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MODELING THE SPREAD OF ALFALFA STEM NEMATODES:

INSIGHTS INTO THEIR DYNAMICS AND CONTROL

by

Scott G. Jordan

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Mathematical Sciences

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Logan, Utah

2018

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ABSTRACT

Modeling the Spread of Alfalfa Stem Nematodes:
Insights into their Dynamics and Control

by

Scott G. Jordan, Doctor of Philosophy

Utah State University, 2018

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Department: Mathematics and Statistics

Alfalfa is a major cash crop in the western United States, where fields that are infested with the alfalfa stem nematode (*Ditylenchus dipsaci*) can be found. With no nematicides available to control alfalfa stem nematode spread, growers can use nematode resistant varieties of alfalfa to manage nematode populations in a field. A deterministic, discrete-time, host-parasite model is presented that describes the spread of alfalfa stem nematodes on resistant hosts that was fit to experimental data obtained in Weber County, Utah. Numerical results obtained from simulations with the model are used to compare how varying levels of resistance can affect harvest yield.

Resistant varieties can also affect the invasion speeds of epidemics in crops. A continuous time, spatial model is presented that describes how these resistant varieties affect invasion speeds in general crop systems. Speeds of traveling wave fronts are determined for simple epidemics in crops that contain a mixture of resistant and non-resistant hosts. For the model, the wave speeds are found to be proportional to the fraction of resistant individuals. The conclusions are reached through the application of the linear conjecture and verified by comparing the results with numerical solutions of the non-linear model.

The speed of invasion for the alfalfa stem nematode can be determined through the moment generating function associated with the contact distribution of the dispersal process. We present a spatial model for the spread of alfalfa stem nematodes that uses a Gaussian as the contact distribution, parameterized by experimental data. With

this we proceed to approximate the speed of nematode invasive fronts in absence of advection, i.e. without nematode transport through flood irrigation. The parameterized probability kernel is then used to calculate front speeds when resistant varieties of alfalfa are introduced. We found that, unsurprisingly, invasive speeds are relatively low and cannot support the rapid dispersal of the disease among fields as seen in practice. However, this result leads to conjecture that changing current irrigation practices, from flood to sprinkle irrigation, could effectively contribute to control the spread of alfalfa stem nematodes.

Resistant varieties of alfalfa can be used to effectively control the spread of the alfalfa stem nematode. In this work we have shown that using resistant varieties of alfalfa can increase yield up to 83%, they can slow down invasion speeds of nematodes, and switching from flood to sprinkler irrigation could effectively contribute to the control of the alfalfa stem nematode.

(71 pages)

PUBLIC ABSTRACT

Modeling the Spread of Alfalfa Stem Nematodes:
Insights into their Dynamics and Control

Scott G. Jordan

Alfalfa is a major cash crop in the western United States, where fields that are infested with the alfalfa stem nematode (*Ditylenchus dipsaci*) can be found. With no nematicides available to control alfalfa stem nematode spread, growers can use nematode resistant varieties of alfalfa to manage nematode populations in a field. A deterministic, discrete-time, host-parasite model is presented that describes the spread of alfalfa stem nematodes on resistant hosts that was fit to experimental data obtained in Weber County, Utah. Numerical results obtained from simulations with the model are used to compare how varying levels of resistance can affect harvest yield.

Resistant varieties can also affect the invasion speeds of epidemics in crops. A continuous time, spatial model is presented that describes how these resistant varieties affect invasion speeds in general crop systems. Speeds of traveling wave fronts are determined for simple epidemics in crops that contain a mixture of resistant and non-resistant hosts. For the model, it was found that the wave speeds will slow down as highly nematode resistant varieties of alfalfa are used.

The speed of invasion for the alfalfa stem nematode can be determined by using a mathematical relationship that is known as the contact distribution. We present a spatial model for the spread of alfalfa stem nematodes that uses a Gaussian distribution as the contact distribution of the alfalfa stem nematodes, which was determined by experimental data. Using this contact distribution we are able to approximate the speed of nematode invasive fronts in absence of advection, i.e. without nematode transport through flood irrigation. The contact distribution is then used to calculate front speeds when resistant varieties of alfalfa are introduced. We found that, unsurprisingly, invasive speeds are relatively low and cannot support the rapid dispersal of the disease

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Chapter 1

INTRODUCTION

1.1 Importance of alfalfa

In the history of alfalfa, western states have played an important part that has led to its current status as the nations' 4th largest commodity [Putnam et al. 2000, Sumner and Rosen 2011]. Alfalfa has become a critical cash crop in these western states. Many farmers and ranchers depend on alfalfa as a mainstay crop because it has a high biomass production, which makes it a great animal feed. As the demand for alfalfa increases, so does the need for farmers to produce quality alfalfa.

While alfalfa is often characterized as being of “low value”, its true economic impact is much greater than just its gross receipts. Alfalfa is the beginning of a complex food chain, and affects many industries from dairying to wool and beef production. To an end, alfalfa plays an important role in the creation of milk, cheese, ice cream, honey, leather, etc. The many end-uses are worth billions of dollars more than the value of the crop itself [Putnam et al. 2001]. Alfalfa is the humble beginning of all these great things that people enjoy.

There are many benefits of planting alfalfa. For example, it creates a year-round canopy that helps protect the soil from erosion [Putnam et al. 2001]. It also leaves behind nitrogen in the soil which improves the soil structure for the crop that follows [Putnam et al. 2001]. The primary use of alfalfa is in dairy production [Putnam et al. 2001]. However, alfalfa is also used extensively as feed for horses, sheep, and other animals. Without alfalfa, many farms and ranches would fail [Putnam et al. 2001]. That failure would be seen in grocery stores and food chains all over the United States.

1.2 General nematode biology

Alfalfa is attacked by a pest known as the alfalfa stem nematode, *Ditylenchus dipsaci*. It is a microscopic, colorless, non-segmented roundworm that attacks and reproduces inside alfalfa [Evans et al. 2008]. In general, nematodes are pseudocoelomate, unsegmented worm-like animals, commonly described as filiform or thread-like, a characteristic reflected by the taxon name *nema* (Greek, *nema*=thread) and its nominative plural *nemata* [Decraemer and Hunt 2006]. Nematodes are the most numerous Metazoa, a zoological group comprising of multicellular, eukaryotic organisms, on earth [Decraemer and Hunt 2006]. They are either free living or parasites of plants. Although they occur in almost every habitat, they are essentially aquatic animals. They depend on moisture for their movement. Soil moisture, relative humidity, and other environmental factors directly affect their survival. In adverse environmental conditions, such as extreme heat or cold, alfalfa stem nematodes can survive in an anhydrobiotic state, which is characterized by controlling how the body loses water [Decraemer and Hunt 2006]. Even though nematodes can have a variety of lifestyles they have a relatively conserved body plan. The body consists of an external cylinder (the body wall) and an internal cylinder (the digestive system) separated by a pseudocoelomic cavity filled with fluid under pressure. The internal cylinder also contains a number of cells and other organs. About 99% of known nematodes have a long, thin cylindrical body shape, which is round in cross-sections and tapered towards the ends [Decraemer and Hunt 2006]. The body length of plant-parasitic nematodes is usually smaller than 1 mm in length.

Life cycles of nematodes typically include an egg stage, four juvenile stages, and lastly the adult stage. The egg is usually cylindrical with a chorion/eggshell of varying thickness. Most nematodes moult four times before becoming an adult [Decraemer and Hunt 2006]. In some groups of nematodes one juvenile stage is more resistant to environmental stress than the others. This juvenile stage is specialized for dispersal to infect new host plants or for surviving adverse environmental conditions. This stage is typically called the infectious stage.

1.3 Alfalfa stem nematode biology

Ditylenchus dipsaci is commonly known as the stem and bulb nematode. It has one of the widest impacts on agriculture. The maxim 'where a plant is able to live, a nematode is able to attack it' describes the problem very well. The host range of

Ditylenchus dipsaci includes more than 300 plant species. More than 30 physiological races of the nematode are known [Duncan and Moens 2006]. Many of those races are host-specific and others are widely polyphagous, able to feed on various kinds of food. It is a serious pest of clover, pea, celery, garlic, onion, strawberry, alfalfa, and many others. Races of *Ditylenchus dipsaci* are named after the crop from which they were identified or after a major host [Duncan and Moens 2006].

The alfalfa stem nematode, (ASN), is a race of *Ditylenchus dipsaci* that is a plant parasite of alfalfa that can dramatically reduce plant stand and forage yields, raising considerable concern in alfalfa producers. The nematodes feed in the parenchymatous tissues of stems, where all life stages occur [Duncan and Moens 2006]. They can also be found in foliage, inflorescences, buds, rhizomes, and stolons. Symptoms of stem nematode parasitism in alfalfa are stunted and swollen stems, stem necrosis, white flagging of leaves and stems, crown rot, and stand decline [Evans et al. 2008, Gray and Franc 1993]. These symptoms are exacerbated by low temperatures [Williams-Woodward and Gray 1999]. The effects of ASN infested alfalfa crops result in a lower yield at harvest and consequently induce economic losses [Nicol et. al. 2011].

As a parasite of above-ground parts of a plant, ASN is not hindered from changes in ambient weather conditions. As a result, ASN is highly resistant to desiccation and is adapted for survival. In the absence of suitable hosts or during harsh environmental conditions nematodes in the soil undergo a physical transformation that allows them to survive in a dormant state called *anhydrobiosis* [Evans et al. 2008]. Anhydrobiosis is when the nematode enters an almost completely desiccated state which stabilizes its cellular structures and protects it from harsh environmental factors, such as extreme heat or cold. Anhydrobiosis can allow ASNs to stay dormant in the soil for long periods of time (years) waiting for the right host plant to appear. As a result, it may take several years of crop rotation to ensure that it is safe enough to plant alfalfa again without the risk of a rapid rise of a nematode outbreak.

It is in the spring, with optimal temperatures around 5°C-18°C, that ASNs are most active [Norton 1978]. It is during this time that they begin to leave infested alfalfa plants in search for nematode-free hosts. It is the fourth-stage juvenile (J4) that is the primary survival and infective stage [Duncan and Moens 2006]. When conditions are prime, ASN migrate to germinating host plants and invade hypocotyls or petioles,

entering through the stomata or penetrating the epidermis. Once the J4 enters a new host it proceeds to moult into an adult. Reproduction and population growth can occur very rapidly. A single female can lay 200-500 eggs in its lifetime [Duncan and Moens 2006]. The offspring quickly goes through the four juvenile stages until they reach adulthood in about 19-23 days [Evans et al. 2008]. Eventually, the J4 stage will leave the stem and go back into the soil to repeat the cycle [Evans et al. 2008, Norton 1978]. This rapid population growth can result in severe crop damage even with an initial low density population. As the season progresses, however, reproduction slows down as a result of the rising temperatures and lower soil moisture [Williams-Woodward and Gray 1999].

As previously discussed, infestation can cause alfalfa plants to decay. As they decay this directly affects the plants ability to produce high yielding and quality hay during the field season (summer). Similarly, as winter approaches and temperatures decrease, the nematodes become less active [Williams-Woodward and Gray 1999]. Masses of anhydrobiotic ASN can overwinter in dried plant debris in the field [Duncan and Moens 2006]. Plants damaged from ASN may become less likely to survive winter dormancy and may not reach their yield potential the following field season. This is because once a plant becomes infected, it stays infected.

1.4 Methods of control

In the past, chemical pesticides have been used as a control method for nematodes. Some examples are Carbofuran and Methyl Bromide. These pesticides have been deemed harmful by the EPA and have since been removed from the approved pesticide list. With the removal it have become vital that strategies are found to control ASN populations within a field to help prevent unnecessary economic loss. The main practices used to control the effects of ASNs are crop rotation and the use of nematode resistant varieties of alfalfa.

Crop rotation is defined as the replacement of the current crop with a different crop. As for the case of alfalfa growers with an ASN infestation, crop rotation is when the alfalfa is replaced by a non-host of the ASN, such as barley, wheat, sorghum, or corn [Evans et al. 2008]. Without a host crop for reproduction the nematode population in the soil will decrease over time [Evans et al. 2008, Gray and Franc 1993]. After a number of years, usually determined by the grower, alfalfa is planted again with

the hope that the nematode population in the soil has decreased enough allowing alfalfa to be planted again without a sudden resurgence of nematodes. Crop rotation works well for ASN because they are specific to their host. ASN attacks and reproduces only inside alfalfa (*Medicago sativa*) and sainfoin (*Onobrychis viciifolia*) plants [Evans et al. 2008]. Typically, a 2-3 year crop rotation is sufficient to suppress the ASN population [Gray and Franc 1993, Jordan et al. 2017]. For some farmers, crop rotation may be burdensome because it may require additional equipment for another crop type, another crop may not be as profitable as alfalfa, or the environmental impact of crop rotation may not be desirable [Brankatschk and Finkbeiner 2015].

Some questions that arise are, what can farmers do to increase the time between crop rotations, and what can they do to minimize yield loss due to ASN infestation? The use of resistant varieties of alfalfa can help answer these questions. Resistant varieties of alfalfa are designed to affect how nematodes mature and reproduce within the plant [Schomaker and Been 2006], effectively slowing down the ASN infestation throughout a field. Resistance is defined as a plants ability to withstand, oppose, lessen, or overcome the attack of a pathogen [Rhode 1972]. A plant resistant to nematodes resists attack or exhibits little damage and reduces the nematode population [Giebel 1974]. There are four main types of resistance that can be utilized. (i) The plant may produce toxins that are harmful to the nematodes. (ii) The plant may fail to provide adequate conditions for the nematode to survive. (iii) Plants can secrete chemicals that will repel nematodes. (iv) Plants hypersensitivity will cause the nematodes to die [Giebel 1974]. Hypersensitivity is when the cells around the nematodes undergo necrosis, thereby trapping the nematodes and preventing further infestation and reproduction. The exact plant defense mechanisms used by alfalfa plants against ASN is not clear. Given the high genetic variability of alfalfa it can be challenging to determine the specific mechanism, and with this variability resistance is evaluated at the plant population level. It is also possible that different varieties may have different defense mechanisms against ASN. What is clear is that varieties that have been classified as resistant reduce the negative effects of an ASN infestation. Thus, allowing farmers to grow alfalfa for longer periods of time between crop rotations. Also, resistant varieties of alfalfa can be more tolerant to ASN. In other words, resistant varieties will not be stunted like non-resistant varieties, which allows for greater yields at harvest.

In Chapter 2, a deterministic, discrete-time model was used to explore how different levels of resistance to nematodes in alfalfa plants affects the yield produced at harvest. To do this, an extension of the model used in [Jordan et al. 2017] is used along with data obtained from experiments conducted in Weber County, Utah. The model describes harvest yield based off of the number of plants and the approximate weight of each plant, which depends on nematode infestation and the resistance rating. A comparison is presented to show how the varying levels of nematode resistance will affect the harvest yield of the alfalfa crop.

After determining how the resistant varieties of alfalfa affected yield, I considered how these varieties affect the spread of the nematodes throughout a field. In order to answer that question we needed to explore a new model that takes into account space and time. Spatial continuous models for disease spread, i.e. models that assume individuals continuously distributed in space, have been widely used as a realistic approach to understanding how crop disease dispersal progresses, [Madden et al. 2011]. One characteristic that makes this approach interesting is that it describes the wave-like expanding traveling fronts of diseases moving at speeds that can be determined, see [Madden et al. 2011] and [Ruan 2007] for extensive reviews.

In Chapter 3, the goal was to determine *how the speed of propagation of a simple epidemic in crops was affected by the introduction of resistant individuals?* First, we need to clarify that what characterizes a “resistant individual” is the set of specific artificially modified traits that allow the individual to fight the invasion of clearly identified micro or macro parasites. That is to say, the attributes of a resistant individual are specific to each crop-pest system under consideration. Although the model described in Chapter 3 does not make reference to a particular crop system, we stress that it was motivated by the attributes of nematode-resistant alfalfa varieties designed to control stem nematodes [Jordan et al. 2017]. In that case, resistant individuals are *not* immune to the attacks of nematodes but are designed to diminish the damage on the hosts so that farmers can still recover a significant fraction of normal yield from each plant. As a consequence, infected resistant hosts have a decreased rather than zero transmission rate.

We examine a one-dimensional spatial model for simple epidemics (SI), as defined

in [Mollison 1972], with the addition of two classes: resistant-susceptible and resistant-infected individuals. The model uses a generalization of the mass action term, introduced by D.G. Kendall in [Kendall 1957], where the factor corresponding to the infectives is replaced by a spatial average of infectives. The speeds of traveling wave solutions for the linearized model can be determined in relation to those in the system that does not include resistant individuals. Then the so-called “linear conjecture” [van den Bosch and Metz and Diekmann 1990, Sattenspiel 2009], which has been used for instance to successfully approximate the speed of disease fronts for fungal crop diseases in two spatial dimensions [Metz and van den Bosch 1995], is used to conclude that the speeds found are a good approximation to those in the non-linear model. We validate this approximation by comparing the results with the speeds obtained from numerical computations of the non-linear system.

Chapter 4 outlines the details of an experiment designed to approximate the contact distribution of the ASN, which to the best knowledge of the authors has not been estimated before. In the experiment alfalfa stem nematodes were placed at varying distances from nematode-free alfalfa plants. After six weeks the alfalfa plants were inspected for nematode presence. The plant counts at each distance were then used for the fitting of a Gaussian distribution. This approximated contact distribution is then used in the model from Chapter 3 to estimate invasion speeds for the ASN when a mixture with resistant varieties of alfalfa is used.

Chapter 2

YIELD TO THE RESISTANCE: THE IMPACT OF NEMATODE RESISTANT VARIETIES ON ALFALFA YIELD

The content of this chapter has been published in *Natural Resource Modeling*.

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2.1 Introduction

The alfalfa stem nematodes (ASN), *Ditylenchus dipsaci*, is a major threat to alfalfa production. It is a microscopic roundworm that infests alfalfa. Once infested, the alfalfa plant is stunted and as a result harvest yield declines, which in turn causes economic loss. This is a problem since alfalfa is a major cash crop of the western United States and as such many aspects of our lives depend on its production (e.g., dairy production, feed for ranches, honey production, etc.)

It is vital that strategies are found to control ASN populations within a field to help prevent unnecessary economic loss. Since there are no nematicides currently available to use, the main practices used to control the effects of ASNs are crop rotation and the use of nematode resistant varieties of alfalfa. Crop rotation is defined as the replacement of the current crop with a different crop. As for the case of alfalfa growers with an ASN infestation, crop rotation is when the alfalfa is replaced by a non-host of the ASN. Some examples of non-host crops are wheat and barley. Typically, a 2-3 year crop rotation is sufficient to suppress the ASN population [Gray and Franc 1993, Jordan et al. 2017]. The downside of crop rotation is that farmers will have to grow a crop that does not profit them as much as alfalfa would. Some questions that arise are, what can farmers do to increase the time between crop rotations, and what can they do to minimize yield loss due to ASN infestation? The use of resistant varieties of alfalfa can help answer

these questions. Resistant varieties of alfalfa are designed to affect how nematodes mature and reproduce within the plant [Schomaker and Been 2006], effectively slowing down the ASN infestation throughout a field. Thus, allowing farmers to grow alfalfa for longer periods of time between crop rotations. Also, resistant varieties of alfalfa can be more tolerant to ASN. In other words, resistant varieties will not be stunted like non-resistant varieties, which allows for greater yields at harvest.

Seinhorst (1967) was one of the first people to come up with a model that would show the relationship between nematode density and plant growth. Since then many authors have used adaptations of Seinhorst's equations to model nematode population growth within a field [van den Berg and Rossing 2005, Ehwaeti et al. 2000].

In this paper, a deterministic, discrete-time model is used to explore how different levels of resistance to nematodes in alfalfa plants affects the yield produced at harvest. To do this, an extension of the model used in [Jordan et al. 2017] is used along with data obtained from experiments conducted in Weber County, Utah. The model describes harvest yield based off of the number of plants and the approximate weight of each plant, which depends on nematode infestation and the resistance rating. A comparison is presented to show how the varying levels of nematode resistance will affect the harvest yield of the alfalfa crop.

2.2 Resistant Varieties of Alfalfa

Resistance is defined as a plants ability to withstand, oppose, lessen, or overcome the attack of a pathogen [Rhode 1972]. A plant resistant to nematodes resists attack or exhibits little damage and reduces the nematode population [Giebel 1974]. There are four main types of resistance that can be utilized. (i) The plant may produce toxins that are harmful to the nematodes. (ii) The plant may fail to provide adequate conditions for the nematode to survive. (iii) Plants can secrete chemicals that will repel nematodes. (iv) Plants hypersensitivity will cause the nematodes to die [Giebel 1974]. Hypersensitivity is when the cells around the nematodes undergo necrosis, thereby trapping the nematodes and preventing further infestation and reproduction.

In alfalfa, resistance is expressed as necrosis, reduced gall formation, and reduced reproduction of nematodes [Rhode 1972]. Resistant varieties of alfalfa will help to slow

down the spread of a nematode population throughout a field. They will also help to lessen the economic loss incurred because of the infestation.

Breeding programs have been developed to produce resistant varieties of alfalfa. What a breeding program does to produce a new variety is take a current one that has desirable characteristics, like pest resistance, then it is cross pollenated with a variety that does not have those same characteristics. The result is a new variety that has characteristics from both parent plants. These programs came into existence after the first nematode resistant gene was cloned, (*Hs^{pro1}* from wild beet) [Gheysen and Jones 2006]. Plant breeding does not guarantee that all seeds produced will be resistant to nematodes. This is due to the genetic diversity of the alfalfa plant. To account for this, each variety produced is given a resistant rating. These resistance ratings correspond to a percentage range that describes the approximate number of seeds contained in the bag that will be resistant to nematodes. Table 2.1 shows the different resistance ratings according to the National Alfalfa and Forage Alliance 2016 Alfalfa Varieties Ratings Leaflet. For example, if a bag of alfalfa seeds is purchased and it is classified as having moderate resistance, then approximately 15 – 30% of the seeds will be resistant to nematodes, while the remaining percentage will not be.

Resistance Ratings: Percentage of resistant seed used in field	
Percentage	Resistance Class
0-5%	Susceptible
6-14%	Low Resistance
15-30%	Moderate Resistance
31-50%	Resistance
>50%	High Resistance

TABLE 2.1: Resistance ratings adapted from National Alfalfa and Forage Alliance 2016 Alfalfa Variety Ratings Leaflet. The percentage column represents the approximate percentage of seeds in a bag that will be resistant to nematodes for each resistance class.

2.3 The Model

2.3.1 Model Formulation

Changes in the model studied in [Jordan et al. 2017] have been made to account for the use of resistant varieties and to calculate yield at harvest. While resistant varieties of alfalfa are used it is necessary to keep track of both resistant and non-resistant alfalfa

plants. Let S_t and I_t be the number of non-resistant healthy and infested alfalfa plants at time $t = 0, 1, 2, \dots$, where the time unit within a year is chosen to be equal to one month (1 unit of time = one month), and corresponds to the interval between harvests during the summer. Let \hat{S}_t and \hat{I}_t be the number of resistant healthy and infested plants at time t . Also, let W_t be the average density of nematodes in the rhizosphere surrounding one plants' roots at time t .

In the model, the density of nematodes in the rhizosphere of one plant changes due to either nematodes immigrating from other hosts or because they die with average rate μ_W . Considering the total area, A , of the field to be relatively small, it can be assumed that the average nematode contribution from each infested plant to the rhizosphere of any other one (healthy or infested), C , is proportional to the number of surviving nematodes coming out of the infested plant, c . This allows the approximation $C = c/(\text{total number of plants in the area } A)$, which is justified in part from the observation that, in addition to nematode dispersal through flood irrigation, the tools employed in harvesting for cutting the plants are also responsible for the nematode transport over relatively large distances [Evans et al. 2008]. Thus, the total number of new nematodes surrounding a host's root becomes $C \times (\text{number of infested hosts})$, with the number of infested hosts given by $I_{t-1} \times A$. The model uses a relative value of $A = 1$, which corresponds to the 1 acre.

Therefore, the density of nematodes in *one* host's rhizosphere at time t can then be described by

$$W_t = (1 - \mu_W)W_{t-1} + CI_{t-1} + \beta C\hat{I}_{t-1}, \quad (2.1)$$

where μ_W is the death rate of nematodes and β represents a reduction in the nematode contribution from resistant infested plants. Since β is a reduction in the nematode contribution it follows that $0 \leq \beta \leq 1$. Notice that nematode contribution comes from both resistant and non-resistant plants. The contribution from a resistant plant will be less than that of a non-resistant plant.

Next, the density of non-resistant healthy and infested plants can be approximated with the equations,

$$S_t = S_{t-1}e^{-aW_{t-1}}, \quad (2.2)$$

$$I_t = (1 - \mu_I)I_{t-1} + (1 - e^{-aW_{t-1}}) S_{t-1}. \quad (2.3)$$

To approximate the density of resistant healthy and infested plants the following equations are used.

$$\hat{S}_t = \hat{S}_{t-1}e^{-aW_{t-1}}, \quad (2.4)$$

$$\hat{I}_t = (1 - \mu_I)\hat{I}_{t-1} + (1 - e^{-aW_{t-1}})\hat{S}_{t-1}, \quad (2.5)$$

where $e^{-aW_{t-1}}$ represents the probability that a healthy host is not reached by any nematode in its rhizosphere, a is a parameter measuring the nematode efficiency in finding the host's root, μ_I is the death rate of non-resistant infested plants, and $\mu_{\hat{I}}$ is the death rate of resistant infested plants. Notice the equations (2) – (5) all depend W_t . This provides a connection between resistant and non-resistant plants.

The equations have in addition to the trivial stable equilibrium, $(S^*, I^*, \hat{S}^*, \hat{I}^*, W^*) = (0, 0, 0, 0, 0)$, an unstable one at $(S^*, I^*, \hat{S}^*, \hat{I}^*, W^*) = (S_0, 0, \hat{S}_0, 0, 0)$. This simply tells us that nematode infestation will stop only when all healthy hosts are depleted and eventually die. If mortality of nematode-infested hosts is neglected then the infestation will stop only when all plants are contaminated.

Stability of the point $(S^*, I^*, \hat{S}^*, \hat{I}^*, W^*) = (S_0, 0, \hat{S}_0, 0, 0)$ can be determined by looking at the Jacobian Matrix for this system of five equations. After evaluating the Jacobian at the equilibrium point it can be seen that not all conditions of the Jury Test are met [Edelstein-Keshet 2005]. Thus, this equilibrium point is unstable.

During computations the model has the following assumptions: mortality of nematode-infested hosts will be neglected, new nematodes will not be introduced into the field by means of runoff irrigation from other infested fields or from man's activities, and the initial nematode population comes from the use of infested seeds.

2.3.1.1 Calculating Yield

Yield is calculated as a dry weight of the alfalfa that was cut over a certain area. It is generally expressed in tons per acre. The model calculates the yield at harvest by multiplying the number of plants in each category (non-resistant healthy, non-resistant infested, resistant healthy, and resistant infested) by an average weight per plant. Depending on the category the weight of the plant may be reduced. For example, the weight

of an infested alfalfa plant will be less than a non-infested plant due to stem stunting caused by nematodes. The degree of stem stunting depends on how long the plant has been infested by nematodes. In other words, the longer the plant has been infested the less it will weigh at harvest. A nematode resistant alfalfa plant will not experience the same degree of stem stunting as a non-resistant plant. This is due to resistant varieties being tolerant to the nematodes. Harvest yield is then found by adding together the yields from each category. A total yield for the year can then be found by summing the yield totals for all the harvests in the year.

2.3.2 Model Fitting

2.3.2.1 Experimental Data

Data was provided by a Utah State University Extension agent in Weber County, Utah and was obtained by an experiment where 10 varieties of alfalfa were planted in a known nematode infested field and the harvest yield was tracked over 4 years. The objectives of the experiment were to:

- i) determine the level of stem nematode resistance of the nine alfalfa varieties that are marketed as being highly resistant to stem nematodes,
- ii) evaluate the economic advantage of growing an alfalfa variety that exhibits high resistance to alfalfa stem nematodes when growing in a field that has stem nematodes, and
- iii) determine how the level of stem nematodes effects stand longevity.

The different varieties used in the experiment are Ranger, DKA 43-22 RR, Producers Choice PGI424, Producers Choice PGI557, WL 363, Americas Alfalfa 445NT, Croplan Denali 4.10 RR, Eureka 4R200 RR, Pioneer 54V09, and Pioneer 54Q25. Ranger is in the susceptible class of resistance of alfalfa while all the other varieties are marketed as having high resistance towards ASN. Data was collected for the growing seasons in 2012, 2013, 2014 and 2015.

Plots containing six replications of ten alfalfa varieties were established in a field of newly planted alfalfa in the spring of 2012. The planting date was March 27. The field was heavily infested with stem nematode two years previous. Due to heavy weed

Variety	Cut										
	1	2	3	4	5	6	7	8	9	10	11
Ranger	2.28	1.87	3.01	1.29	0.83	2.20	1.24	0.72	2.41	2.24	1.62
DKA 43-22	2.29	1.93	3.17	1.72	1.09	2.61	1.66	1.01	2.68	2.33	1.83
PGI 424	2.29	1.97	3.30	1.65	1.23	2.48	1.75	1.25	2.72	2.34	1.85
PGI 557	2.28	2.2	3.36	1.77	1.25	2.62	1.76	1.10	2.66	2.25	1.79
WL 363	2.28	2.2	3.43	1.86	1.27	3.00	1.80	1.21	2.75	2.39	1.75
AA 445 NT	2.27	2.12	3.21	1.70	1.07	2.43	1.73	1.25	2.96	2.33	1.92
CD 4.10 RR	2.26	2.18	3.21	1.65	1.20	2.88	1.85	1.08	3.04	2.22	1.81
Eureka 4R200	2.27	1.98	3.21	1.66	1.12	2.81	1.75	1.17	2.96	2.36	1.75
P 54V09	2.28	2.22	3.45	1.75	1.31	2.88	1.53	1.14	3.13	2.14	1.89
P54Q25	2.22	2.13	3.42	1.67	1.11	2.93	1.68	1.11	2.77	2.20	1.74

TABLE 2.2: Yield Data in tons/acre from Weber County. Data is for 2012-2015 growing seasons with three cuts per year, except 2012 which only had two cuts. Cuts 1 and 2 correspond to July 20 and September 17 in 2012. Cuts 3-5 correspond to June 7, July 8, and August 15 of 2013. Cuts 6-8 correspond to May 30, July 2, and August 7 of 2014. Cuts 9-11 correspond to June 8, July 7, and August 17 of 2015. Ranger is in the susceptible class while the other nine varieties are marketed as being highly resistant.

growth only two cuttings happened in 2012. For years 2013, 2014, and 2015 there were three cuttings. The cuttings were around the beginning of June, July, and August. The average dry weight (tons/acre) for each variety was recorded at each cutting. Table 2.2 shows the average dry weight for each variety at each cutting for the 2012-2015 growing seasons.

2.3.2.2 Initial Conditions

The common measurement of field size is an acre, which is a unit of land area equal to 43,560 square feet. The density of alfalfa plants can vary from field to field but it is approximated to be between 5 and 10 plants per square foot. The average number of plants per acre was estimated by first taking 5 plants per square foot and multiplying that by 43,560 square feet to get how many plants are in one acre. The process was repeated for 6, 7, 8, 9, and 10 plants per square foot. Those values were averaged to get 326,700 plants per acre.

As a first approximation, the model uses the following initial conditions: $S_0 + \hat{S}_0 = 326700$, $I_0 + \hat{I}_0 = 0$, and $W_0 = 2000$. W_0 comes from fitting the data to the model. The resistance rating of the alfalfa seeds describes the proportion of the seeds that are resistant to the ASN. For example, if a bag of alfalfa seeds has a resistance rating of

40%, then approximately 40% of the seeds will be resistant to the nematodes. This corresponds to having about 40% of the plants being resistant. Letting α represent the resistance rating, the initial conditions become,

$$S_0 = 326700(1 - \alpha), \quad \hat{S}_0 = 326700\alpha, \quad I_0 = 0, \quad \hat{I}_0 = 0, \quad W_0 = 2000. \quad (2.6)$$

2.3.2.3 Parameter Values

The parameter a describes the nematodes efficiency in finding a host's roots. According to [Griffin and Waite 1971] nematode attraction is the same between non-resistant and resistant plants. Thus, the fitted value for a is appropriate to use in equations (2.2) and (2.3) as well as equations (2.4) and (2.5) since nematode attraction will not be biased based on if the plant is resistant or non-resistant.

The average contribution of nematodes from each infested plant to the rhizosphere of any other plant is described by C . Since resistant varieties limit nematode reproduction within a plant, the nematodes that are contributed by a resistant plant will be reduced compared to the contribution of a non-resistant plant. The parameter β accounts for the nematode reduction that happens in a resistant plant.

Parameters γ and λ are the weight reduction in non-resistant and resistant plants respectively due to nematodes and g represents the average weight per plant.

Parameter	Description	Approx. Value	Source
a	nematode efficiency in finding host's root (area per nematode)	0.001	[Jordan et al. 2017]
C	incoming nematode density per infested plant	1.202	[Jordan et al. 2017]
μ_W	death rate of nematodes (density per time)	0.411	[Boelter et al. 1985]
β	Reduction in nematode contribution from resistant plants	0.10	This paper
γ	weight reduction in infested non-resistant plants (grams)	0.38	This paper
λ	weight reduction in infested resistant plants (grams)	0.15	This paper
g	approximate plant weight (grams)	11.5	This paper

TABLE 2.3: Parameters for the model and their estimated values. The unit of time used to approximate the rates is 30 days.

2.3.2.4 Fitting to Data

Values for parameters a and C were found from fitting equations (2.1), (2.2), and (2.3) to data which does not include resistant varieties [Jordan et al. 2017]. Fitted values for W_0 , β , γ , λ , and g can be found in Table 2.3.

These parameters can be used in simulations to see how varying the resistant rating will affect the harvest yield of a field. Figure 2.1 shows the results of the fitting process. The box plots represent the data of the nine highly resistant varieties obtained in Weber County, UT and the red squares are simulated values. An anomaly was noticed in the 2015 data. The yield from the third cut of that year were significantly higher than the first two years. To explore the anomaly, the model was fit first to all 9 cuts and then second to 8 cuts to see how the model adapted. The differences in the fitting can be found in Figure 2.1. The main differences seen are in the improved approximations for the yield in the 2nd and 3rd cuts of 2013 and 2014. The approximations for the other cuts are similar for both 9 and 8 cuts. This means that the model can be fit to the data without using the data anomaly found in the last cut of 2015, resulting in a better overall fit.

2.3.3 Results

2.3.3.1 Harvest Yield

Farmers are concerned about how well their fields will produce over the years they grow alfalfa. The total yield produced over the growing season in a year is a measure of how well a field performed. The model will output a yield total for the entire year for a set number of years. This allows a farmer to get an idea of what the yield of their field will be based on the resistance rating used and the number of years they plan to grow alfalfa.

Panel (A) of Figure 2.2 shows the averaged results for total harvest yield from simulating growing alfalfa continuously for 3, 4, 5, or 6 years for each resistant class. The model needs to produce averaged results because each resistance class has a percentage range of resistance. Those ranges are outlined in Table 2.1. For example, to get an average total yield for the low resistant class the model will use a percentage rating at the lower end of its range, which is 6%, to produce harvest yields totals. Then the model

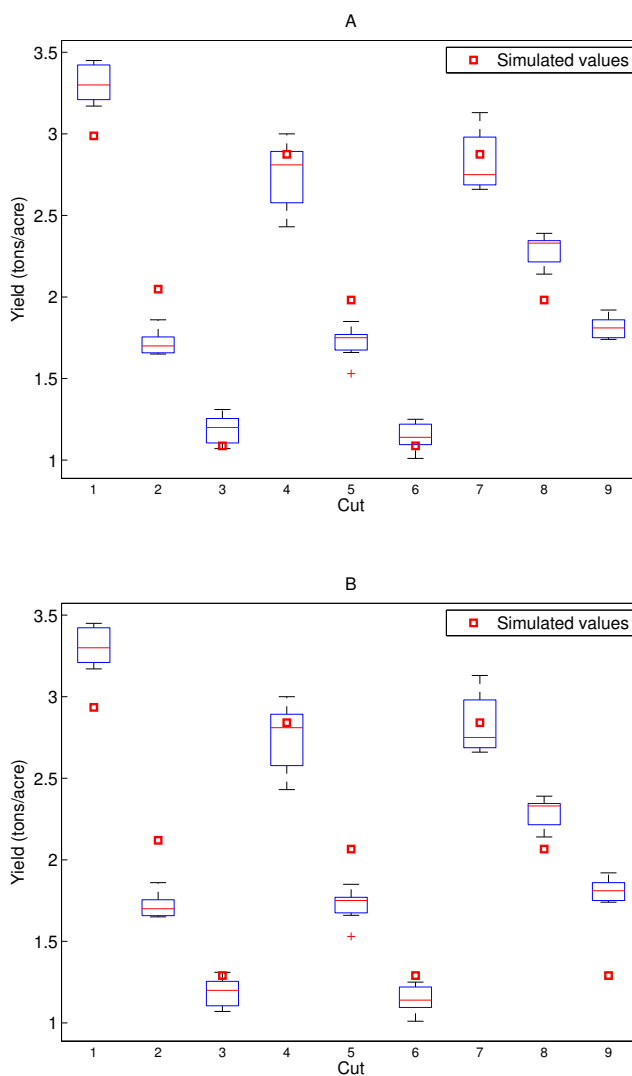


FIGURE 2.1: Computations were ran to fit parameters to yield data of the nine highly resistant varieties for years 2013, 2014, and 2015. There were three harvests each year which makes a total of 9 cuts. (A) represents the fitting of only 8 cuts and (B) is all 9 cuts. The box plots represent the data obtained in Weber County, UT and the red squares are from the fitting process. Fitting without the yield data from the last cut in 2015 improves the overall fit. Thus, the model parameters are calculated from using 8 cuts.

will produce harvest yield totals using a percentage at the high end of its range, which is 14%. Those results are then averaged to get an average total harvest yield for the low resistance class. This process is then repeated for every other resistant class.

Figure 2.2 shows that for each resistance class the relationship between time grown and total harvest yield is linear, suggesting that the yield does not change from year to year. Thus, the average harvest yield per year for each resistance class is the same

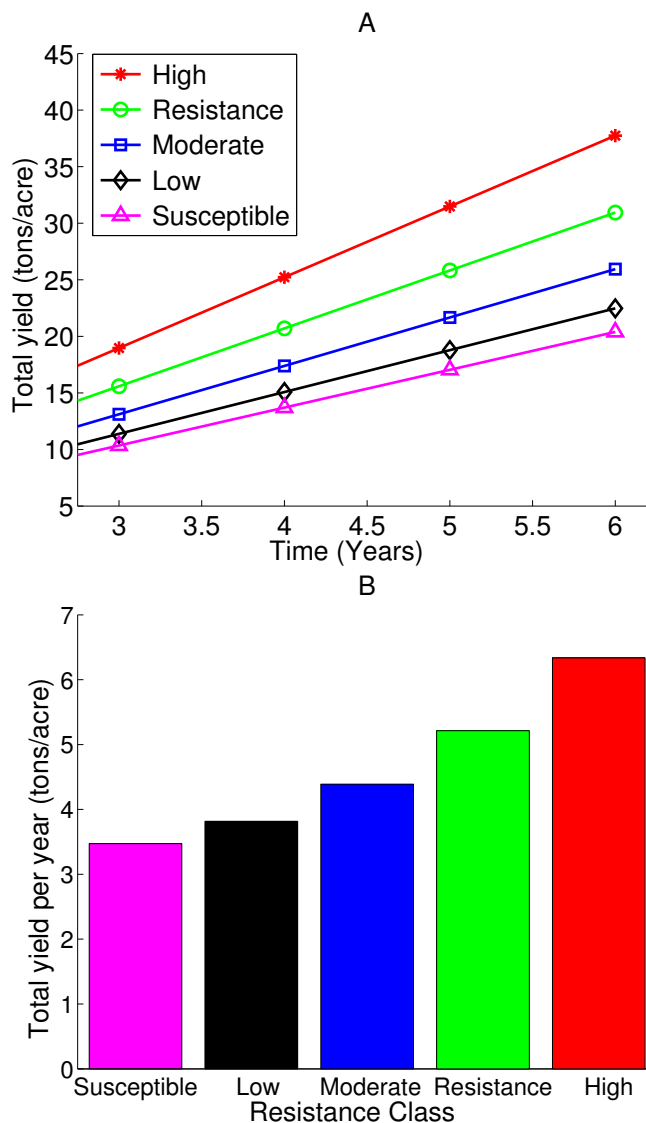


FIGURE 2.2: Model computations for continuously growing alfalfa for 3, 4, 5, or 6 years. Panel (A) shows the total yield (tons/acre) for each resistance class. It can be seen that the relationship between time grown and total harvest yield is linear, suggesting that the yield does not change from year to year. Thus, the average harvest yield per year for each resistance class is the same regardless of the length of time alfalfa is grown.

Panel (B) shows the total yield (tons/acre) per year for each resistance class.

regardless of the length of time alfalfa is grown. Panel (B) of Figure 2.2 shows the average yield (tons/acre) per year obtained for each resistant class.

To see how the total yield per year was affected by the parameter β model computations were made with $0 \leq \beta \leq 1$ over 3 years. The results are shown in Figure 2.3. Panel (A) shows the total yield per year as a function of β value and the resistance rating. Panel (B) shows what happens to the total yield per year as β varies and the resistance rating is held constant. Notice that the total yield per year does not change

as β varies and the resistance rating remains constant. Thus, varying β and keeping the resistance rating fixed has a negligible effect on the total yield per year. For a more biological meaning recall that harvest yield is based on the number of plants in each category. The resistant plants are tolerant to nematodes, which means that they will stunt less compared to a non-resistant one. Thus, more resistant plants implies a better yield. Figure 2.3 shows that the β value does not significantly alter the number of plants in each category enough for the yield to be affected. Thus, varying the nematode contribution from the resistant infested plants and keeping the resistance rating constant has a negligible effect on harvest yield.

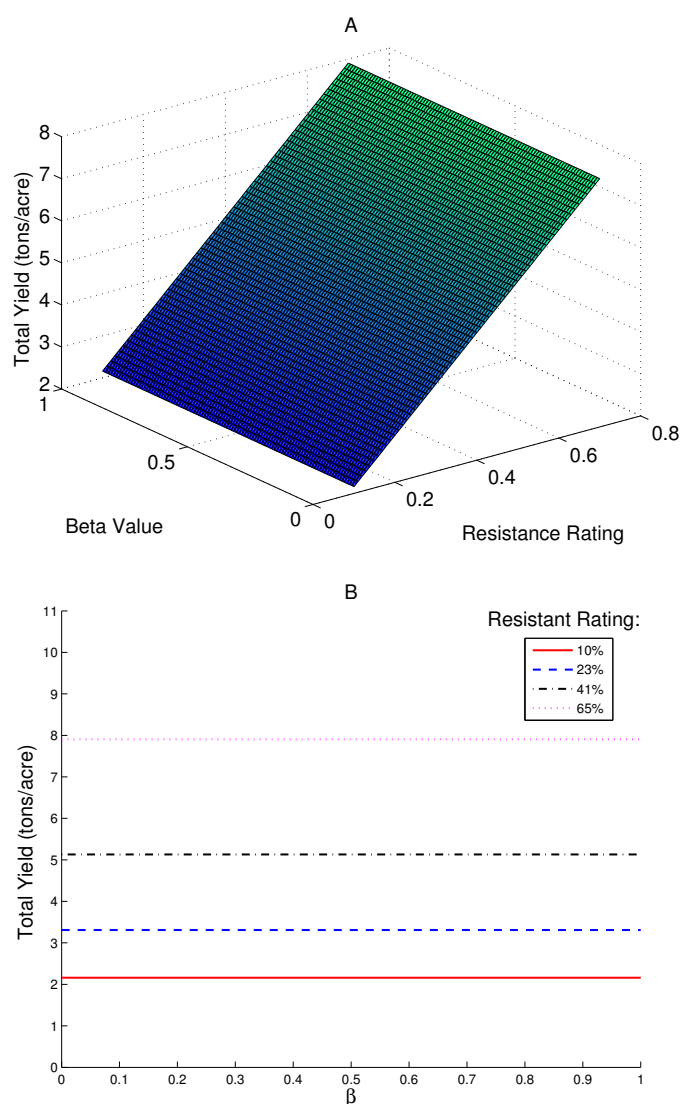


FIGURE 2.3: Computations were made for varying β values and resistant ratings. Panel (A) shows the total yield (tons/acre) per year as a function of resistance ratings and β . Panel (B) shows that varying the β value and keeping the resistance rating constant has a negligible effect on the total yield per year.

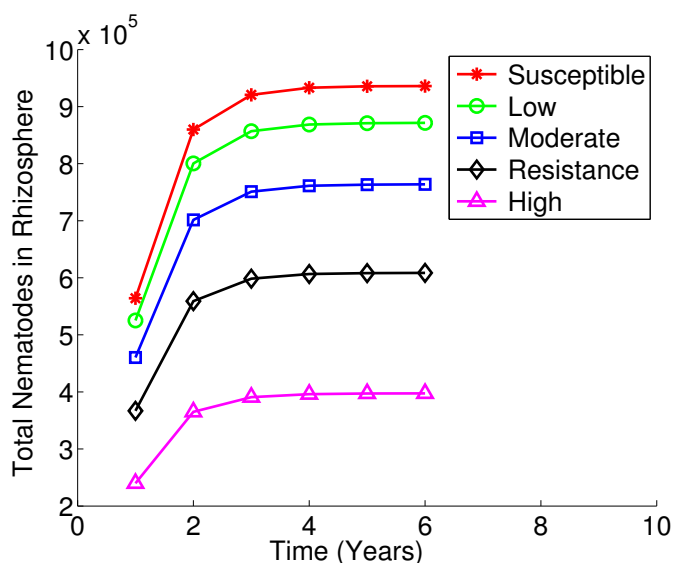


FIGURE 2.4: Total nematode population in one plant’s rhizosphere. The figure shows the nematode population at the last harvest of the growing year. The nematode population increases very rapidly at first, and as time continues the nematode reproduction slows down. This is due to resistant plants inhibiting nematode reproduction.

2.3.3.2 Nematode Population

Recall that W_t describes the nematode population in the rhizosphere of one alfalfa plant at time t . The model keeps track of the nematode population at the time of the last harvest every year alfalfa is grown for each of the resistance classes. Figure 2.4 shows how resistant varieties of alfalfa will affect the nematode population. It shows that as resistance increases the nematode population decreases. The nematode population increases very rapidly at first, and as time continues the nematode reproduction slows down. This is due to resistant plants inhibiting nematode reproduction. Thus, nematode resistant varieties of alfalfa can slow down nematode infestations.

2.4 Conclusions and Discussion

The alfalfa stem nematode (ASN) is a major concern among farmers in the western United States. It attacks alfalfa resulting in an economic loss to these farmers. Without the use of nematicides, other methods are needed to control the ASN. The novelty here is a model that demonstrates the relationship between the different resistance ratings and harvest yield in tons per acre. This is accomplished by tracking the number of plants in a field and dividing them into four categories: non-resistant healthy, non-resistant infested, resistant healthy, and resistant infested. Yield was then calculated based on

the number of plants in each category. This process was repeated for varying levels of nematode resistance and then a comparison was made.

The model was fit to data obtained from Weber County, Utah. The model shows how different resistance ratings affect yield at harvest. It was found that higher resistance ratings allow for higher yields at harvest and lower nematode population in the field. The model presented in this paper provides a way for farmers to have an idea of what resistance rating to use that is best for their needs.

Panel (A) of Figure 2.2 shows how the resistance ratings play a role in the total yield accumulated over 3, 4, 5, and 6, years of continuously growing alfalfa. This shows that the higher the resistance rating the better the yield will be over the lifetime of the alfalfa field. It can be seen that the difference between using the susceptible class and the highly resistance class could result in approximately 15 – 20 more tons per acre in yield when growing alfalfa for 6 years. The relationship between growing time and harvest yield is linear, suggesting that the change in harvest yield per year for each resistance class is the same regardless of the time grown. Panel (B) of Figure 2.2 shows the average yearly yield (tons/acre) for each resistance class. Having the average yearly yield will allow a comparison to be made between different resistance classes. This will help farmers to know what to expect when changing from one resistance class to another.

Table 2.4 shows the approximate percentage change in yield (tons/acre) when moving from one resistance class of alfalfa to another. The chart reads the approximate percentage change in yield when moving from the resistance class in the left column to the resistance class along the top row. For example, moving from a susceptible class to a high resistance class can approximately increase the yield of an alfalfa yield by 83%.

The use of resistant varieties not only helps control nematode populations in a fields, it helps lessen the economic losses that are incurred by the nematode infestation. Knowing how resistant varieties of alfalfa affects yield is a great tool that can be used when making crop management decisions.

Percentage change in yield between resistance classes						
		To resistance class				
		Susceptible	Low	Moderate	Resistant	High
From resistance class	Susceptible	0%	10%	27%	51%	83%
	Low	-9%	0%	15%	37%	67%
	Moderate	-21%	-13%	0%	19%	45%
	Resistant	-33%	-27%	-16%	0%	22%
	Highly	-45%	-40%	-31%	-18%	0%

TABLE 2.4: Percentage change in yield (tons/acre) between resistance classes of alfalfa. The table shows changes in yield by going from the resistance class in left column to the resistance class along top row.

Chapter 3

INFLUENCE OF RESISTANT VARIETIES ON THE SPEED OF PROPAGATION OF SIMPLE EPIDEMICS IN CROPS

The content of this chapter has been published in *Applied Mathematics Letters*. Authors are Luis Gordillo and Scott Jordan.

Gordillo, L.F., and Jordan, S., “Influence of resistant varieties on the speed of propagation of simple epidemics in crops.” *Applied Mathematics Letters* 68 (2017): 129-134.

3.1 Introduction

Since the introduction of genetically engineered (GE) crops in the United States in the mid-90s, their advantages and disadvantages have been continuously scrutinized. With the assessment of environmental, economic and social impacts of GE crops, new and intricate challenges for their future beneficial use have emerged [NAP 2010]. It is of particular interest, from the managerial point of view, to be able to generate estimates of future effects when new technology of this type is introduced to fight crop diseases. The development of GE crop resistance to nematodes, bacteria, or viruses requires that it be determined, at least approximately, how their introduction would affect the dynamics of pest dispersal, and therefore how to design better introduction strategies.

Spatial continuous models for disease spread, i.e. models that assume individuals continuously distributed in space, have been widely used as a realistic approach to understanding how crop disease dispersal progresses, [Madden et al. 2011]. One characteristic that makes this approach interesting is that it describes the wave-like expanding traveling fronts of diseases moving at speeds that can be determined, see [Madden et al. 2011] and [Ruan 2007] for extensive reviews.

The goal of this paper is to determine *how is the speed of propagation of a simple epidemic in crops is affected by the introduction of resistant individuals?* First, we need to clarify that what characterizes a “resistant individual“ is the set of specific artificially modified traits that allow the individual to fight the invasion of clearly identified micro or macro parasites. That is to say, the attributes of a resistant individual are specific to each crop-pest system under consideration. Although the model described below does not make reference to a particular crop system, we stress that it was motivated by the attributes of nematode-resistant alfalfa varieties designed to control stem nematodes [Jordan et al. 2017]. In that case, resistant individuals are *not* immune to the attacks of nematodes but are designed to diminish the damage on the hosts so that farmers can still recover a significant fraction of normal yield from each plant. As a consequence, infected resistant hosts have a decreased rather than zero transmission rate.

We examine a one-dimensional spatial model for simple epidemics (SI), as defined in [Mollison 1972], with the addition of two classes: resistant-susceptible and resistant-infected individuals. The model uses a generalization of the mass action term, introduced by D.G. Kendall in [Kendall 1957], where the factor corresponding to the infectives is replaced by a spatial average of infectives. The speeds of traveling wave solutions for the linearized model can be determined in relation to those in the system that does not include resistant individuals. Then the so-called “linear conjecture” [van den Bosch and Metz and Diekmann 1990, Sattenspiel 2009], which has been used for instance to successfully approximate the speed of disease fronts for fungal crop diseases in two spatial dimensions [Metz and van den Bosch 1995], is used to conclude that the speeds found are a good approximation to those in the non-linear model. We validate this approximation by comparing the results with the speeds obtained from numerical computations of the non-linear system.

3.2 Theoretical framework

Let us consider a sessile population distributed along the real line with constant density N , and let $x = x(s, t)$ and $y = y(s, t)$ be the densities of susceptible and infected individuals at location s and time t . We examine a disease for which the only individual transitions allowed are of the type *susceptible* \rightarrow *infective*, generally known as a *simple epidemic*, or SI. The associated differential equation is given by $\partial_t y = \beta x \bar{y}$, where \bar{y} is an spatial average of infectives, [Mollison 1972].

We introduce now a second class of susceptible individuals, $x_r = x_r(s, t)$, which we call the *resistant variety*, that is assumed to be perfectly mixed with the original susceptibles. This hypothesis is reasonable for systems where seeds of both types are mixed before sowing, as in the case of alfalfa fields, for instance. We let two specific attributes characterize this class of individuals: (i) when exposed to the disease, individuals trigger a defense mechanism that minimizes the damage produced by the infection, and (ii) their capacity to propagate the infection is reduced.

Case 1. Let $y_r = y_r(s, t)$ be the density of resistant individuals infected at location s and time t , and examine first the case where the infection rate associated to the infected resistant variety is negligible, i.e. consider the simplified model

$$\partial_t y = \beta x \bar{y}, \quad (3.1)$$

$$\partial_t y_r = \beta x_r \bar{y}. \quad (3.2)$$

Let us assume that a traveling wave solution exists for this system, and that the transient effects of its buildup from an initial focus have already faded. We first look at the linearization of the total epidemic in the front of the wave,

$$\partial_t (y + y_r) = \beta N \bar{y}, \quad (3.3)$$

where $N = x + x_r + y + y_r$ is constant. We recall the initial assumption of a perfect mixture of resistant and non-resistant individuals, which implies that susceptibles of both types have the same chance of becoming infected. This means that $y_r/(y + y_r) = \alpha$ is a constant value in time and location. Equation (3.3) can then be rewritten as

$$\partial_t (y + y_r)(s, t) = \beta N (1 - \alpha) \int_{-\infty}^{\infty} (y + y_r)(s - u, t) dF(u), \quad (3.4)$$

where $dF(u)$ is a (symmetrical) contact distribution. Under the condition that this contact distribution is exponentially bounded, traveling wave solutions to (3.4) have been well studied, see for instance [Daniels 1975, Medlock and Kot 2003, Mollison 1972]. It follows from the theory that the speeds for traveling wave solutions in this case, say c , should satisfy the relation $c/((1 - \alpha)\beta N) = \psi(\theta)/\theta$, where

$$\psi(\theta) = \int_{-\infty}^{\infty} e^{\theta u} dF(u)$$

is the moment generation function for the contact distribution.

Case 2. We now consider the case where infected resistant individuals can pass on the disease, but in a lesser degree than a non-resistant individual. In this case we arrive at an extension of the system (3.1)-(3.2), given by

$$\partial_t y = \beta x \bar{y} + \beta_r x \bar{y}_r, \quad (3.5)$$

$$\partial_t y_r = \beta x_r \bar{y} + \beta_r x_r \bar{y}_r, \quad (3.6)$$

where $0 \leq \beta_r < \beta$. We consider a traveling wave solution as before, with the linear approximation in the front of the wave now given by

$$\partial_t (y + y_r) = (\beta \bar{y} + \beta_r \bar{y}_r) N. \quad (3.7)$$

Uniform mixing of resistant and non-resistant individuals allows the last equation to be rewritten as

$$\partial_t (y + y_r) = (\beta(1 - \alpha) + \alpha\beta_r)(\bar{y} + \bar{y}_r) N, \quad (3.8)$$

where $0 \leq \alpha \leq 1$ has the same meaning as in Case 1. Again, it follows that the speed of propagation of the linear epidemic model should satisfy

$$\frac{c}{(\beta(1 - \alpha) + \alpha\beta_r) N} = \frac{\psi(\theta)}{\theta}. \quad (3.9)$$

The conditions for the *linear conjecture* of van den Bosch et al.

[van den Bosch and Metz and Diekmann 1990] are satisfied in this scenario, and according to this conjecture the asymptotic wave speed of the traveling front in the non-linear model should be equal to the minimum wave speed, which happens to be that from the linearization, i.e. that determined by equation (3.9).

3.3 Comparison with the non-linear model

In the previous Section, the theoretical predictions concerning the effect of resistant varieties on the speed of a simple epidemic traveling front were deduced using the model linearization and the linear conjecture. Now we verify that these predictions are valid for the non-linear model by using a computational approach. Firstly, a contact distribution that corresponds to the observed characteristics of the disease has to be selected. For

our example we arbitrarily choose a Gaussian, i.e. $dF(u) = \left[\exp(-u^2/4Dt)/\sqrt{4\pi Dt} \right] du$, $D = 1/2$, with the sole purpose of illustrating the validity of the theoretical results. Similarly, we do not specify the units for space, and β is taken equal to one.

Figures 3.1(a) and 3.1(b) are snapshots of traveling wave solutions for the non-linear model with the vertical axis showing the relative density of infected $(y + y_r)/N$, normalized by letting $N = 1$. Figure 3.1(a) is obtained from a mixture 1:1 of non-resistant and resistant individuals. It is assumed that infected resistant hosts do not turn infectious, i.e. $\beta_r = 0$. For Figure 3.1(b) it is assumed that only non-resistant individuals are present. The continuous curves in both panels show the traveling fronts after a time T that ensures the absence of transient effects. The curves in dash-dots are the fronts after time $2T$ has elapsed. It is apparent from the Figures that the distance traveled during the time interval $[T, 2T]$ by the front in (b) is twice that of (a). In Figure 3.2 the assumption that infected resistant hosts are incapable of transmitting the disease is dropped. We assume now partial infectiousness with $\beta_r = 0.2\beta$. If we want that the speed of the traveling wave to be the same as that in Figure 3.1(a) then the non-resistant:resistant proportion must be changed. From $(1 - \alpha)\beta + \alpha\beta_r = 1/2$, we find $\alpha = 0.625$, which is the proportion of resistant individuals in the total population. With these parameters, the corresponding snapshot of the traveling wave becomes identical to that in Figure 3.1(a).

3.4 Conclusions

We have incorporated into the classical one-dimensional model of a spatial simple epidemic (SI) the possibility of having infectious resistant individuals. We framed the model context to that of a crop disease assuming that (i) resistant and non-resistant individuals are homogeneously mixed, (ii) resistant individuals become infectious at a decreased rate of infectiousness, and (iii) the death rate of individuals due to the disease is slow in relation to the process of replacement (crop rotation or field re-sowing). These attributes are satisfied in the case of alfalfa, where the use of resistant varieties is the most viable way to control the invasion of alfalfa nematodes that spreads along the rows of sown plants.

The novelty here is the establishment of an analytical relationship between the

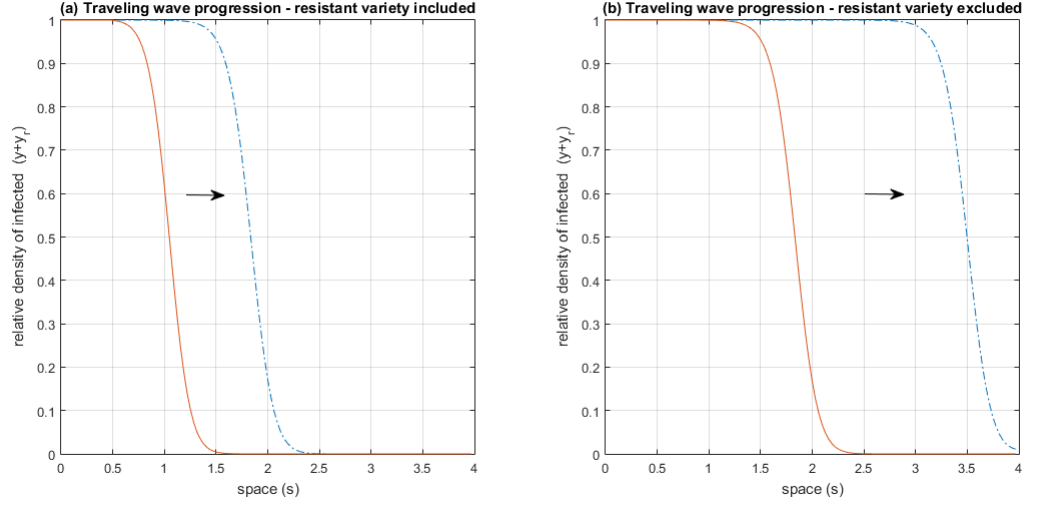


FIGURE 3.1: Traveling wave solutions for the non-linear model, equations (3.5) and (3.6), including resistant hosts (a), and without resistant hosts (b). For the computations we assumed that $\beta = 1$ and $\beta_r = 0$, i.e. resistant infected individuals are not infectious. The fronts represented by the continuous curves are obtained after computing for a fixed time T (both panels) that ensures the removal of transient effects. The fronts represented by dash-dot curves are obtained after a time $2T$ (both panels). The resistant proportion of hosts used in (a) is $\alpha = 1/2$. It becomes apparent from comparing both panels that the traveling front in (b) moves forward twice the distance of the traveling front in (a) during the time interval $[T, 2T]$, in agreement with the results for the linearized model. The contact distribution used is $dF(u) = [\exp(-u^2/2t)/\sqrt{2\pi t}] du$.

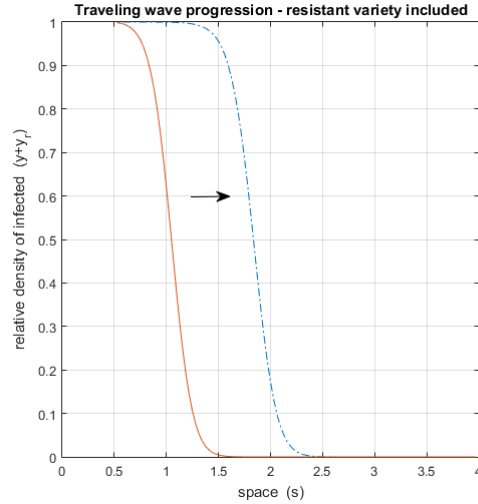


FIGURE 3.2: Traveling wave solutions for the non-linear model, equations (3.5) and (3.6), where infected resistant plants present a reduced infectious rate. For the computations $\beta = 1$ and $\beta_r = 0.2$, i.e. a reduction in the infectious rate of 80%, which is plausible in some varieties of resistant alfalfa. If we wish to halve the speed of the traveling front, then the resistant proportion can be computed from the left hand side of equation (3.9), which gives $\alpha = 0.5/0.8 = 0.625$. The picture shows the same result as Figure 3.1(a), i.e. the same front speed is obtained. The computations were made with the same specifications as Figure 3.1.

propagation speed of traveling wave fronts in crop fields with and without resistant individuals. The main conclusion is that the speed of disease front depends proportionally on the relative fraction of resistant individuals originally in the field. Although this result could be intuitively clear for an experienced grower, the exact analytical relation, equation (3.9), which involves partial infectivity from infected resistant varieties becomes significant given the non-linear nature of the spatial process of infection. We also notice from equation (3.9) that the linear relation between c and α has slope $(-\beta + \beta_r)k$, where $k > 0$. This means that increases in the proportion of resistant seed might confer little reduction in the traveling wave speed if the resistant variety is of low quality, as it would be expected. The results are obtained by first using the linearization of the model, and then extending to the full non-linear model through the linear conjecture, [Metz and van den Bosch 1995, van den Bosch and Metz and Diekmann 1990]. The validity of the conclusion is then verified by numerically solving the non-linear model and comparing the propagation speeds of traveling fronts. Our results are a theoretical complement to the findings in [van den Bosch et al. 1990], which are elaborated for the *susceptible* \rightarrow *infected* \rightarrow *removed* (SIR) case for two spatial dimensions. It was found there that the speed of traveling fronts in a crop field with uniform mixing of resistant and non-resistant types are proportional to the logarithm of $1 - \alpha$, where α is the proportion of the resistant type. The theory and applications there elaborated and further described in [Metz and van den Bosch 1995] are inspired in fungal crop diseases for which the spores are dispersed in the canopy over short distances, creating local patches of high infestation. In contrast, alfalfa nematodes are expelled from the stems of an infected plant and reach the roots of new hosts using a combination of chemotaxis and transport through irrigation water flow along plant rows.

Currently, there are several varieties of alfalfa that are resistant to the stem nematode, but measures of resistance can vary. There is no standard for the classification of alfalfa varieties as “resistant” among manufacturers. It is known, for instance, that some declare a variety resistant if 51% of plants test negative for the presence of nematodes in screening trials. In addition, it is common practice among growers to commercialize non-certified seed, which often carries mixtures of resistant and non-resistant plants. These two circumstances suggest that the results obtained here could be used to supplement the planning of control strategies.

Chapter 4

A MODEL FOR THE DISPERSAL OF THE ALFALFA STEM NEMATODE

The content of this chapter was submitted to be published in the International Journal of Agronomy. The authors are Scott Jordan, Luis Gordillo, and Ricardo Ramirez.

4.1 Introduction

In absence of approved pesticides that target alfalfa stem nematode (ASN) exclusively, the control of its spread is currently based on two practices: crop rotation and introduction of resistant varieties of alfalfa. Only alfalfa plants can host ASN, which have developed a mechanism of anhydrobiosis to overcome dry conditions.

Resistant varieties of alfalfa are designed to affect how nematodes mature and reproduce within the plant [Schomaker and Been 2006]. Resistance is defined as a plants ability to withstand, oppose, lessen, or overcome the attack of a pathogen [Rhode 1972]. A plant resistant to nematodes resists attack or exhibits little damage and reduces the nematode population [Giebel 1974]. There are four main types of resistance that can be utilized. (i) The plant may produce toxins that are harmful to the nematodes. (ii) The plant may fail to provide adequate conditions for the nematode to survive. (iii) Plants can secrete chemicals that will repel nematodes. (iv) Plants hypersensitivity will cause the nematodes to die [Giebel 1974]. Hypersensitivity is when the cells around the nematodes undergo necrosis, thereby trapping the nematodes and preventing further infestation and reproduction. The exact plant defense mechanisms used by alfalfa plants against ASN is not clear. Given the high genetic variability of alfalfa it can be challenging to determine the specific mechanism, and with this variability resistance is evaluated at the plant population level. It is also possible that different varieties may have different defense

mechanisms against ASN. What is clear is that varieties that have been classified as resistant reduce the negative effects of an ASN infestation.

Mathematical models describing the spread of ASN on alfalfa have been studied in [Jordan et al. 2017, Jordan 2017]. These models, which do not include a component for spatial spread and are discrete in time, are focused on finding the best crop rotation period to control nematode infestations as well as determining the impact of resistant varieties on alfalfa harvest yield. In [Jordan et al. 2017], it was found that the best rotation period to use is 2-3 years, and in [Jordan 2017] it was found that using a highly nematode resistant variety of alfalfa can increase yield, measured in tons/acre, up to 83%. A different approach was taken in [Gordillo and Jordan 2017] by modeling nematode dispersal through the consideration of susceptible and infected plant classes and a non-local process dispersal. This allows to approximate speeds in the ASN's invasive traveling fronts, and mainly how they change under the introduction of resistant varieties of alfalfa. The model proposed in [Gordillo and Jordan 2017] depends on the concept of *contact distribution* to determine how far the nematodes' search for a new host extend, without being transported by water flow, once they leave the infected plant where they were born. In this paper we report the results of an experiment designed to approximate this contact distribution for ASN, which to the best knowledge of the authors has not been estimated before. Then the spatial model proposed in [Gordillo and Jordan 2017] is used to estimate invasion speeds for the ASN when a mixture with resistant varieties of alfalfa is used.

4.2 Materials and methods

4.2.1 Data collection

The goal was to gather data on the distances that nematodes move in a controlled environment. Nematodes were placed at varying distances from nematode-free alfalfa plants. After six weeks the alfalfa plants were inspected for nematode presence. The plant counts at each distance were then used for the fitting of a Gaussian distribution.

In the experiment, sets of two 12 ounce Solo cups were connected using 3/4 inch diameter PVC pipes. The pipes were cut in half to make a trough and were super glued so that the top of the trough was level with the top of the cup. Semicircles were cut out of the cups where the PVC pipes were connected to allow for an unobstructed access

to the cup from the trough. The cups were connected using PVC bridges of different lengths, which were 1, 1.5, 2, and 2.5 in. In total, 36 two-cup units were used. Alfalfa plants were then transplanted from a 3 year field in Cache County, Utah into the cups, one plant per cup. The field was stem nematode free and the variety of the alfalfa plants were Round Up Ready. Miracle Grow All Purpose Garden Soil was used to transplant the plants into the Solo cups. Soil was also placed in the PVC bridges. The sets of cups were super glued to three 2 by 2 feet wooden board for stability in transportation. Each wood board had three sets of cups at each distance, see Figure 4.1 Alfalfa stem nematode infested plants were collected from fields in Millard County, Utah. Samples were taken from multiple fields that showed signs of a nematode infestation, see Figure 4.1.



FIGURE 4.1: **Left:** Alfalfa plants transplanted into Solo cups. **Right:** A picture of an alfalfa field in Millard County, Utah. Stunted plants reveal nematode infestation. The spread of the nematodes following a preferential direction is apparent.

Nematodes were extracted from the infested plants using a Baermann Funnel technique. A tube was attached to a funnel and was clamped off. A mesh was placed at the mouth of the funnel. Cut up alfalfa material was placed on top of the mesh gate. The funnel was then filled with water. The alfalfa soaked in the water for 6-8 hours, which allowed the nematodes to exit the plant debris and then float down past the mesh gate, see Figure 4.2. The nematode solution was then collected and examined for the presence of nematodes. A 5 mL solution containing approximately 200 nematodes was placed in the middle of each PVC bridge that connected two cups, see Figure 4.2. Before the nematodes were placed in the bridges, each plant was given 75 mL of water to saturate the soil with water so that the nematodes could start traveling to the alfalfa plants.

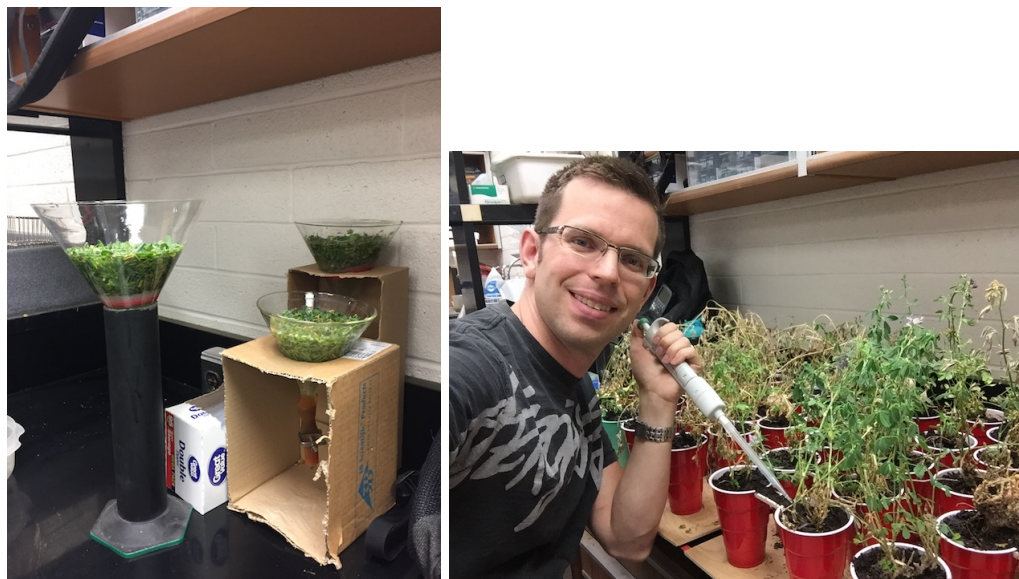


FIGURE 4.2: **Left:** Cut up alfalfa material in a Baermann Funnel for nematode collection and later release. **Right:** Solution containing nematodes placed in the middle of each PVC bridge.

The plants were then placed in an incubator that was set to 19° Celsius, which is the optimal temperature for nematode movement, [Norton 1978], see Figure 4.3. Lights were set to 12 hour light/dark intervals in the incubator. They would come on at 6 am and turn off at 6 pm. The plants were left in the incubator for six weeks. This was chosen because the life span of a nematode is 45-73 days [Hafez 1998]. This allows for only one generation of nematodes to interact with the plants. Plants were given 75 mL of water once a week for the duration of the experiment.

After the six weeks the alfalfa plants were taken out of the cups, chopped up, and then placed in dishes containing water. They were inspected under a microscope to determine if nematodes were present, see Figure 4.3. Data were collected for the number of plants at each distance that were infested. Figure 4.4 shows the number of plants at each distance that were infested by nematodes. We notice that the data collected at distance 0.5 in shows unexpected results. It is possible that the low counting at this distance was related to the orientation of the plants in the incubator. The cups corresponding to the 1 in distance were near the back of the incubator, where the incubator fan was located.



FIGURE 4.3: **Left:** Connected cups with alfalfa plants placed in an incubator. The plants were tested for infection six weeks after nematode release. **Right:** Alfalfa plants cut up and inspected to determine if nematodes are present.

4.2.2 Model Framework

The following is a brief overview of the model found in [Gordillo and Jordan 2017]. In a sessile population distributed along the real line and with constant density N we denote with $x(s, t)$ and $y(s, t)$ the densities of non-resistant susceptible and infected individuals at location s and time t , respectively. If we assume that the only individual state transitions allowed are from the class susceptible to the class infective then we can approximate the dynamics of the disease with a commonly known “SI model“. By using the subscript r to further introduce a resistant class in the hosts we can write the equations for the model as

$$\partial_t y = \beta x \bar{y} + \beta_r x \bar{y}_r \quad (4.1)$$

$$\partial_t y_r = \beta x_r \bar{y} + \beta_r x_r \bar{y}_r, \quad (4.2)$$

where β and β_r represent the transmission rates associated with non-resistant and resistant hosts, respectively. The \bar{y} represents the spatial average of infectives [Mollison 1972], which is given by

$$\bar{y}(x, t) = \int_{-\infty}^{\infty} y(s - u, t) dF(u), \quad (4.3)$$

where $dF(u)$ is a symmetrical contact distribution. By assuming a perfect mixture of resistant and non-resistant individuals, susceptibles of both classes have the same chance

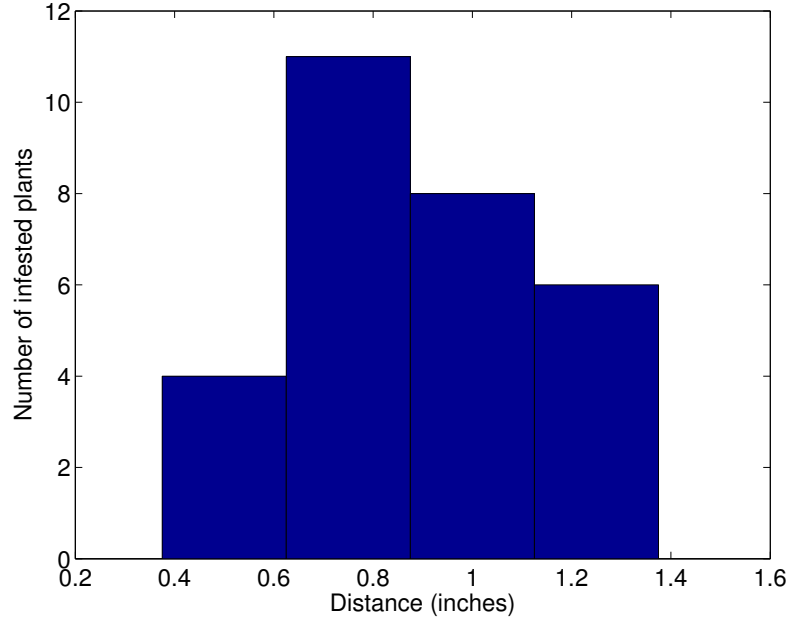


FIGURE 4.4: Number of infested plants observed at different distances (inches) from the nematode source. The countings at 0.5 in appear as outliers, presumably due to the position of the cups in the incubator.

of becoming infested. It also follows that $y_r/(y + y_r) = \alpha$ is a constant value in time and location. Equations (4.1) and (4.2) can be combined by linear approximations and uniform mixing of resistant and non-resistant individuals and be written as

$$\partial_y(y + y_r)(s, t) = (\beta(1 - \alpha) + \alpha\beta_r)(\bar{y} + \bar{y}_r)N. \quad (4.4)$$

For the case where the contact distribution $dF(u)$ is exponentially bounded traveling wave solutions to equation (4.4) have been well studied, see for instance [Daniels 1975, Mollison 1972]. The speed of a traveling wave solution, c , should satisfy the relation

$$\frac{c}{(\beta(1 - \alpha) + \alpha\beta_r)N} = \frac{\psi(\theta)}{\theta}, \quad (4.5)$$

where

$$\psi(\theta) = \int_{-\infty}^{\infty} e^{\theta u} dF(u)$$

is the moment generating function for the contact distribution.

The conditions for the *linear conjecture* are satisfied in our case [van den Bosch and Metz and Diekmann 1990], and therefore the asymptotic wave speed

of the traveling front in the non-linear model should be equal to the minimum wave speed obtained from the linearization, determined by equation (4.5).

4.3 Results

4.3.1 Parameter estimation

We proceed to fit a Gaussian distribution, i.e. $dF(u) = \exp(-u^2/4Dt)/\sqrt{4\pi Dt}$, using the data obtained from the experiment. The parameter D is the diffusion coefficient associated with nematode dispersal, with $D = \sigma^2/2t$. A Gaussian distribution is exponentially bounded and thus wave speeds can be calculated.

We recall that in the experiments, the origin is the only source of nematodes from which they disperse. It is reasonable to assume that any plant located at the source will get infected with probability one. But for the anomaly at 0.5 in, the normalized frequency histogram suggests that a Gaussian curve could be a good fit. In order to see how this data abnormality affects the fitting of a Gaussian we explore the distribution obtained by using values within the range of the extreme frequencies for infested plants, i.e. between values 0 and 1 with steps of 1/16 (16 was the number of surviving plants at the 0.5 in). Table 4.1 shows how the standard deviation changes with different number of infested plants at 0.5 in.

From Table 4.1 we see that the standard deviation changes are less than 0.0925. We can interpret this as the data at 0.5 in does not produce significant variations on the final contact distribution. Figure 4.5 shows the probability curves when fitting with 0, 4, and 16 plants. The boxes in the figure represent the range of values obtained from fitting with plant counts at the 0.5 in distance that range from 0 to 16 plants. It shows the extreme cases for the contact distribution as well as the curve that comes from using the plant count of 4 that comes from the data.

We estimate the diffusion constant by using the relation $D = \sigma^2/2t = 0.8093^2/(2 \cdot 6) = 0.0546 \text{ in}^2/\text{week}$, where $t = 6$ is the time of observation in weeks. The transmission rate β can be approximated by

$$\beta = (\text{number of effective contacts by one infective nematode per unit of time})/N,$$

see [Hethcote 2000], for instance. In our case, there were 29 infected out of 65 total

Number of infected plants	Standard Deviation	Error
0	0.8387	1.1881
1	0.8308	1.0968
2	0.8233	1.0060
3	0.8161	0.9158
4	0.8093	0.8263
5	0.8028	0.7376
6	0.7966	0.6502
7	0.7906	0.5646
8	0.7848	0.4814
9	0.7793	0.4023
10	0.7740	0.3301
11	0.7690	0.2702
12	0.7641	0.2323
13	0.7594	0.2274
14	0.7548	0.2574
15	0.7504	0.3123
16	0.7462	0.3815

TABLE 4.1: Standard deviation and error for fitting Gaussian curves to the data with different plant counts at 0.5 in. The far right column describes the 2-norm of the error vector between the observed data points and the values from the probability density. The row in bold is the actual observed plant count.

Parameter	Description	Units
β	transmission rate for non-resistant plants	(week) ⁻¹
β_r	transmission rate for resistant plants	(week) ⁻¹
α	Resistance rating	dimensionless
N	Plant density	(inches) ⁻¹
D	Nematodes diffusivity	(inches) ² (week) ⁻¹

TABLE 4.2: Parameters for the model.

surviving plants. Therefore, $\beta = (29/6)/65 = 0.0744$ (week)⁻¹. Recall that for our model we are considering a population that is distributed along the real line with constant density N . Current seeding and farming practices allow for fields to have varying densities. For our model computations we chose the value of $N = .5$ (inches)⁻¹. This corresponds to a density of one plant per two inches. Table 4.2 contains all the model parameters along with their units.

4.3.2 Effect of resistant varieties on front speeds

Equation (4.5) can be used to express the minimum speed of a traveling wave solution, c , in terms of the moment generating function of the contact distribution, ψ , by minimizing $\psi(\theta)/\theta$. According to the Linear Conjecture, this minimum wave speed

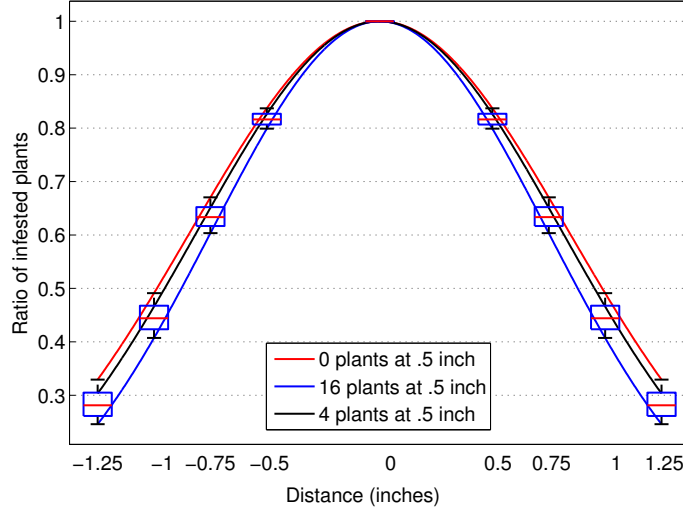


FIGURE 4.5: Extreme cases for fitting the probability density curve when using 0 (red) and 16 (blue) plants at distance 0.5 in. We observe that the count of infested plants count at 0.5 inches do not severely affect the fit. The error boxes show the values for the distribution obtained from fitting with plant counts that range from 0 to 16.

is equal the asymptotic wave speed of the non-linear model.

The moment generating function of the Gaussian distribution is given by $\psi(\theta) = e^{Dt\theta^2}$, and from

$$\frac{d}{d\theta} \left(\frac{\psi(\theta)}{\theta} \right) = \left(2Dt - \frac{1}{\theta^2} \right) e^{Dt\theta^2} = 0 \quad (4.6)$$

we see that the minimum of $\psi(\theta)/\theta$ is reached at $\theta = 1/\sqrt{2Dt}$. From equation (4.5) we obtain the expression for the minimum speed

$$c = (\beta(1 - \alpha) + \alpha\beta_r)N(\sqrt{12D})e^{1/2}, \quad (4.7)$$

where α represents the resistance rating of the alfalfa variety. By adjusting the parameter α to the different resistant classes we obtain the associated wave speeds.

The parameter value β_r represents the transmission rate from resistant infected plants to susceptible plants. Resistant varieties of alfalfa contain a phenotype that will effect the reproduction of nematodes, [Rhode 1972]. This implies that $0 \leq \beta_r \leq \beta$. Since the exact defense mechanism is not known, and it can vary between varieties, β_r can be difficult to approximate. To understand how wave speed changes for different values of β_r , model computations were made as β_r changes from 0 to β . Figure 4.6 shows the wave speed (inches/week) as β_r and α vary. In the figure we can see that as β_r approaches β

the wave speed becomes constant regardless the resistant variety used. As this happens, equation (4.7) transforms into $c = \beta N(\sqrt{12D})e^{1/2}$ (inches/week), which does not depend on the resistant rating of the alfalfa plants. We know that this will not occur because resistant varieties affect nematode reproduction within the plant, and consequently affect the transmission rate from resistant infected to susceptible plant, [Rhode 1972]. From the figure we can also see that as β_r increase the wave speed decreases, as seen from equation (4.7).

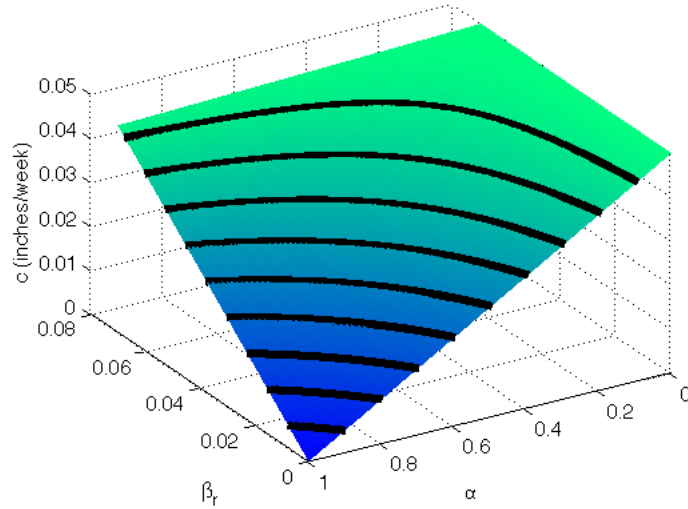


FIGURE 4.6: Wave speed, c (in/week), as function of the transmission rate for the resistant varieties, β_r (1/week), and the resistance rating, α . The surface is computed using the relation (7). The graph also shows the contour curves for a fixed speed (black curves). Parameter values used: $D = 0.0546$ (in²/week), $N = 0.5$ (1/in), and $\beta = 0.0744$ (1/week).

Figure 4.7 shows the traveling waves solutions of the system of equations (4.1) - (4.2) for the different resistant classes of alfalfa. The figure shows the infected plant densities at time T and time $T + 24$. The difference of 24 weeks was chosen as it is approximately the length of the growing season in one year. From the figure we can see that the more significant reductions in the wave speed come from using a variety of alfalfa that has a higher resistance rating.

Now that we have the wave speeds for different resistance classes we can look at how changing from one class to another will affect the wave speed. This is important to look at because growers of alfalfa may want to adjust their crop management according to their specific field needs. Table 4.3 shows the percentage change in wave speed when moving from one resistance class to another. The table reads the change in wave speed

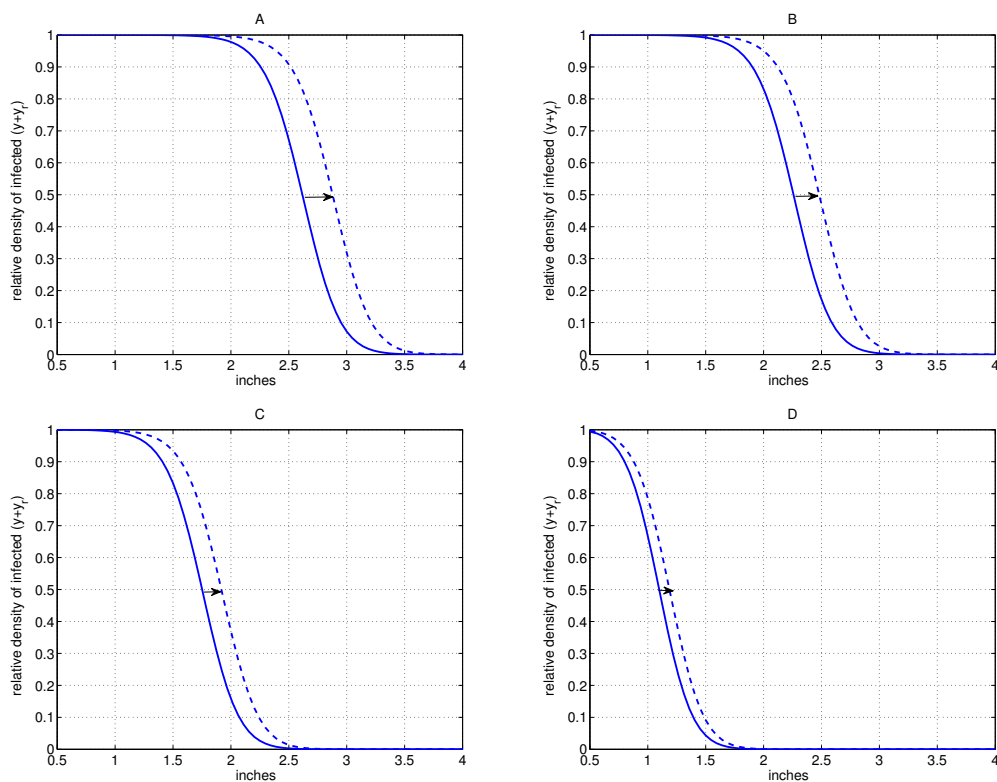


FIGURE 4.7: Snapshots of traveling fronts, taken at times after transient effects had disappeared, show the effects of resistant classes on wave speeds. Continuous and broken curves represent fronts at times T and $T + 24$, respectively, where the latter is taken as the approximate length of the growing season for alfalfa measured weeks. The panels exhibit simulations that include the presence of hosts from Low (A), Moderate (B), Resistant (C), and High (D) classes of resistant alfalfa.

when moving from a resistance class in the left column to a resistance class along the top row. A negative percentage indicates a reduction in wave speed, while a positive indicates an increase in wave speed. From the table we can see that moving from a susceptible class to a highly resistant class can approximately decrease the wave speed by 64%.

4.4 Conclusions and discussion

Spatial continuous models for disease spread have been widely used to understand the crop disease dispersal process [Madden et al. 2011]. This approach describes the wave-like expanding traveling fronts of diseases moving at speeds to be determined, see [Madden et al. 2011] and [Ruan 2007]. The novelty in this paper is that we used experimental data to approximate the contact distribution for the alfalfa stem nematodes.

To gather the data we transplanted alfalfa plants into Solo cups that were connected

Percentage change in wave speed between resistance classes						
		To resistance class				
		Susceptible	Low	Moderate	Resistant	High
From resistance class	Susceptible	0%	-8%	-21%	-39%	-64%
	Low	8%	0%	-14%	-34%	-61%
	Moderate	26%	16%	0%	-23%	-55%
	Resistant	64%	51%	30%	0%	-41%
	Highly	179%	157%	121%	70%	0%

TABLE 4.3: Percentage change in wave speed (inches/week) between resistance classes of alfalfa. The table shows changes in wave speed by going from the resistance class in left column to the resistance class along top row. For this table $D = 0.0546$, $N = 0.5$, $\beta = 0.0744$, and $\beta_r = 0$. β_r was chosen to be 0 to demonstrate the best possible case for the alfalfa plants.

in sets of two by PVC pipe. Nematodes were collected from infested plants in Millard County, Utah. These nematodes were extracted from the plants and placed in the center of the PVC bridge that connected two alfalfa plants. After six weeks the alfalfa plants were inspected to see which ones were infected. These data were then used to approximate the contact distribution for the alfalfa stem nematodes.

This contact distribution was then used in the model described in [Gordillo and Jordan 2017]. Wave speeds were then calculated for different resistant classes. We conclude that using varieties that have higher resistance ratings can reduce the wave speed and quantify the magnitude of those reductions, see Table 4.3. For example, switching from the susceptible class to highly resistant class can approximately decrease the wave speed by 64%.

The data from the experiment showed an abnormality at 0.5 in. In order to see how the infected plant count at this distance would affect wave speed we made computations with the model that compare the wave speed using the different diffusivity values that came from fitting the contact distribution to the data. The results showed that the biggest difference in wave speed from using different diffusivity values was 0.0051 in/week. Also, no significant variations to the percentage changes in Table 4.3 were detected after adjusting different diffusivity values obtained. This shows that even though the plant count at 0.5 in was abnormal, the model was robust.

In agreement with practice, the model shows that nematode invasion speeds are too low and cannot support the rapid dispersal of the disease as seen in the field. This

leads us to presume that other mechanisms are in play that allow the efficient dispersal of nematodes, including nematode transport through the field by the tractor that harvests the alfalfa, and the consistent use of non-certified seed by farmers. The latter, also known as “brown bag” seed, has the potential to come from fields that have been contaminated with nematodes. In that case, it is possible that seeds carry nematodes attached, and farmers inadvertently re-infect their own field or the fields of the farmers who bought the seed. Another main driving mechanism supporting rapid nematode dispersal is the use of flood irrigation, which is the practice of opening gates at the top of the field that allow water to flow into the field. The gates are left open during a prescribed amount of time and then closed. It is speculated that the traveling water front is what is responsible for transporting the nematodes throughout the field. A supporting argument for this is that in sprinkler irrigated fields, where water is sprayed into the air so small water droplets fall into the ground, it is rare to spot a nematode problem. Our findings support the conjecture that changing from flood to sprinkler irrigation could effectively contribute to the control of the spread of the alfalfa stem nematode.

Chapter 5

CONCLUSIONS

The alfalfa stem nematode (ASN) is a major concern among farmers in the western United States. It attacks alfalfa resulting in an economic loss to these farmers. Without the use of nematicides, other methods are needed to control the ASN. The novelty of Chapter 2 is a model that demonstrates the relationship between the different resistance ratings and harvest yield in tons per acre. This is accomplished by tracking the number of plants in a field and dividing them into four categories: non-resistant healthy, non-resistant infested, resistant healthy, and resistant infested. Yield was then calculated based on the number of plants in each category. This process was repeated for varying levels of nematode resistance and then a comparison was made.

The model was fit to data obtained from Weber County, Utah. The model shows how different resistance ratings affect yield at harvest. It was found that higher resistance ratings allow for higher yields at harvest and lower nematode population in the field. The model presented in this paper provides a way for farmers to have an idea of what resistance rating to use that is best for their needs.

The model helps us to understand how resistant varieties will affect harvest yield. It shows that when higher resistance ratings are used, the better the yield will be over the lifetime of the alfalfa field. An example of this is that changing from the susceptible class to the highly resistant class could result in approximately 15–20 more tons per acre in yield when growing alfalfa for 6 years. Another aspect that we learn from the model is that the relationship between growing time and harvest yield is linear, suggesting that the change in harvest yield per year for each resistance class is the same regardless of the time grown. We can use this knowledge to make a comparison between different resistance classes. This will help farmers to know what to expect when changing from one resistance class to another. Table 2.4 shows the approximate percentage change

in yield (tons/acre) when moving from one resistance class of alfalfa to another. From the table we can see that moving from a susceptible class to a high resistance class can approximately increase alfalfa yield by 83%. The use of resistant varieties not only helps control nematode populations in fields, it helps lessen the economic losses that are incurred by the nematode infestation. Knowing how resistant varieties of alfalfa affects yield is a great tool that can be used when making crop management decisions.

In Chapter 3, we incorporated into the classical one-dimensional model of a spatial simple epidemic (SI) the possibility of having infectious resistant individuals. We framed the model context to that of a crop disease assuming that (i) resistant and non-resistant individuals are homogeneously mixed, (ii) resistant individuals become infectious at a decreased rate of infectiousness, and (iii) the death rate of individuals due to the disease is slow in relation to the process of replacement (crop rotation or field re-sowing). These attributes are satisfied in the case of alfalfa, where the use of resistant varieties is the most viable way to control the invasion of alfalfa nematodes that spreads along the rows of sown plants.

The novelty in Chapter 3 is the establishment of an analytical relationship between the propagation speed of traveling wave fronts in crop fields with and without resistant individuals. The main conclusion is that the speed of disease front depends proportionally on the relative fraction of resistant individuals originally in the field. Although this result could be intuitively clear for an experimented grower, the exact analytical relation is novel. This relation involves partial infectivity from infected resistant varieties and becomes significant given the non-linear nature of the spatial process of infection. We notice from equation (3.9) that the linear relation between c and α has slope $(-\beta + \beta_r)k$, where $k > 0$. This means that increases in the proportion of resistant seed might confer little reduction in the traveling wave speed if the resistant variety is of low quality, as would be expected. The results are obtained by first using the linearization of the model, and then extending to the full non-linear model through the linear conjecture, [Metz and van den Bosch 1995, van den Bosch and Metz and Diekmann 1990]. These results though intuitive provide a validation of the modeling approach. The validity of the conclusion is then verified by numerically solving the non-linear model and comparing the propagation speeds of traveling fronts. Our results are a theoretical complement to the findings in [van den Bosch et al. 1990], which are elaborated for

the *susceptible* \rightarrow *infected* \rightarrow *removed* (SIR) case for two spatial dimensions. It was found there that the speed of traveling fronts in a crop field with uniform mixing of resistant and non-resistant types are proportional to the logarithm of $1 - \alpha$, where α is the proportion of the resistant type. The theory and applications there elaborated and further described in [Metz and van den Bosch 1995] are inspired in fungal crop diseases for which the spores are dispersed in the canopy over short distances, creating local patches of high infestation. In contrast, alfalfa nematodes are expelled from the stems of an infected plant and reach the roots of new hosts using a combination of chemotaxis and transport through irrigation water flow along plant rows.

Currently, there are several varieties of alfalfa that are resistant to the stem nematode, but measures of resistance can vary. There is no standard for the classification of alfalfa varieties as “resistant” among manufacturers. It is known, for instance, that some declare a variety resistant if 51% of plants test negative for the presence of nematodes in screening trials. In addition, it is common practice among growers to commercialize non-certified seed, which often carries mixtures of resistant and non-resistant varieties. These two circumstances suggest that the results obtained in chapter 3 could be used to supplement the planning of control strategies.

In Chapter 4 we discussed how spatial continuous models for disease spread have been widely used to understand the crop disease dispersal process [Madden et al. 2011]. This approach describes the wave-like expanding traveling fronts of diseases moving at speeds to be determined, see [Madden et al. 2011] and [Ruan 2007]. The novelty in Chapter 4 is that we used experimental data to approximate the contact distribution for the alfalfa stem nematodes, which will help us to determine the wave speeds of an ASN infestation.

To gather the data we transplanted alfalfa plants into Solo cups that were connected in sets of two by PVC pipe. Nematodes were collected from infested plants in Millard County, Utah. These nematodes were extracted from the plants and placed in the center of the PVC bridge that connected two alfalfa plants. After six weeks the alfalfa plants were inspected to see which ones were infected. These data were then used to approximate the contact distribution for the alfalfa stem nematodes.

This contact distribution was then used in the model described in Chapter 3. Wave speeds were then calculated for different resistant classes. We conclude that using varieties that have higher resistance ratings can reduce the wave speed and quantify the magnitude of those reductions, see Table 4.3 . For example, switching from the susceptible class to highly resistant class can approximately decrease the wave speed by 64%.

The data from the experiment showed an abnormality at 0.5 in. In order to see how the infected plant count at this distance would affect wave speed we made computations with the model that compare the wave speed using the different diffusivity values that came from fitting the contact distribution to the data. The results showed that the biggest difference in wave speed from using different diffusivity values was 0.0051 in/week. Also, no significant variations to the percentage changes in Table 4.3 were detected after adjusting different diffusivity values obtained. This shows that even though the plant count at 0.5 in was abnormal, the model is robust.

In agreement with practice, the model shows that nematode invasion speeds are too low and cannot support the rapid dispersal of the disease as seen in the field. This leads us to presume that other mechanisms are in play that allow the efficient dispersal of nematodes, including nematode transport through the field by the tractor that harvests the alfalfa, and the consistent use of non-certified seed by farmers. The latter, also known as “brown bag” seed, has the potential to come from fields that have been contaminated with nematodes. In that case, it is possible that seeds carry nematodes attached, and farmers inadvertently re-infect their own field or the fields of the farmers who bought the seed. Another main driving mechanism supporting rapid nematode dispersal is the use of flood irrigation, which is the practice of opening gates at the top of the field that allow water to flow into the field. The gates are left open during a prescribed amount of time and then closed. It is speculated that the traveling water front is what is responsible for transporting the nematodes throughout the field. A supporting argument for this is that in sprinkler irrigated fields, where water is sprayed into the air so small water droplets fall into the ground, it is rare to spot a nematode problem. Our findings support the conjecture that changing from flood to sprinkler irrigation could effectively contribute to the control of the spread of the alfalfa stem nematode.

In this dissertation we specifically looked at how these resistant varieties affected harvest yield and invasion speed. These questions have not yet been addressed before using the mathematics contained in this dissertation. The end goal is to provide some helpful insights about managing a nematode infested alfalfa field. Since alfalfa is a major commodity in the United States it is of vital importance that advances are made in the management strategies of alfalfa to ensure that quality alfalfa is produced to meet the needs to the country. We believe that the results in this dissertation can help in the advancement of these crop management practices.

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APPENDICES

APPENDIX A
PERMISSION LETTER

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APPENDIX B
CURRICULUM VITA

SCOTT JORDAN

Department of Mathematics and Statistics 3900 Old Main Hill • Logan, Utah 84322

Email: scottjordan@aggiemail.usu.edu

EDUCATION

Utah State University *August 2015 - Expected graduation May 2018*
 Doctor of Philosophy (PhD) in Pure and Applied Mathematics
 Advisor: Dr. Luis Gordillo
 Cumulative GPA: 3.83/4.00

Utah State University *August 2013 - May 2015*
 Master of Science (M.S) in Mathematics
 Advisor: Dr. Luis Gordillo
 Cumulative GPA: 3.78/4.00

Brigham Young University Idaho *May 2009 - April 2013*
 Bachelor of Science (B.S) in Applied Mathematics
 Minor in Engineering
 Cumulative GPA: 3.73/4.00

EXPERIENCE

Utah State University August 2013 - Present
Graduate Teaching Assistant *Logan, UT*

Instructor of record for undergraduate courses in mathematics:

1. Math 1060: Trigonometry (2 Sections each semester) - Fall 2013, Spring 2014, Spring 2015, Spring 2017, Summer 2017 (1 section)
2. Math 1100: Calculus Techniques - Summer 2016
3. Math 1210: Calculus 1 - Fall 2014, Spring 2016
4. Math 2210: Calculus 3 - Spring 2018
5. Math 2270: Linear Algebra - Fall 2017

Teaching Assistant/Recitation Leader:

1. Math 1210: Calculus 1 - Fall 2015
2. Math 2250: Linear Algebra and Differential Equations - Fall 2016

-Duties include: prepare and present lectures, write lesson plans, grade papers, hold office hours, advise students, write and give exams and quizzes.

Brigham Young University Idaho January 2015 - Present
Online Instructor *Rexburg, ID*

Instructor for online courses

1. Math 111: Trigonometry (Full semester and block versions)-Fall 2016 (Pilot Instructor), Winter 2017, Spring 2017, Summer 2017, Fall 2017, Winter 2018
2. Math 100G: Personal Finance - Winter 2015, Spring 2015, Winter 2016, Spring 2016
3. GS 120: Pathway Life Skills - Fall 2015

- Online Course Representative (OCR) - Math 111. Work with Course Council to develop curriculum to enhance student learning
- Provided guidance for students to help them learn mathematical concepts.
- Graded assignments and provided feedback to help students improve their mathematical skills.

RESEARCH

Utah State University August 2015 - Present
PhD research

Project 1: Yield to the Resistance: The Impact of Nematode Resistant Varieties on Alfalfa Yield.

Project 2: Influence of resistant varieties on the speed of propagation of simple epidemics in crops.

Project 3: A model for the dispersal of the alfalfa stem nematodes.

Supervisor: Dr. Luis Gordillo (Mathematics)

Collaborators: Dr. Ricardo Ramirez (Biology) and Dr. Claudia Nischwitz (Biology)

Utah State University January 2014 - April 2015
Master's research

Project: Managing the spread of alfalfa stem nematodes (*Ditylenchus Dipsaci*): The relationship between crop rotation and pest re-emergence.

Supervisor: Dr. Luis Gordillo (Mathematics)

Collaborators: Dr. Ricardo Ramirez (Biology) and Dr. Claudia Nischwitz (Biology)

PUBLICATIONS

1. **Yield to the Resistance: The Impact of Nematode Resistant Varieties on Alfalfa Yield**
Jordan S., Natural Resource Modeling. 2017;00:e12150.
<https://doi.org/10.1111/nrm.12150>
2. **Influence of resistant varieties on the speed of propagation of simple epidemics in crops.**
L.F. Gordillo, S. Jordan, Applied Mathematics Letters, Volume 68, June 2017, Pages 129-134
3. **Managing the spread of alfalfa stem nematodes (*Ditylenchus Dipsaci*): The relationship between crop rotation and pest re-emergence.**
S. Jordan, C. Nischwitz, R. Ramirez, L.F. Gordillo, Natural Resource Modeling, 30(2) (2017)
4. **A model for the dispersal of the alfalfa stem nematodes.**
Scott Jordan, Ricardo Ramirez, and Luis F. Gordillo
In Progress

INVITED TALKS

Managing the spread of alfalfa stem nematodes (*Ditylenchus Dipsaci*) using Crop Rotation and Resistant Varieties
Brigham Young University - Idaho, June 1, 2017

PRESENTATIONS

1. **A model for the dispersal of the alfalfa stem nematodes.**
Oral presentation at the 2018 MAA Intermountain Section Meeting on March 23-24, 2018
2. **Yield to the Resistance: The Impact of Nematode Resistant Varieties on Alfalfa Yield.**
Poster presentation at the 2015 Society for Mathematical Biology Annual Meeting on July 17, 2017
3. **Yield to the Resistance: The Impact of Nematode Resistant Varieties on Alfalfa Yield.**
Poster presentation at the 2017 Society for Industrial and Applied Mathematics Annual Meeting on July 11, 2017
4. **Yield to the Resistance: The Impact of Nematode Resistant Varieties on Alfalfa Yield.**
Poster presentation at the Student Research Symposium at Utah State University on April 13, 2017
5. **Yield to the Resistance: The Impact of Nematode Resistant Varieties on Alfalfa Yield.**
Oral presentation at the MAA Intermountain Section Meeting on April 7, 2017
6. **Modeling the spread of alfalfa stem nematodes (*Ditylenchus Dipsaci*): The relationship between crop rotation and pest re-emergence.**
Poster presentation at the 2016 Society for Industrial and Applied Mathematics Annual Meeting at Westin Boston Waterfront on July 12, 2016
7. **Modeling the spread of alfalfa stem nematodes (*Ditylenchus Dipsaci*): The relationship between crop rotation and pest re-emergence.**
Poster presentation at the 2015 Society for Mathematical Biology Annual Meeting at Georgia State University on July 1, 2015
8. **Modeling the spread of alfalfa stem nematodes (*Ditylenchus Dipsaci*): The relationship between crop rotation and pest re-emergence.**
Oral presentation at the Student Research Symposium at Utah State University on April 9, 2015
9. **Modeling the spread of disease using delay differential equations**
Poster session at the Brigham Young University Idaho Research and Creative Works Conference on April 4, 2013
10. **Modeling the spread of disease using delay differential equations**
Oral presentation at the MAA Intermountain Section Meeting at Brigham Young University - Idaho on March 30, 2013

EXTRA-CURRICULAR ACTIVITIES

Society of Industrial and Applied Mathematics USU Chapter

- President (2016-2017)-Invite speakers, work with a team of students to organize activities, organized and ran calculus review, organized field trip to Idaho National Lab, organized professional development seminars
- Treasurer (2014-2016)- Organized calculus reviews, integration bees, complete funding requests, and handled funds for the organization

Utah State University Mathbio Lab

- Journal club to expand knowledge in the field of Mathematical Biology
- Participate in professional development activities to improve speaking and writing skills.

Science Unwrapped

Presentations after a community event focusing on science at Utah State University.

- Displayed poster titled "Modeling the spread of alfalfa stem nematodes (*Ditylenchus Dipsaci*): The relationship between crop rotation and pest re-emergence."
- Displayed Netlogo simulations that demonstrated soil erosion.
- Displayed Netlogo simulations that demonstrated the synchronization of flocking birds using agent based modeling.

AWARDS

SIAM USU Chapter Outstanding Student Award

For the 2016-2017 Academic Year

Graduate Student Department Service Award

Utah State University Department of Mathematics and Statistics Awards Meeting on April 15, 2016

SIAM Student Travel Award

\$650 used to travel to the SIAM 2017 Annual Conference

\$500 used to travel to the SIAM 2016 Annual Conference

Landahl Travel Award

\$100 used to travel to the SMB 2017 Annual Conference

\$100 used to travel to the SMB 2015 Annual Conference

Excellent Oral Communicator

Student Research Symposium at USU on April 9, 2015

Third place poster in the Mathematical and Economic Analysis Session

BYU-I Research and Creative Works Conference on April 4, 2013

First place in the Integration Bee

Department of Mathematics at BYU-I March 2011

MEMBERSHIPS

Society of Industrial and Applied Mathematics USU Chapter

American Mathematical Society

Society for Mathematical Biology

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Claudia Nischwitz - PhD committee member in Biology
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