  \hspace{1cm} (5.2.48)  

We need to show that equation (5.2.48) holds for both cases of the max operator:

$$s_{\min} - s_{\min} = 0 < s^0,$$  \hspace{1cm} (5.2.49)  

and

$$-\eta \nu_0 e^{-\tau^*} < s^0.$$  \hspace{1cm} (5.2.50)  

Both inequalities (5.2.49) and (5.2.50) hold since $0 < s_{\min} \leq s^0$. Therefore the initial condition (5.2.43) is in the domain of attraction of the stable steady state (5.2.44) $\forall \tau > 0$. □

By substituting (5.2.38) into equation (5.2.32), we obtain a set of coupled ODE's for the zeroth order regular functions $\bar{v}_{u,0}(\theta)$ and $\bar{u}_{0}(\theta)$:

$$\frac{d\bar{v}_{u,0}(\theta)}{d\theta} = \kappa_u \bar{u}_{0}(\theta) - \bar{v}_{u,0}(\theta).$$  \hspace{1cm} (5.2.51)
\[
\frac{d\tilde{u}_0(\theta)}{d\theta} = \max(s_{\text{min}}, 1 - \eta \tilde{v}_{u,0}) - \tilde{u}_0(\theta),
\]

with initial conditions (5.2.29). Equations (5.2.51) and (5.2.52) can be re-written using standard matrix notation:

\[
\frac{d}{d\theta} \begin{bmatrix}
\tilde{v}_{u,0}(\theta) \\
\tilde{u}_0(\theta)
\end{bmatrix} = \begin{bmatrix}
-1 & \kappa_u \\
-\eta & -1
\end{bmatrix} \begin{bmatrix}
\tilde{v}_{u,0}(\theta) \\
\tilde{u}_0(\theta)
\end{bmatrix} + \begin{bmatrix}
0 \\
1
\end{bmatrix},
\]

or, in the case when the carrying capacity is \(s_{\text{min}}\),

\[
\frac{d}{d\theta} \begin{bmatrix}
\tilde{v}_{u,0}(\theta) \\
\tilde{u}_0(\theta)
\end{bmatrix} = \begin{bmatrix}
-1 & \kappa_u \\
0 & -1
\end{bmatrix} \begin{bmatrix}
\tilde{v}_{u,0}(\theta) \\
\tilde{u}_0(\theta)
\end{bmatrix} + \begin{bmatrix}
0 \\
\frac{s_{\text{min}}}{s_{\text{min}}}
\end{bmatrix}
\]

The eigenvalues of the constant coefficient matrix of the RHS of (5.2.53) and (5.2.54) are,

\[
\lambda_{1,2} = -1 \pm i\sqrt{\frac{\kappa_u}{\eta}},
\]

and

\[
\lambda_{1,2} = -1,
\]

respectively. Since the eigenvalues of (5.2.55) and (5.2.56) have negative real parts, the steady state for the zeroth order approximation of \(\tilde{v}_{u,0}\) and \(\tilde{u}_0\) is a stable attractor. The analytic solutions of (5.2.53) and (5.2.54), with initial conditions (5.2.29) are

\[
\tilde{v}_{u,0}(\theta) = e^{-\theta} \left( \nu^0_u - \frac{\kappa_u}{\kappa_u \eta + 1} \right) \cos(\sqrt{\kappa_u \eta} \theta) + \\
\quad + \frac{\kappa_u}{\sqrt{\kappa_u \eta} \eta + 1} \left( \frac{\nu^0_u}{\kappa_u \eta + 1} \right) \sin(\sqrt{\kappa_u \eta} \theta) + \frac{\kappa_u}{\kappa_u \eta + 1},
\]

and

\[
\tilde{u}_0(\theta) = -\frac{e^{-\theta}}{\kappa_u} \left( \sqrt{\kappa_u \eta} \left( \nu^0_u - \frac{\kappa_u}{\kappa_u \eta + 1} \right) \sin(\sqrt{\kappa_u \eta} \theta) - \\
\quad - \kappa_u \left( \frac{\nu^0_u}{\kappa_u \eta + 1} \right) \cos(\sqrt{\kappa_u \eta} \theta) + \frac{1}{\kappa_u \eta + 1} \right),
\]

and

\[
\tilde{v}_{u,0}(\theta) = e^{-\theta} (\nu^0_u - \kappa_u s_{\text{min}}) + \kappa_u (\tilde{u}^0 - s_{\text{min}}) e^{-\theta} + \kappa_u s_{\text{min}}.
\]

\[
\tilde{u}_0(\theta) = e^{-\theta} (\tilde{u}_0^0 - s_{\text{min}}) + s_{\text{min}}.
\]
respectively. We use this and previous results to assemble the complete leading order approximation for the solution of the set of ODEs (5.1.3) - (5.1.7):

\[
\nu_\theta(\theta, \tau) = e^{-\theta} \left( \left[ \nu^0_\mu - \frac{\kappa_\mu}{\kappa_\mu + 1} \right] \cos(\sqrt{\kappa_\mu} \eta \theta) + \right.
\left. + \frac{\kappa_\mu}{\sqrt{\kappa_\mu} \eta} \left[ \nu^0_\nu - \frac{1}{\kappa_\nu \eta + 1} \right] \sin(\sqrt{\kappa_\nu} \eta \theta) \right) + \frac{\kappa_\mu}{\kappa_\nu \eta + 1} + O(\varepsilon),
\]

(5.2.61)

\[
\nu_\nu(\theta, \tau) = \nu^0_\nu e^{-\tau} + O(\varepsilon),
\]

(5.2.62)

\[
\bar{u}(\theta, \tau) = -e^{-\theta} \left( \sqrt{\kappa_\nu} \eta \left[ \nu^0_\nu - \frac{\kappa_\mu}{\kappa_\nu \eta + 1} \right] \sin(\sqrt{\kappa_\nu} \eta \theta) - \right.
\left. - \kappa_\nu \left[ \nu^0_\nu - \frac{1}{\kappa_\nu \eta + 1} \right] \cos(\sqrt{\kappa_\nu} \eta \theta) \right) + \frac{1}{\kappa_\nu \eta + 1} + O(\varepsilon),
\]

(5.2.63)

\[
\bar{w}(\theta, \tau) = \bar{w}^0 e^{-\tau} + O(\varepsilon),
\]

(5.2.64)

\[
s(\theta, \tau) = -e^{-\theta} \left( \left[ \nu^0_\nu - \frac{\kappa_\mu}{\kappa_\nu \eta + 1} \right] \cos(\sqrt{\kappa_\nu} \eta \theta) + \right.
\left. + \frac{\kappa_\mu}{\sqrt{\kappa_\nu} \eta} \left[ \nu^0_\nu - \frac{1}{\kappa_\nu \eta + 1} \right] \sin(\sqrt{\kappa_\nu} \eta \theta) \right) + \frac{1}{\kappa_\nu \eta + 1} +
\]

\[+ \Pi_0 s(\tau) + O(\varepsilon).
\]

(5.2.65)

Let us refer to the above solution as Case A, that is, when the forest volume is less than the critical volume. The leading order approximation when the forest volume is greater than or equal to the critical volume is

\[
\nu_\nu(\theta, \tau) = \nu^0_\nu e^{-\tau} + O(\varepsilon),
\]

(5.2.66)

\[
\bar{u}(\theta, \tau) = e^{-\theta} (\nu^0_\nu - \kappa_\mu s_{\text{min}}) + \kappa_\mu (\bar{u}^0 - s_{\text{min}}) \theta e^{-\theta} + \kappa_\mu s_{\text{min}} + O(\varepsilon),
\]

(5.2.67)

\[
\bar{w}(\theta, \tau) = \bar{w}^0 e^{-\tau} + O(\varepsilon),
\]

(5.2.68)

\[
s(\theta, \tau) = s_{\text{min}} + O(\varepsilon),
\]

(5.2.69)

and will be referred to as Case B. It is easy to see that as \( \theta \to \infty \), Case A tends to the steady state (4.2.8):

\[
SS_1 \rightarrow \left\{ \begin{array}{l}
\nu^*_\mu = \frac{\kappa_\mu}{\kappa_\mu \eta + 1}, \\
\nu^*_\nu = 0, \\
\bar{u}^* = \frac{1}{\kappa_\eta \eta + 1}, \\
\bar{w}^* = 0, \\
s^* = \frac{1}{\kappa_\eta \eta + 1}.
\end{array} \right.
\]

(5.2.71)

where as Case B tends to:
A special case arises when the forest site becomes saturated with trees. In this case the system will have oscillatory behavior. The approximate solution for such a site will utilize both Case A and B solutions. The Case A solution is used when the site has total volume less than the critical forest volume and the Case B solution when it has total volume greater than or equal to the critical volume.

We next will obtain an approximate solution for the Case 2.

5.2.5 Case 2 of Section 5.1.2

By substitution of (5.2.27) and (5.2.28) into (5.1.9) - (5.1.13), and comparing like terms (multiplying zero power of $\epsilon$), as we did before, we obtain problems for terms in the leading order approximation for regular and boundary functions for Case 2 (we also use leading order initial conditions (5.2.29), as well as (5.2.30)):

\[
\frac{d\bar{v}_{u,0}(\theta)}{d\theta} = \kappa_u \bar{u}_0(\theta) - \bar{v}_{u,0}(\theta) - \frac{\rho}{\mu} \bar{v}_{w,0}(\theta) \bar{v}_{u,0}(\theta), \tag{5.2.73}
\]

\[
\frac{d\bar{v}_{w,0}(\theta)}{d\theta} = \kappa_w \bar{w}_0(\theta) - \gamma \bar{v}_{w,0}(\theta) + \frac{\rho}{\mu} \frac{\kappa_w}{\kappa_u} \bar{w}_{u,0}(\theta) \bar{v}_{u,0}(\theta), \tag{5.2.74}
\]

\[
\frac{d\bar{u}_0(\theta)}{d\theta} = \bar{s}_0(\theta) - \bar{u}_0(\theta) - \frac{\rho}{\mu} \bar{v}_{w,0}(\theta) \bar{u}_0(\theta), \tag{5.2.75}
\]

\[
\frac{d\bar{w}_0(\theta)}{d\theta} = -\gamma \bar{w}_0(\theta) + \frac{\rho}{\mu} \bar{v}_{w,0}(\theta) \bar{u}_0(\theta), \tag{5.2.76}
\]

\[
\Pi_0 v_u(\tau) = \Pi_0 v_w(\tau) = \Pi_0 \bar{u}(\tau) = \Pi_0 \bar{w}(\tau) = 0. \tag{5.2.77}
\]

We find the leading order approximation for the regular part of the seedling equation to be

\[
\bar{s}_0(\theta) = \max(s_{\text{min}}, 1 - \eta(\bar{v}_{u,0}(\theta) + \bar{v}_{w,0}(\theta))). \tag{5.2.78}
\]

and the boundary layer part, as before, by expanding $s_0(\theta)$ in the Taylor series about $\theta=0$:  

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\[ \frac{d \Pi_0 s(\tau)}{d \tau} = - \Pi_0 s(\tau) - \frac{1}{1 - \eta(v_0 + \nu_0)} \Pi_0 s(\tau)^2, \]
\[ = - \Pi_0 s(\tau) - \frac{1}{k^0} \Pi_0 s(\tau)^2. \tag{5.2.79} \]

Using (5.2.29) we obtain the initial condition for (5.2.79):

\[ \Pi_0 s(0) = s^0 - \max(s_{\text{min}}, 1 - \eta(v_0 + \nu_0)) = s^0 - k^0 \tag{5.2.80} \]

The solution to (5.2.79) with condition (5.2.80) is,

\[ \Pi_0 s(\tau) = \frac{k^0(k^0 - s^0)}{k^0 - s^0 + s^0 e^{\tau}}. \tag{5.2.81} \]

We can easily see that the additional condition (5.2.30) on \( \Pi_0 s \) is also satisfied. We can substitute (5.2.78) into (5.2.75), thus, reducing our system to 4 nonlinear coupled ODEs for the regular part of the leading order approximation:

\[ \frac{d \tilde{v}_w,0(\theta)}{d \theta} = \kappa_u \tilde{v}_u,0(\theta) - \nu_u,0(\theta) - \frac{\rho}{\mu} \nu_w,0(\theta) \tilde{v}_u,0(\theta), \]
\[ \frac{d \tilde{v}_w,0(\theta)}{d \theta} = \kappa_u \tilde{v}_w,0(\theta) - \frac{\gamma}{\mu} \nu_w,0(\theta) + \frac{\rho \kappa_u}{\mu} \nu_w,0(\theta) \tilde{v}_w,0(\theta), \]
\[ \frac{d \tilde{u}_0(\theta)}{d \theta} = \max(s_{\text{min}}, 1 - \eta(\tilde{v}_u,0(\theta) + \tilde{v}_w,0(\theta))) - \tilde{u}_0(\theta) - \frac{\rho}{\mu} \nu_w,0(\theta) \tilde{u}_0(\theta), \]
\[ \frac{d \tilde{w}_0(\theta)}{d \theta} = - \frac{\gamma}{\mu} \tilde{w}_0(\theta) + \frac{\rho}{\mu} \nu_w,0(\theta) \tilde{u}_0(\theta). \tag{5.2.82} \]

System (5.2.82), with initial conditions (5.2.29), approximates the original model (5.1.9) - (5.1.13) under conditions that the seedling reestablishment rate coefficient \( \sigma \) is much greater than the death rate coefficient for uninfected trees.

We will next present examples of both Case 1 and 2 for various parameters.
5.3 Examples of the ODE system

In this section we explore a variety of cases of the ODE system with different parameter values.

5.3.1 Example 1 (low initial forest volume and tree count, no infected trees)

In this example we consider a forest site with low forest volume and tree count at initial instant of time. There are no infected trees in this site. Figures 5.3.2-5.3.4 show the behavior of the site, while a discussion of the results follows at the end of this section. We list the parameters and initial values below, and along the right hand side of each Figure.

Domain:
\[ \theta \in [0,4] \quad \text{(time)} \]

Initial Values:
\[
\begin{align*}
\nu_\nu(0) &= 0.02 \quad \text{(initial uninfected volume)} \\
\nu_\omega(0) &= 0.0 \quad \text{(initial infected volume)} \\
\tilde{u}(0) &= 0.2 \quad \text{(initial uninfected total trees)} \\
\tilde{w}(0) &= 0.0 \quad \text{(initial infected total trees)} \\
s(0) &= 0.1 \quad \text{(initial seedling count)}
\end{align*}
\]

Resource Consumption:
\[
\begin{align*}
\kappa_\nu &= 0.1 \quad \text{(rate of increase in size of uninfected tree)} \\
\kappa_\omega &= 0.05 \quad \text{(rate of increase in size of infected tree)}
\end{align*}
\]

Parameters:
\[
\begin{align*}
\mu &= .05 \quad \text{(constant proportional to death rate of uninfected trees)} \\
\gamma &= 1 \quad \text{(constant proportional to death rate of infected trees)} \\
\rho &= 0 \quad \text{(pathogen virulence)} \\
\eta &= 10 \quad \text{(competition between seedlings and adult trees)} \\
\sigma &= 2 \quad \text{(constant proportional to seedling reestablishment)}
\end{align*}
\]

For this example the re-establishment rate coefficient of seedlings, \( \sigma = 2 \), is fast compared to the death rate coefficient of uninfected trees, \( \mu = .05 \). The inequality (4.2.35):

\[
\begin{align*}
2 + 4 \frac{\sigma}{\mu} + 2 \left( \frac{\sigma}{\mu} \right)^2 &> \frac{\kappa_\nu \eta \sigma}{\mu}, \\
2 + 4 \frac{2}{.05} + 2 \left( \frac{2}{.05} \right)^2 &> \frac{.1 \times 10 \times 2}{.05},
\end{align*}
\]

\[ 3362 > 40. \]
is clearly satisfied, therefore the trajectories tend to the stable steady state (4.2.32).

\[ S_{(Ex.1)} \rightarrow \left\{ \begin{array}{l}
\nu^* = \frac{1}{1 \times 10^4} = .05, \\
\bar{u}^* = \frac{1}{1 \times 10^4} = .5, \\
\bar{s}^* = \frac{1}{1 \times 10^4} = .5.
\end{array} \right. \]

Figure 5.3.2: This plot shows a site that initially has a low forest volume and tree count. There are no infected trees. The plot shows the evolution of the total volume of trees. The forest evolves to the steady state (4.2.32).
Figure 5.3.3: This plot shows the evolution of the total number of adult trees and seedlings. The parameters are the same as in Figure 5.3.2.

![Plot of the seedling carrying capacity](image)

At the initial instant of time the forest site has a large amount of open space with few new seedlings, \( s(0) = .1 \). This particular choice of initial seedling count is much less than the initial carrying capacity of the site, \( k(0) = 1 - \eta v(0) = 1 - 10 \times .02 = .8 \). Hence, during the initial period, and because of the fact that the rescaled reestablishment rate for seedlings is large, \( \sigma_\mu = 40 \), the seedling count increases rapidly filling the large open space in the forest site. The forest volume for this site remains below the critical volume and the seedling count tends to a steady state well above the minimum of \( s_{min} \). It is seen that for this case the asymptotic solution (5.2.61), (5.2.63) and (5.2.65) accurately represents the numerical solution (A.2.15), (A.2.17) and (A.2.19).

5.3.2 Example 2 (low initial forest volume and tree count with infected trees)

In this example we consider a forest site with low initial forest volume and tree count. There are infected trees in this site.
Domain:
\[ \theta \in [0, 4] \] (time)

Initial Values:
\[ \nu_w(0) = 0.01 \] (initial uninfected volume)
\[ \nu_w(0) = 0.01 \] (initial infected volume)
\[ \hat{u}(0) = 0.1 \] (initial uninfected total trees)
\[ \hat{w}(0) = 0.1 \] (initial infected total trees)
\[ s(0) = 0.1 \] (initial seedling count)

Resource Consumption:
\[ \kappa_w = 0.1 \] (rate of increase in size of uninfected tree)
\[ \kappa_w = .05 \] (rate of increase in size of infected tree)

Parameters:
\[ \mu = .05 \] (constant proportional to death rate of uninfected trees)
\[ \gamma = 1 \] (constant proportional to death rate of infected trees)
\[ \rho = 10 \] (pathogen virulence)
\[ \eta = 10 \] (competition between seedlings and adult trees)
\[ \sigma = 2 \] (constant proportional to seedling reestablishment)

The site seen in Figures 5.3.5-5.3.7, responds quickly to the high death rate of the infected forest. The forest volume and tree count are initially reduced, which causes a slightly larger spike in the seedling count than Example 1. The infected trees die at a much faster rate than the uninfected trees, and in a short amount of time are completely removed from the forest. Because both the death of infected trees and reestablishment of seedlings have rate coefficients much larger than the death rate of uninfected trees, the asymptotic solution (5.2.61) - (5.2.65) for Case 1 is used to compare with the numerical solution (A.2.15) - (A.2.19). Again by noting the parameter settings and inequality (4.2.12):

\[
\frac{\kappa_w \rho}{\kappa_w \eta + 1} < \frac{(\frac{\gamma}{\mu})^2}{1 + \frac{\gamma}{\mu}},
\]

\[
.05 \frac{10}{.05} \frac{10}{.05} \frac{10}{.05} \frac{10}{.05} < \frac{(\frac{1}{.05})^2}{1 + \frac{1}{.05}},
\]

we find the system evolves to the steady state.
Using coefficients (4.2.26) evaluated with given parameter values we find that the Routh-Hurwitz conditions (4.2.27) - (4.2.31) hold. This steady state is therefore stable. We can confirm this by checking that the eigenvalues of the Jacobian matrix (4.2.23) have negative real parts. We find,

eigenvalues of $J(SS_{(E.x.2)}) \Rightarrow [-40.03, -20.85, -14.15, -0.987 + 1.01i, -0.987 - 1.01i]$.

Figure 5.3.5: This plot shows a forest site with the same initial low volume and tree count as Example 1, however in this example half of the forest volume and tree count are infected with disease. The forest evolves to the steady state (4.2.8).
Thus far, we have discussed two examples. First, a site with no disease and low initial forest volume and tree count. After a rapid introduction of seedlings, caused by a low initial seedling count and high initial carrying capacity, the site evolved to a steady state. Second, we produced a
The site behavior shown in Figures 5.3.8-5.3.10 responds quickly to the large open space in the forest, as in our previous example. However, this site corresponds to Case 2, where only the reestablishment of seedlings have rate much larger than the death rate of uninfected trees. At initial instant of time there is a very small portion of the forest site infected, \( v_{w}(0) = 0.001 \), with the same pathogen virulence, \( \rho = 10 \), as Example 1. Because the death rate of infected trees is only twice that of uninfected trees, \( \gamma = 0.1 \) and \( \mu = 0.05 \), respectively, the disease successfully spreads to other uninfected trees. The forest soon reaches a steady state. This site will always
have infected trees. The forest volume is always below the critical volume, hence seedlings will always have enough resources to exceed the minimum of $s_{min}$. The leading order set of 4 ODEs (5.2.82) is solved numerically, with the regular and boundary parts of the asymptotic solution for the seedlings (5.2.78) and (5.2.81), respectively. This compares well with the numerical solution of (4.2.15) -(4.2.19). By decreasing $\epsilon$ we may see that the asymptotic solution tends to the numerical. By noting the parameters and inequality (4.2.12):

$$\frac{\kappa_w \rho}{\kappa_u \eta + 1} \geq \frac{(\frac{\gamma}{\mu})^2}{1 + \frac{1}{10}}$$
$$\frac{.05}{10 + \frac{1}{.05}} \geq \frac{(\frac{1}{10})^2}{1 + \frac{1}{10}}$$

$5 > 1.33,$

we see that this site will tend to the non-trivial steady state described in (4.2.14) -(4.2.18):

$$d_1 = \left(\frac{\rho}{\mu}\right)^2 \left(\frac{\gamma}{\mu}\right)^2 + \kappa_w \eta = \left(\frac{10}{.05}\right)^2 \left(\frac{.1}{.05}\right)^2 + .05 \times 10 = 1.8E5,$$

$$d_2 = 2 \left(\frac{\gamma}{\mu}\right)^2 \frac{\rho}{\mu} + \kappa_w \frac{\rho}{\mu} \left(\frac{\gamma}{\mu} + \eta - \frac{\rho}{\mu}\right) = 2 \left(\frac{1}{.05}\right)^2 \frac{10}{.05} + .05 \times 10 \left(\frac{1}{.05} \times 10 - \frac{10}{.05}\right) = -100,$$

$$d_3 = \left(\frac{\gamma}{\mu}\right)^2 \left(1 + \kappa_u \eta\right) - \kappa_w \frac{\rho}{\mu} \left(\frac{\gamma}{\mu} + 1\right) = \left(\frac{1}{.05}\right)^2 \left(1 + .1 \times 10\right) - .05 \times 10 \left(\frac{1}{.05} + 1\right) = -22,$$

$$v^*_{\nu} = \frac{-d_2 + \sqrt{d_2^2 - 4d_1 d_3}}{2d_1} = \frac{-d_2 + \sqrt{-100^2 - 4 \times 1.8E5 \times (-22)}}{2 \times 1.8E5} = 0.0113;$$

$$v^*_\eta = \frac{(1 - \rho v^*_\nu) \kappa_u}{\kappa_u \eta + (1 + \rho v^*_\nu)^2} = \frac{(1 - 10 \times 0.0113) \times 1}{1 \times 10 + (1 + 10 \times 0.0113)^2} = 0.00759.$$

$$\bar{u}^* = v^*_\nu \left(1 + \frac{\rho v^*_\nu}{\mu \kappa_u}\right) = 0.00759 \left(1 + \frac{10 \times 0.0113}{.05 \times .05}\right) = 0.248.$$

$$\bar{w}^* = v^*_\nu \left(\frac{\gamma}{\mu \kappa_w} - \frac{\rho v^*_\nu}{\mu \kappa_u}\right) = 0.0113 \left(\frac{1}{.05 \times .05} - \frac{10 \times 0.00759}{.05 \times 1}\right) = 0.281,$$

$$s^* = 1 - \eta (v^*_\nu + v^*_\nu) = 1 - 10 (0.00759 + 0.0113) = 0.811.$$

The steady state (4.2.8) is unstable, as can be seen from the Routh-Hurwitz matrix (4.2.30), using coefficients (4.2.26):
\[ \begin{vmatrix} a_1 & 1 & 0 & 0 \\ a_3 & a_2 & a_1 & 1 \\ a_5 & a_4 & a_3 & a_2 \\ 0 & 0 & a_5 & a_4 \end{vmatrix} = \begin{vmatrix} 21 & 1 & 0 & 0 \\ -243 & 8 & 21 & 1 \\ -440 & -491 & -243 & 8 \\ 0 & 0 & -440 & -491 \end{vmatrix} = -4.69 \times 10^{-7} < 0 \]

Figure 5.3.8: This plot shows a site with low initial forest volume and tree count. This example coincides with Case 2, where only the rate coefficient for reestablishment of seedlings \( \sigma = 1 \) is much greater than the death rate coefficient of uninfected trees \( \mu = 0.05 \). Note that this site also represents the PDE model of Example 1 of Section 3.3.1, where we have chosen the same parameters. Trajectories from both examples tend to the same steady state \((4.2.14)\) to \((4.2.18)\).

The eigenvalues of the Jacobian matrices \((4.2.22)\) and \((4.2.23)\) are,

- Eigenvalues of \( J(SS_{\text{trivial}}) \to [-20.05, 3.85, -2.85, -0.972 + 1.024i, -0.972 - 1.024i] \).
- Eigenvalues of \( J(SS_{\text{nontrivial}}) \to [-20.06, -4.75, -1.47 + 1.59i, -1.47 - 1.59i, -2.01] \).

Notice the second eigenvalue of \( J(SS_{\text{trivial}}) \) is positive, confirming this steady state is now unstable. The nontrivial steady state is stable since all real parts of the eigenvalues are negative.
Figure 5.3.9: This plot shows the evolution of the total number of adult trees and seedlings. The parameters are the same as in Figure 5.3.8.

Figure 5.3.10: This plot shows the evolution of the seedling carrying capacity. The parameters are the same as in Figure 5.3.8.

We will next show a site that exhibits oscillatory behavior and the effects of disease on such a site.
5.3.4 Example 4 (large initial forest volume and medium tree count with no diseased trees)

In this example we consider a forest site at initial instant of time with a larger volume and the same tree count as in Example 1. As in Example 1 there are no infected trees in this site. We list the parameters and initial values below, and along the right hand side of each Figure.

Domain: 
\[ \theta \in [0, 16] \]  
(time)

Initial Values:
- \( w(0) = 0.03 \) (initial uninfected volume)
- \( v_w(0) = 0.0 \) (initial infected volume)
- \( \bar{u}(0) = 0.2 \) (initial uninfected total trees)
- \( \bar{w}(0) = 0.0 \) (initial infected total trees)
- \( s(0) = 1E^{-8} \) (initial seedling count)

Resource Consumption:
- \( \kappa_u = 0.1 \) (rate of increase in size of uninfected tree)
- \( \kappa_w = 0.05 \) (rate of increase in size of infected tree)

Parameters:
- \( \mu = 0.1 \) (constant proportional to death rate of uninfected trees)
- \( \gamma = 0.2 \) (constant proportional to death rate of infected trees)
- \( \rho = 0 \) (pathogen virulence)
- \( \eta = 80 \) (competition between seedlings and adult trees)
- \( \sigma = 1 \) (constant proportional to seedling reestablishment)
Figure 5.3.11: This plot shows an example of a forest site with a larger volume and the same number of trees as Example 1. This pertains to a mid-aged forest with few young trees. There is no disease in this forest site. As the forest evolves, stable oscillations occur.

Figure 5.3.12: This plot shows the evolution of the total number of adult trees and seedlings. The parameters are the same as in Figure 5.3.11.
Figure 5.3.13: This plot shows the projection of the phase space on the plane of variables: volume of the forest and the seedling count. The parameters are the same as in Figure 5.3.11.

Figure 5.3.14: This plot shows the projection of the phase space on the plane of variables: total number of trees on the site forest and the seedling count. The parameters are the same as in Figure 5.3.11.
Figure 5.3.15: This plot shows the projection of the phase space on the plane of variables: total number of trees and the volume of trees on the site. The parameters are the same as in Figure 5.3.11.

Figure 5.3.16: This plot shows the evolution of the carrying capacity. The parameters are the same as Figure 5.3.11.
Figure 5.3.17: This plot shows the projection of the phase space on the plane of variables: total number of trees and the volume of trees in the site. Several trajectories are shown that differ by initial values of the total volume of trees. These trajectories reflect the stability of the two limit cycles and steady state. The parameters are the same as in Figure 5.3.11.

As shown in the Figures 5.3.11-5.3.16, this forest has evolved to a state of oscillations. At the initial instant of time this forest site is saturated with trees. Seedlings will remain at \( s_{\text{min}} \) until the critical volume is reached, \( \theta \approx 1.5 \). On Figure 5.3.13, the maximum forest volume attained by the trajectory is the critical volume, \( \frac{1}{\eta} = .0125 \). We use the same small seedling carrying capacity of \( s_{\text{min}} = 1e - 008 \), as in our PDE model of Section 3.3. Though the trajectory has tended to a stable limit cycle, the steady state (4.2.32) exists, as can be seen by inequality (4.2.12):

\[
\frac{\kappa w \frac{L}{\mu}}{\kappa w \eta + 1} < \frac{(\frac{\gamma}{\mu})^2}{1 + \frac{\gamma}{\mu}},
\]

\[
.05 \frac{L}{\mu} < \frac{(\frac{1}{1})^2}{1 + \frac{1}{1}},
\]

\[
.1 \times 80 + 1 < \frac{1}{1},
\]

\[
0 < 1.33,
\]

This steady state is stable by the inequality (4.2.35):
\[
2 + 4 \frac{\sigma}{\mu} + 2 \left( \frac{\sigma}{\mu} \right)^2 > \frac{\kappa_\nu \eta \sigma}{\mu},
\]

\[
2 + 4 \frac{1}{1} + 2 \left( \frac{1}{1} \right)^2 > \frac{1 \times 80 \times 1}{1},
\]

\[
242 > 80,
\]

with eigenvalues for the trivial solution:

\[
\text{eigenvalues of } J(SS_{\text{Ex.41}}) \Rightarrow [-10.83, -0.586 + 2.823i, -0.586 - 2.823i].
\]

Figure 5.3.18: This plot shows the three dimensional phase space of variables: total number of trees, the total volume of trees in the site and the seedling count. The trajectories shown are the same as those in Figure 5.3.17.

The outside trajectory, starting at point A, tends to the stable limit cycle, whereas, the trajectory starting at point C tends to the steady state. Notice, the initial point B, which is located just outside the dashed circle and tends to the stable limit cycle. This implies the existence of an unstable limit cycle which is depicted by the dashed line.

In our next example we will show the effect of disease on a site that is in a state of oscillation.
5.3.5 Example 5 (large initial forest volume and medium tree count with introduction of infected trees, high pathogen virulence)

In this example we consider a forest site with the same initial volume and tree count at initial instant of time as in Example 4. At time $\theta = 4$ an infectious agent is introduced in the forest. The parameters and initial values are listed below, and along the right hand side of each Figure.

Domain:
$\theta \in [0, 20]$ (time)

Initial Values:
- $v_u(0) = 0.03$ (initial uninfected volume)
- $v_i(0) = 0.0$ (initial infected volume)
- $\tilde{u}(0) = 0.2$ (initial uninfected total trees)
- $\tilde{w}(0) = 0.0$ (initial infected total trees)
- $s(0) = 1E-8$ (initial seedling count)

Resource Consumption:
- $\kappa_u = 0.1$ (rate of increase in size of uninfected tree)
- $\kappa_w = 0.05$ (rate of increase in size of infected tree)

Parameters:
- $\mu = .1$ (constant proportional to death rate of uninfected trees)
- $\gamma = .2$ (constant proportional to death rate of infected trees)
- $\rho = 0.60$ (pathogen virulence)
- $\eta = 80$ (competition between seedlings and adult trees)
- $\sigma = 1$ (constant proportional to seedling reestablishment)

As shown in the Figures 5.3.19- 5.3.24, the oscillatory behavior of the ODE model of Figures 5.3.11- 5.3.16 can be disrupted by introducing an infectious disease to a portion of the forest site. At time $\theta = 4$, 20% the forest site is infected with a highly infectious disease, $\rho = 60$. Recall the parameter $\rho$ governs the virulence of the pathogen. With the diseased portion now infecting other trees in the site, the evolution of the forest has been altered. We are able to break the cyclic pattern of the forest site.
Figure 5.3.19: This plot shows the oscillatory evolution of our previous example. The site has a large initial uninfected forest volume and small forest tree count with no infected trees at time $t = 0$. At time $t = 0$ a highly infectious pathogen is introduced, $p = 60$, in the site, where 20% of the forest becomes infected. This particular perturbation changes the cyclic pattern of the forest. Notice the stable limit cycle after the pathogen is introduced has become a positive attractor (stable focus).

After the disease is introduced, and because the inequality (4.2.12) is satisfied, the stable forest will have a segment of infected trees that remain. This steady state is obtained by equations (4.2.14)-(4.2.18), where we find,

$$SS_{(Ex.5)} \rightarrow \begin{cases} v^*_{u} = 0.00212, \\ v^*_{w} = 0.00549 \\ \bar{u}^* = 0.091 \\ \bar{w}^* = 0.15 \\ s^* = 0.391. \end{cases}$$

As we have seen before the trivial steady state has become unstable.
Figure 5.3.20: This plot shows the evolution of the total number of adult trees and seedlings. The parameters are the same as Figure 5.3.19.

Figure 5.3.21: This plot shows the projection of the phase space on the plane of variables: volume of the forest and the seedling count. The parameters are the same as in Figure 5.3.19.
Figure 5.3.22: This plot shows the projection of the phase space on the plane of variables: total number of trees on the site forest and the seedling count. The parameters are the same as in Figure 5.3.19.

Figure 5.3.23: This plot shows the projection of the phase space on the plane of variables: total number of trees and the volume of trees in the site. The parameters are the same as in Figure 5.3.19.
Figure 5.3.24: This plot shows the evolution of the carrying capacity. The parameters are the same as in Figure 5.3.19.

We will now show this same site where the pathogen virulence is slightly lower.

**5.3.6 Example 6 (large initial forest volume and medium tree count with introduction of infected trees, decreased pathogen virulence)**

In this example we consider a forest site with the same initial volume and tree count at initial instant of time as in Example 4. At time $\theta = A$ an infectious agent is introduce in the forest. The parameters and initial values are listed below, and along the right hand side of each Figure.

**Domain:**

$\theta \in [0, 30]$ (time)

**Initial Values:**

$v_u(0) = 0.03$ (initial uninfected volume)

$v_i(0) = 0.0$ (initial infected volume)

$\tilde{n}(0) = 0.2$ (initial uninfected total trees)

$\tilde{w}(0) = 0.0$ (initial infected total trees)

$s(0) = 1E - 8$ (initial seedling count)
Resource Consumption:

- $\kappa_u = 0.1$ (rate of increase in size of uninfected tree)
- $\kappa_w = 0.05$ (rate of increase in size of infected tree)

Parameters:

- $\mu = 0.1$ (constant proportional to death rate of uninfected trees)
- $\gamma = 0.2$ (constant proportional to death rate of infected trees)
- $\rho = 0.40$ (pathogen virulence)
- $\eta = 80$ (competition between seedlings and adult trees)
- $\sigma = 1$ (constant proportional to seedling reestablishment)

Figure 5.3.25: This plot shows an example with the same initial forest distribution as Figures 5.3.19-5.3.24. At time $\theta = 4$, an infectious pathogen with a slightly less virulence, $\rho = 0.40$, than that represented in Example 5 is introduced in the site, where 20% of the forest becomes infected. Notice the forest site responses by lowering the forest tree count and volume, followed by an increase in the amplitude of the subsequent seedling count peaks. The trajectory soon settles into a limit cycle as before, but with an increase in amplitude.
Figure 5.3.26: This is a plot of the total trees and seedlings on the site. The parameters are the same as in Figure 5.3.25.

Figure 5.3.27: This plot shows the projection of the phase space on the plane of variables: volume of the forest and the seedling count. The parameters are the same as in Figure 5.3.25.
Figure 5.3.28: This plot shows the projection of the phase space on the plane of variables: total number of trees on the site forest and the seedling count. The parameters are the same as in Figure 5.3.25.

Figure 5.3.29: This plot shows the projection of the phase space on the plane of variables: total number of trees and the volume of trees in the site. The parameters are the same as in Figure 5.3.25.
Figure 5.3.30: This plot shows the evolution of the carrying capacity. The parameters are the same as in Figure 5.3.25.

As shown in the Figures 5.3.25-5.3.30, the oscillatory behavior of the ODE model of Figures 5.3.11-5.3.16 can be disrupted by introducing an infectious disease to a portion of the forest site. At time $\theta = A$, 20% the forest site is infected with an infectious disease, $p = 40$, half as infectious as Example 5. With the diseased portion infecting other trees in the site but with a lesser virulence, the evolution of the forest has only slightly been altered. We are not able to break the cyclic pattern of the forest site. The oscillations remain, but with a larger amplitude. Notice the forest has a portion of infected trees that remains with an oscillatory pattern. The stable steady state for the trivial trajectory remains unstable, therefore an unstable limit cycle does not exist in this site.
Chapter 6

Conclusion

The introduction of disease into a forest site has been modeled to show that the effect is not completely destructive to the forest system. Factors that were shown to affect the behavior of the forest system were, mortality of infected trees caused by the type of disease, pathogen virulence and competition for resources between adult trees and seedlings.

When the rate coefficients for mortality of uninfected and infected trees has the same order of magnitude, the forest system tended to a steady state with infected trees. Whereas, trees on a forest site infected by a highly necrotic disease died out of the system, leaving no diseased trees in the forest. When competition for resources between adult trees and seedlings was high, the forest site showed oscillatory behavior. These oscillations, in both forest volume and tree count, were shown to be altered by pathogen virulence. When the infectious agent had a relatively low virulence the amplitude of oscillation increased, while a higher virulence broke the oscillatory behavior and the system tended to a steady state.

Although diseased trees are generally considered to be undesirable, from this model the introduction of an infectious agent in the forest system can be an effective tool to control over-growth or saturation of a forest site and can contribute to the successful rehabilitation of forest systems.
Appendix A

Numerical schemes

A.1 Numerical scheme for solving the IPDE model

The method of finite differences is used to produce an approximation for the boundary value problem consisting of a set of integro-partial differential equations (we write them out once again for convenience).

\[ \frac{\partial u(\theta, \alpha)}{\partial \theta} + \frac{\partial u(\theta, \alpha)}{\partial \alpha} = -u(\theta, \alpha) - \frac{\rho}{\mu} v_u(\theta) u(\theta, \alpha), \quad (A.1.1) \]

\[ \frac{\partial w(\theta, \alpha)}{\partial \theta} + \frac{\partial w(\theta, \alpha)}{\partial \alpha} = -\gamma \frac{\mu}{\mu} w(\theta, \alpha) + \frac{\rho}{\mu} v_w(\theta) u(\theta, \alpha), \quad (A.1.2) \]

where,

\[ v_u(\theta) = \int_0^{\mu \alpha_{\text{max}}} u(\theta, \alpha) b_u(\alpha) d\alpha, \quad (A.1.3) \]

\[ v_w(\theta) = \int_0^{\mu \alpha_{\text{max}}} w(\theta, \alpha) b_w(\alpha) d\alpha, \quad (A.1.4) \]

\[ \frac{ds(\theta)}{d\theta} = \frac{\sigma}{\mu} s(\theta) \left( 1 - \frac{s(\theta)}{\max(s_{\text{min}}, 1 - \eta (v_u(\theta) + v_w(\theta)))} \right), \quad (A.1.5) \]

Conditions are (3.2.17)-(3.2.20), (3.2.25), (3.2.26), and (3.2.32). We use \( N \) equal time steps \( \Delta \theta \) across the domain \([0, T^*]\) and \( M \) equal time steps \( \Delta \alpha \) across the domain \([0, \mu \alpha_{\text{max}}]\):

\[ \theta_n = n \frac{T^*}{N} \quad \text{for} \quad n = 0, 1, 2 \cdots N \quad (A.1.6) \]

\[ \alpha_m = m \frac{\mu \alpha_{\text{max}}}{M} \quad \text{for} \quad m = 0, 1, 2 \cdots M \quad (A.1.7) \]
The derivatives of the LHS of (A.1.1), (A.1.2), and (A.1.5) are estimated by the Euler method, where we use the first two terms of the Taylor series expansion. For the uninfected tree count $u(\theta, \alpha)$ we find,

$$u(\theta, \alpha + \Delta \alpha) = u(\theta, \alpha) + \frac{\partial u(\theta, \alpha)}{\partial \alpha} \Delta \alpha + \frac{\partial^2 u(\theta, \xi)}{\partial \alpha^2} \Delta \alpha^2, \quad \text{for} \quad \alpha \leq \xi \leq \alpha + \Delta \alpha. \quad (A.1.8)$$

$$u(\theta + \Delta \theta, \alpha) = u(\theta, \alpha) + \frac{\partial u(\theta, \alpha)}{\partial \theta} \Delta \theta + \frac{\partial^2 u(\theta, \xi, \alpha)}{\partial \theta^2} \Delta \theta^2, \quad \text{for} \quad \theta \leq \xi \leq \theta + \Delta \theta. \quad (A.1.9)$$

Equations (A.1.8) and (A.1.9) can be rearranged and combined to obtain

$$\frac{\partial u(\theta, \alpha)}{\partial \theta} + \frac{\partial u(\theta, \alpha)}{\partial \alpha} = \frac{u(\theta_{n+1}, \alpha_m) - u(\theta_n, \alpha_m)}{\Delta \theta} + \frac{u(\theta_n, \alpha_{m+1}) - u(\theta_n, \alpha_m)}{\Delta \alpha} + O(\Delta). \quad (A.1.10)$$

In equation (A.1.10) we have introduced discretized notation and let $\max(\frac{\partial^2 u(\theta, \xi, \alpha)}{\partial \alpha^2} \Delta \alpha, \frac{\partial^2 u(\theta, \xi, \alpha)}{\partial \theta^2} \Delta \theta) = O(\Delta)$. Similarly we find,

$$\frac{\partial w(\theta, \alpha)}{\partial \theta} + \frac{\partial w(\theta, \alpha)}{\partial \alpha} = \frac{w(\theta_{n+1}, \alpha_m) - w(\theta_n, \alpha_m)}{\Delta \theta} + \frac{w(\theta_n, \alpha_{m+1}) - w(\theta_n, \alpha_m)}{\Delta \alpha} + O(\Delta), \quad (A.1.11)$$

$$\frac{ds(\theta)}{d\theta} = \frac{s(\theta_{n+1}) - s(\theta_n)}{\Delta \theta} + O(\Delta \theta). \quad (A.1.12)$$

Though there are many methods to estimate integrals, we choose the simple trapezoidal method [7] to estimate $v_u(\theta_n)$ and $v_w(\theta_n)$ given by equations (A.1.3) and (A.1.4), the total volume of uninfected and infected trees at $\theta_n$, respectively:

$$v_u(\theta_n) = \Delta \alpha \left[ \frac{u(\theta_n, \alpha_0) b_u(\alpha_0) + u(\theta_n, \alpha_M) b_u(\alpha_M)}{2} \right] + \Delta \alpha M^{-1} \sum_{m=1}^{M-1} u(\theta_n, \alpha_m) b_u(\alpha_m) + O(\Delta \alpha^2), \quad (A.1.13)$$

$$v_w(\theta_n) = \Delta \alpha \left[ \frac{w(\theta_n, \alpha_0) b_w(\alpha_0) + w(\theta_n, \alpha_M) b_w(\alpha_M)}{2} \right] + \Delta \alpha M^{-1} \sum_{m=1}^{M-1} w(\theta_n, \alpha_m) b_w(\alpha_m) + O(\Delta \alpha^2). \quad (A.1.14)$$
We can approximate the number of trees at $\mu a_{\text{max}}$ as follows:

\[ u(\theta, \mu a_{\text{max}}) \approx 0, \quad (A.1.15) \]

\[ w(\theta, \mu a_{\text{max}}) \approx 0. \quad (A.1.16) \]

Using (3.2.24), (A.1.15) and (A.1.16) we can simplify (A.1.13) and (A.1.14) to obtain

\[ v_u(\theta_n) = \Delta \alpha \sum_{m=1}^{M-1} u(\theta_n, \alpha_m) b_u(\alpha_m) + O(\Delta \alpha^2). \quad (A.1.17) \]

\[ v_w(\theta_n) = \Delta \alpha \sum_{m=1}^{M-1} w(\theta_n, \alpha_m) b_w(\alpha_m) + O(\Delta \alpha^2). \quad (A.1.18) \]

Substituting (A.1.10), (A.1.11), (A.1.12), (A.1.17) and (A.1.18) into (A.1.1), (A.1.2) and (A.1.5), and solving for $u(\theta_{n+1}, \alpha_m)$, $w(\theta_{n+1}, \alpha_m)$, and $s(\theta_{n+1})$, respectively, we obtain the discretized form:

\[ u_{m+1}^{n+1} = \left[ -1 - \frac{\rho}{\mu} \Delta \alpha \sum_{m=1}^{M-1} w_m^n(b_w)_m \right] + 1 + \frac{\Delta \theta}{\Delta \alpha} u_m^n - \frac{\Delta \theta}{\Delta \alpha} u_{m+1}^n, \quad (A.1.19) \]

\[ w_{m+1}^{n+1} = \left[ \frac{\gamma}{\mu} + \frac{\rho}{\mu} \Delta \alpha \sum_{m=1}^{M-1} w_m^n(b_w)_m \right] + 1 + \frac{\Delta \theta}{\Delta \alpha} w_m^n - \frac{\Delta \theta}{\Delta \alpha} w_{m+1}^n, \quad (A.1.20) \]

\[ s^{n+1} = s^n + \Delta \alpha \frac{\sigma}{\mu} s^n \left( 1 - \frac{s^n}{\max(s_{\text{min}}, 1 - \eta \Delta \alpha \sum_{m=1}^{M-1} (u_m^n(b_u)_m + w_m^n(b_w)_m))} \right), \quad (A.1.21) \]

with initial values (3.2.17)-(3.2.20), (3.2.25), (3.2.26), and (3.2.32).

### A.2 Numerical scheme for solving the ODE model

The method of finite differences is used to produce an approximation for the boundary value problem consisting of a set of ordinary differential equations (we write them out once again for convenience).

\[ \frac{dv_u(\theta)}{d\theta} = \kappa_u \tilde{u}(\theta) - v_u(\theta) - \frac{\rho}{\mu} v_w(\theta) v_u(\theta), \quad (A.2.1) \]

\[ \frac{dv_w(\theta)}{d\theta} = \kappa_w \tilde{w}(\theta) - \frac{\gamma}{\mu} v_w(\theta) + \frac{\rho}{\mu} \frac{\kappa_w}{\kappa_u} v_u(\theta) v_w(\theta). \quad (A.2.2) \]
\[ \frac{d\tilde{u}(\theta)}{d\theta} = s(\theta) - \tilde{u}(\theta) - \frac{\rho}{\mu} v_w(\theta) \tilde{u}(\theta). \]  

(A.2.3)

\[ \frac{d\tilde{v}(\theta)}{d\theta} = -\gamma \tilde{v}(\theta) + \frac{\rho}{\mu} v_w(\theta) \tilde{v}(\theta), \]  

(A.2.4)

\[ \frac{ds(\theta)}{d\theta} = \frac{\sigma}{\mu} s(\theta) \left( 1 - \frac{s(\theta)}{\max(s_{\text{min}}, 1 - \eta(v_u(\theta) + v_w(\theta)))} \right), \]  

(A.2.5)

(A.2.6)

with initial conditions,

\[ v_u(0) = v_u^0, \]
\[ v_w(0) = v_w^0, \]
\[ \tilde{u}(0) = u^0, \]
\[ \tilde{v}(0) = v^0, \]
\[ s(0) = s^0. \]  

(A.2.7)

We use \( N \) equal time steps \( \Delta \theta \) across the domain \([0, T^*] \):

\[ \theta_n = n \frac{T^*}{N} \quad \text{for} \quad n = 0, 1, 2 \cdots \]  

(A.2.8)

The derivatives of the LHS of (A.2.1)-(A.2.5) are estimated by the Euler method, where we use the first two terms of the Taylor series expansion. For the uninfected tree volume \( v_u(\theta) \) we find,

\[ v_u(\theta + \Delta \theta) = v_u(\theta) + \frac{\partial v_u(\theta)}{\partial \theta} \Delta \theta + \frac{\partial^2 v_u(\xi)}{\partial \theta^2} \Delta \theta^2, \quad \text{for} \quad \theta \leq \xi \leq \theta + \Delta \theta. \]  

(A.2.9)

Equation (A.2.9) can be rearranged and combined to obtain

\[ \frac{dv_u(\theta)}{d\theta} = \frac{v_u(\theta_{n+1}) - v_u(\theta_n)}{\Delta \theta} + O(\Delta \theta), \]  

(A.2.10)

Similarly we find,

\[ \frac{dv_w(\theta)}{d\theta} = \frac{v_w(\theta_{n+1}) - v_w(\theta_n)}{\Delta \theta} + O(\Delta \theta). \]  

(A.2.11)

\[ \frac{d\tilde{u}(\theta)}{d\theta} = \frac{\tilde{u}(\theta_{n+1}) - \tilde{u}(\theta_n)}{\Delta \theta} + O(\Delta \theta). \]  

(A.2.12)

\[ \frac{d\tilde{v}(\theta)}{d\theta} = \frac{\tilde{v}(\theta_{n+1}) - \tilde{v}(\theta_n)}{\Delta \theta} + O(\Delta \theta). \]  

(A.2.13)
By substitution (A.2.10)-(A.2.14) into (A.2.1)-(A.2.5), respectively, and solving for \( \nu_u(\theta_n+1) \), \( \nu_w(\theta_n+1) \), \( \tilde{\nu}(\theta_n+1) \), \( \tilde{\nu}(\theta_n+1) \), and \( s(\theta_n+1) \), we obtain the system in discretized form:

\[
\frac{ds(\theta)}{d\theta} = s(\theta_{n+1}) - s(\theta_n) + O(\Delta \theta), \tag{A.2.14}
\]

\[
\left(\begin{array}{l}
(v_u)_n+1 = (v_u)_n + \Delta \theta \left[ \kappa_u \tilde{u}_n - (v_u)_n - \frac{\rho}{\mu} (v_w)_n (v_u)_n \right],
\end{array}\right)
\tag{A.2.15}
\]

\[
\left(\begin{array}{l}
(v_w)_n+1 = (v_w)_n + \Delta \theta \left[ \kappa_w \tilde{w}_n - \gamma (v_w)_n + \frac{\rho \kappa_w}{\mu} (v_u)_n (v_w)_n \right],
\end{array}\right)
\tag{A.2.16}
\]

\[
\tilde{u}_n+1 = \tilde{u}_n + \Delta \theta \left[ s_n - \tilde{u}_n - \frac{\rho}{\mu} (v_w)_n \tilde{u}_n \right], \tag{A.2.17}
\]

\[
\tilde{w}_n+1 = \tilde{w}_n - \Delta \theta \left[ \frac{\gamma}{\mu} \tilde{w}_n - \frac{\rho}{\mu} (v_w)_n \tilde{u}_n \right], \tag{A.2.18}
\]

\[
s_{n+1} = s_n + \Delta \theta \left[ \frac{\sigma}{\mu} s_n \left( 1 - \frac{s_n}{\max(s_{\min}, 1 - \eta ((v_u)_n + (v_w)_n))} \right) \right], \tag{A.2.19}
\]

Initial conditions for this set are (3.2.25), (3.2.26), (3.2.28), (3.2.32), (4.1.14) and (4.1.15).
Bibliography


