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4. A mathematical model describing an outbreak of fire blight

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Abstract. Fire blight is an infectious tree disease caused by the bacteria *Erwinia amylovora* that primarily affects apple and pear varieties. Current methods for reducing fire blight infection are cutting off infected branches and using an antibiotic spray. In this chapter, we outline the economic impact of the disease in Canada and construct three models to investigate the spread of fire blight throughout an orchard. The full model is the most biologically accurate and examines infection through pollinator vectors and through the environment. We introduce two simplified models because of the complexity of the equations in the full model. These models allow for analysis of the basic reproductive ratio, R_0. Latin hypercube sampling was used to perform sensitivity analysis for each R_0 to determine the significance of each parameter in predicting

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the outcome of the disease. Analysis shows that both of the current control methods may have some impact in reducing the spread of fire blight. However, to successfully control the spread of fire blight, a more effective antibiotic spray with less resistance must be developed.

1. Introduction

Canada is one of the largest producers and exporters of agricultural products in the world. Apple production accounts for approximately 10% of this industry, with Canada marketing an estimated 955,276 pounds of apples in 2005 alone [1, 2]. This number, however, is largely reduced due to the loss of crops from storms, infection and disease. Fire blight is one of the most devastating apple diseases in the world. Under optimal weather conditions, fire blight can destroy an entire orchard in a single growing season, which can be economically devastating to the grower and the apple industry [3, 4]. According to Statistics Canada, the annual loss due to fire blight is approximately 5% of total production, which is valued at an estimated $4 million. In Quebec in 2002, an outbreak resulted in the loss of 10,000 trees with an approximated value greater than $800,000. Canada is not the only country facing loss due to this disease [5]. Fire blight is found worldwide in fruit-bearing trees in all countries except Australia and Japan, and with low infection in New Zealand [6].

Fire blight is a contagious bacterial infection that is typically found in fruit-bearing trees, primarily apple, pear and other members of the Rosaceaor rose family (plums, cherry, almond, etc) [5]. The infection is transmitted through gram-negative bacteria, *Erwinia amylovora*, and can infect all parts of the tree including the blossom, leaves, shoots, branches, roots and fruit of the tree. Primary infection is characterized by leaves and limbs that look as though they have been burnt by fire. Leaves become shriveled, curled and brown, and the bark of the tree appears blackened. Secondary infection occurs when the bacterial infection is no longer superficial but has become systemic, leading to death of the tree. This stage of disease is characterized by orange and yellow shoot tips as well as the symptoms of primary infection. At this point in the infection, transmission is high and the infected tree usually dies. Symptoms can appear as early as two weeks after infection has occurred or as late as the following spring, as bacteria can lie dormant within the tree and re-emerge with warm weather [7, 8].

Fire blight can be transmitted in a variety of ways. The primary mode of transmission is through pollinating insects that act as a vector and transmit the bacteria by picking it up from an infected tree and transmitting it to a susceptible tree during blossom season [9]. This is a very effective way for bacteria to spread because they can feed off the sugar of the open blossom, multiply quickly and spread to other uninfected parts of the tree. Humans can also spread the bacteria by picking it up on their clothing or farm equipment and making contact with an uninfected tree [8]. Since this has been recognized as a mode of transmission, greater precautions have been taken to reduce the spread of bacteria through human contact, thereby eliminating this possibility of transmission [6]. Nature plays a significant role in the spread of infection, since bacteria require optimal weather conditions for reproduction and growth. Optimal weather conditions include: a temperature greater than 14°C, but most favorable at approximately 18°C; a wetting event (rain or dew on the leaves) that is greater than 2 mm for the spread of bacteria; and wind speeds less than 20 km/hr, which allow pollinators to access the blossoms and blow infected leaves to susceptible trees. If wind speeds are higher than 20 km/hr, pollinators will stay low to the ground, as they are unable to fly. Hail storms and high winds can also damage the trees and cause open wounds that are further susceptible to infection, and can cause rapid transmission of disease and promote infection [3, 10].

Although there is currently no cure for fire blight, preventative measures can be taken to reduce the spread of disease. Typical spray applications that include copper sulfate and an antibiotic (streptomycin) are applied to trees during optimal weather conditions to target the bacteria when they are most abundant. The antibiotic and chemical compounds are often applied together to have maximal effect; however, the spray efficacy is very low and only deters bacterial growth. In addition, most strains of *Erwinia amylovora* are resistant to streptomycin antibiotic, which is the only registered antibiotic in Canada for this diease [11]. As a result, cutting off limbs is the only effective way of removing infection. This means of control can be economically devastating for growers because they suffer crop and profit loss even if the disease does not kill the tree [5].

2. Modelling fire blight

The main objectives of the models constructed in this chapter are to evaluate whether current controls for fire blight are effective enough to prevent further spread of the disease and what changes can be made in order to slow the progression of infections throughout an orchard. The model examines the efficacy of cutting off infected branches and spraying to reduce infection, which is spread through pollinating insects and the environment. Due to the complexity of the full model, two simplified models that are easier to analyse are also considered.

Fire blight infection is modelled on a daily time scale, which incorporates movement between susceptible and infected, sprayed and unsprayed classes, and infection through pollinators and the environment. The classes for trees and pollinators in a given orchard are defined as follows:

- $S_N(t)$ - Trees that are not sprayed or infected;
- $S_S(t)$ - Trees that are sprayed and are not infected;
- $I_N(t)$ - Trees that are not sprayed and are infected;
- $I_S(t)$ - Trees that are sprayed and are infected;
- $S_B(t)$ - Pollinators that are not carrying bacteria;
- $I_B(t)$ - Pollinators that are carrying bacteria.

In a given orchard, it is assumed that there is a natural death rate, *d*, from all tree classes, and disease death rates from classes of infected trees that are unsprayed and sprayed, given by rates *m* and *M* respectively. There is a birth rate that is proportional to the death rate because farmers replant trees relatively quickly. Movement from an unsprayed to a sprayed class occurs at spraying rate v and wears off at rate *w*. Being in a sprayed class reduces the chance of being infected and of spreading infection by a factor $1 - x$, where x describes the efficacy of the spray. Infection can spread as a result of environmental conditions at rate n and through contact with bacteria-carrying pollinators at rate q_b, yielding infection terms $nS_i(I_N + I_S(1-x))$ and $q_B S_i I_B$, with *i* referring to the sprayed or unsprayed class. It is assumed that the proximity of trees is not a contributing factor in the spread of disease; that is, a tree that is planted next to an infected tree is not more likely to be infected than others that are planted farther away. This assumption is justified by the random search of pollinating insects and the fact that a pollinator does not necessarily lose all of the bacteria that it is carrying when it lands on its first tree after visting an infected tree. Transmission of the infection from a dead tree is not considered because such trees tend to be removed quite quickly from the orchard and thus do not affect transmission. Infected trees can return to the susceptible class at rate c, which describes the successful removal of infected branches. Pollinators have constant birth given by *b*, die at rate *k* and will not die from the disease. They pick up bacteria from an infected tree at rate q_b and lose that bacteria at rate *h*. Although many insects are capable of transmitting fire blight from tree to tree, the model focuses on bees as the primary mode of transmission because it is assumed that there is no other infection in the orchard [12]. Finally, it is assumed that neither trees nor pollinators acquire immunity from the disease.

3. The full model

The full model is given by

$$
\begin{aligned}
S_N' &= -q_B S_N I_B - n S_N (I_N + I_S(1-x)) + c I_n - v S_N + w S_S + d(S_S + I_N + I_S) + M I_S + m I_N \\
S_S' &= -q_B S_S I_B (1-x) - n S_S (I_N + I_S(1-x)) + c I_S + v S_N - w S_S - d S_S \\
I_N' &= q_B S_N I_B + n S_N (I_N + I_S(1-x)) - c I_N - v I_N + w I_S - m I_N - d I_N \\
I_S' &= q_B S_S I_B (1-x) + n S_S (I_N + I_S(1-x)) - c I_S + v I_N - w I_S - M I_S - d I_S \\
S_B' &= b - q_T S_B I_N - q_T S_B I_S (1-x) - k S_B \\
I_B' &= q_T S_B I_N + q_T S_B I_S (1-x) - k I_B.
\end{aligned}
$$

The full model is illustrated in Figure 1

For mathematical tractability, we shall make two separate assumptions on this model, in order to analyse two simplified submodels.

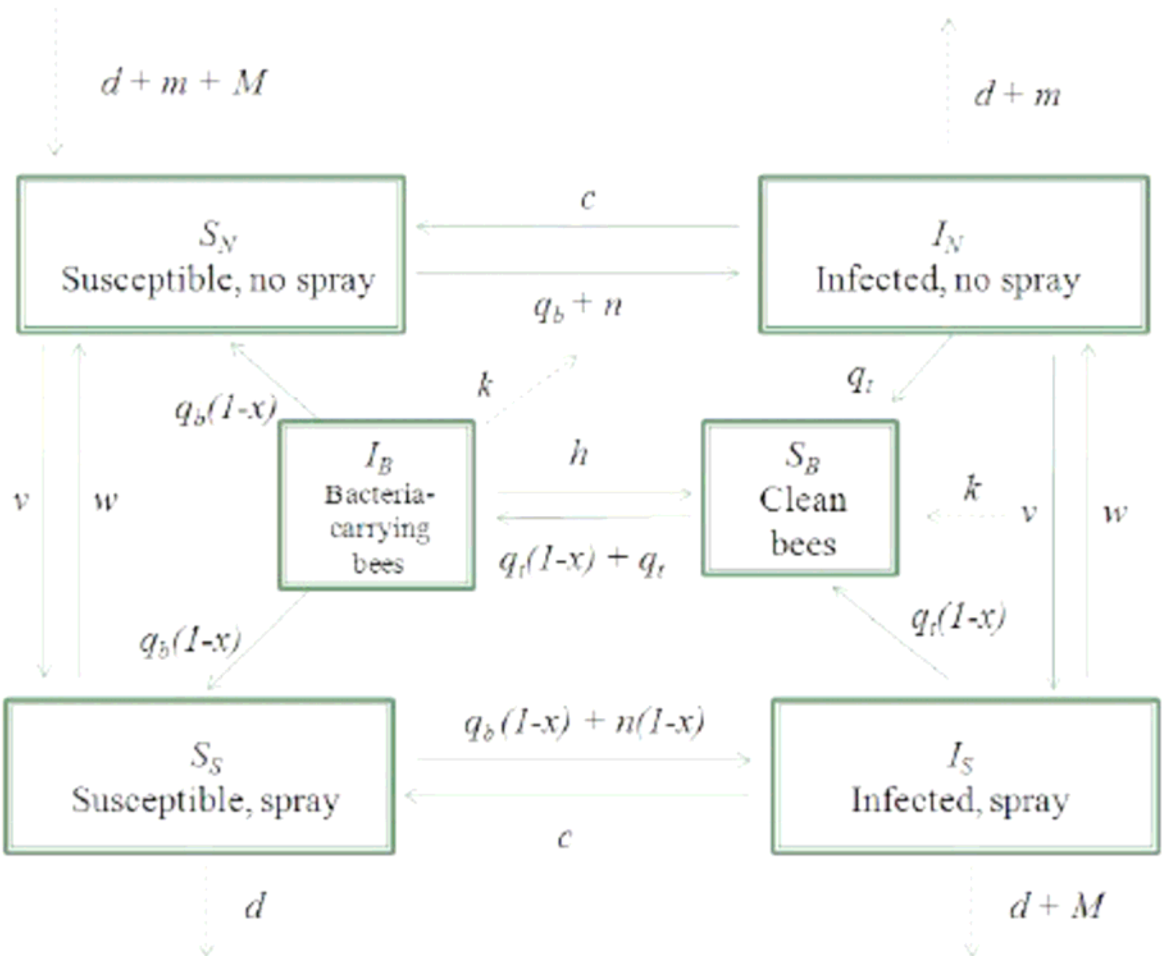

Figure 1. Flow diagram for the full model.

4. Model 2: Constant spray

The first simplified model involves reducing the number of tree classes by assuming that there is a constant amount of spray on all trees at all times. This is a reasonable assumption, because we are interested in the level of infection each year rather than on a daily scale. Thus, an average amount of spray on each tree rather than spray that is applied and wears off should yield similar results. We will refer to this as the CS model.

The flow diagram is given in Figure 2 and equations are modified as follows:

$$
\begin{aligned}
S' &= -q_b I_B S(1-x) + cI - n(1-x)SI + dI + (1-x)mI \\
I' &= q_B I_B S(1-x) - cI + n(1-x)SI - dI - (1-x)mI \\
S'_B &= -q_T S_B I(1-x) + kI_B + hI_B \\
I'_B &= q_T S_B I(1-x) - kI_B - hI_B,
\end{aligned}
$$

where S is the class of all susceptible trees and I is the class of all infected trees. S_B and I_B remain unchanged.

Here, we assume that $S + I = N$, where N is the total size of the orchard and that $S_B + I_B = P$, where P is the total number of bees. The disease-free equilibrium is

$$(S^*, I^*, S_B^*, I_B^*) = (N, 0, P, 0).$$

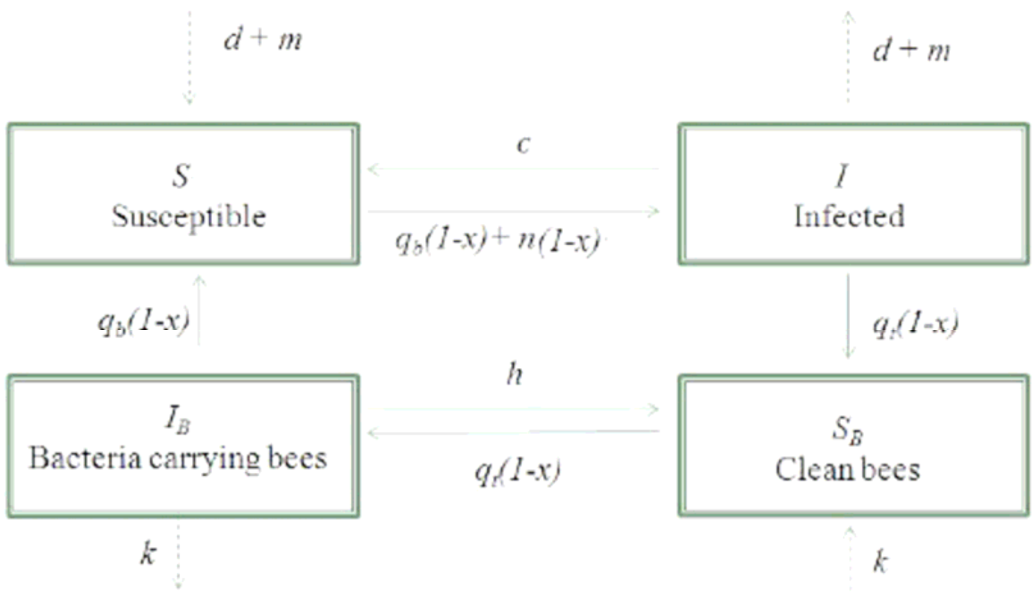

Figure 2. Flow diagram for the CS model.

The Jacobian is

$$J = \begin{bmatrix} (-q_B I_B - nI)(1-x) & c+d+(m-nS)(1-x) & 0 & -q_B S(1-x) \\ (q_B I_B + nI)(1-x) & -c-d+(nS-m)(1-x) & 0 & q_B S(1-x) \\ 0 & -q_T S_B(1-x) & -q_T I(1-x) & k+h \\ 0 & q_T S_B(1-x) & q_T I(1-x) & -k-h \end{bmatrix}.$$

The Jacobian at the disease-free equilibrium is

$$J\big|_{\mathrm{DFE}} = \begin{bmatrix} 0 & c+d+(m-nN)(1-x) & 0 & -q_B N(1-x) \\ 0 & -c-d+(nN-m)(1-x) & 0 & q_B N(1-x) \\ 0 & -q_T P(1-x) & 0 & k+h \\ 0 & q_T P(1-x) & 0 & -k-h \end{bmatrix}.$$

We have

$$\begin{aligned} \det(J-\lambda I) &= (-\lambda)^2((-c-d+(nM-m)(1-x)-\lambda)(-k-h-\lambda) - q_T P(1-x) q_B N(1-x)) \\ &= (-\lambda)^2[\lambda^2 + \lambda(k+h+c+d+(m-nM)(1-x)) - q_T q_B PN(1-x)^2 \\ &\quad + (k+h)(c+d+(m-nN)(1-x))]. \end{aligned}$$

Based on parameter estimates, the coefficient for λ given by $(k+h+c+d+(m-nM)(1-x))$ is always positive. We use the constant-term method to evaluate stability of the disease-free equilibrium and obtain the following R_0, the basic reproductive ratio [13]. If $R_0 > 1$, then the outbreak will persist, whereas if $R_0 < 1$, then the disease will be eradicated.

$$R_0 = N \frac{q_T q_B P(1-x)^2 + (k+h)n}{(k+h)(c+d+m(1-x))}$$

Since data for several parameters was unavailable to run simulations, we use Latin Hypercube Sampling, a method developed by McKay *et al.* [14], to determine which factors may be most influential in predicting the spread of disease. Partial rank correlation coefficients illustrates how influential each parameter is on R_0.

Sensitivity analysis, using the data from Table 1, shows that the most significant parameter in reducing R_0 is the spray efficacy (Figure 3). Cutting off branches is effective in reducing spread of the disease, but not to the same extent as spray efficacy. The orchard size and number of bees increase R_0.

Table 1. Parameter values.

Parameter	Definition	Units	Range (Lower - Upper)
d	Natural death rate of trees	1/day	0.0001 - 0.0002
x	Spray efficacy	%	0 - 1
m	Death rate of infected, unsprayed trees	1/day	0.01 - 0.05
n	Spread of infection through the environment	1/(tree day)	0 - 0.25
w	Rate that spray wears off	1/day	0 - 0.3333
M	Death rate of infected, sprayed trees	1/day	0.005 - 0.025
v	Spraying rate	1/day	0 - 0.3333
q_T	Rate that pollinators pick up bacteria from infected trees	1/(tree day)	0.05 - 0.25
q_B	Rate that bacteria-carrying pollinators transmit bacteria to trees	1/(tree day)	0.05 - 0.25
k	Death rate of bees	1/day	0.0333 - 0.0666
b	Birth rate of bees	Bees/day	N/A
c	Rate that farmers remove infected limbs	1/day	0.2 - 1
N	Orchard size	Trees	1000 - 8000
P	Number of bees	Bees	5000 - 25000

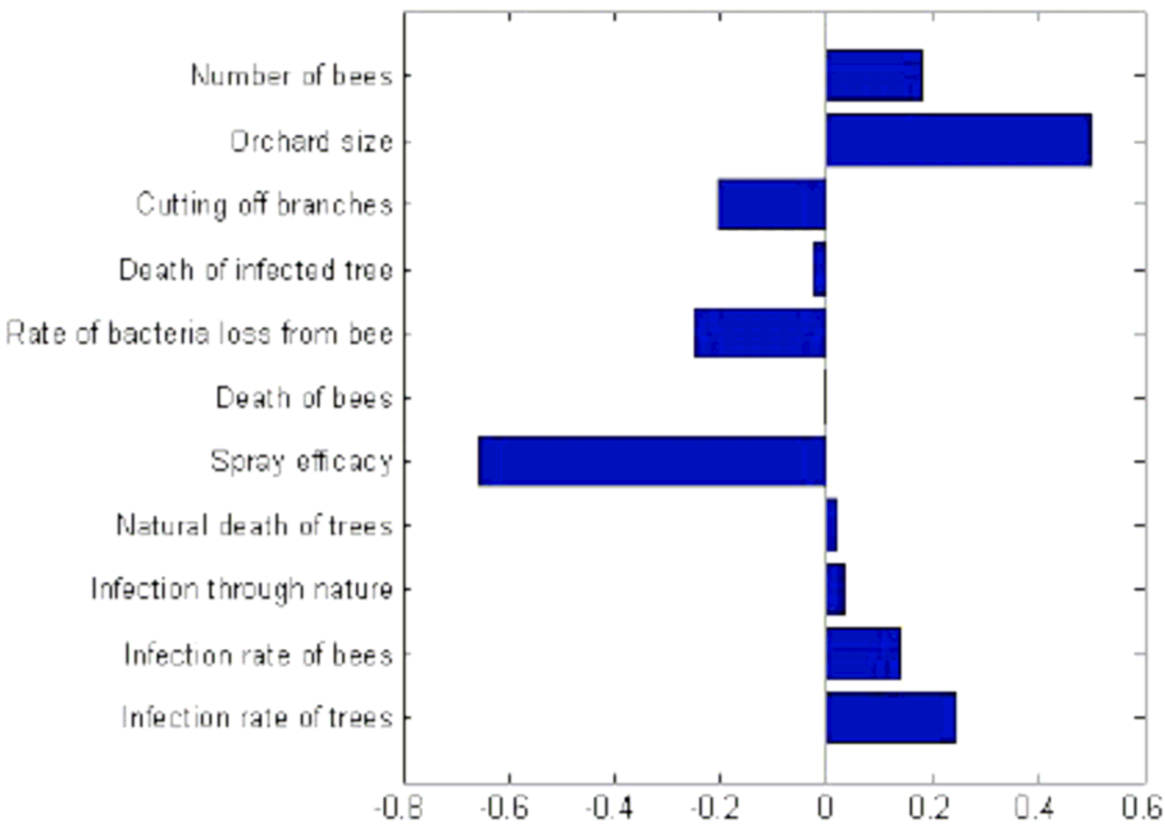

Figure 3. Sensitivity analysis for R_0 for the CS model.

The impact of infection through nature appears insignificant when compared with infection from pollinators.

5. Model 3: Constant number of infectious bees per infected tree

The second simplified model examines the spread of disease where we consider a constant number of bees carrying the infection per infected tree in the orchard. With this additional assumption, the classes S_B and I_B are removed from the model and the parameter that would describe the spread of infection through bees is absorbed into the infection through the nature term. This results in a single infection term for each class of susceptible trees which are given by $nS_N(I_N + I_S)$ and $nS_S(I_N + I_S)(1 - x)$ for unsprayed and sprayed trees respectively. We will refer to this model as the CB model.

The flow diagram is given in Figure 4 and the equations are modified as follows:

$$
\begin{aligned}
S_N' &= -vS_N + cI_N + wS_S - nS_N(I_N + I_S)_m I_N + MI_S + d(S_S + I_N + I_S) \\
S_S' &= vS_N + cI_S - wS_S - nS_S(I_N + I_S)(1 - x) - dS_S \\
I_N' &= -vI_N - cI_N + wI_S + nS_N(I_N + I_S) - dI_N - mI_N \\
I_S' &= vI_N - cI_S - wI_S + nS_S(I_N + I_S)(1 - x) - MI_S - dI_S.
\end{aligned}
$$

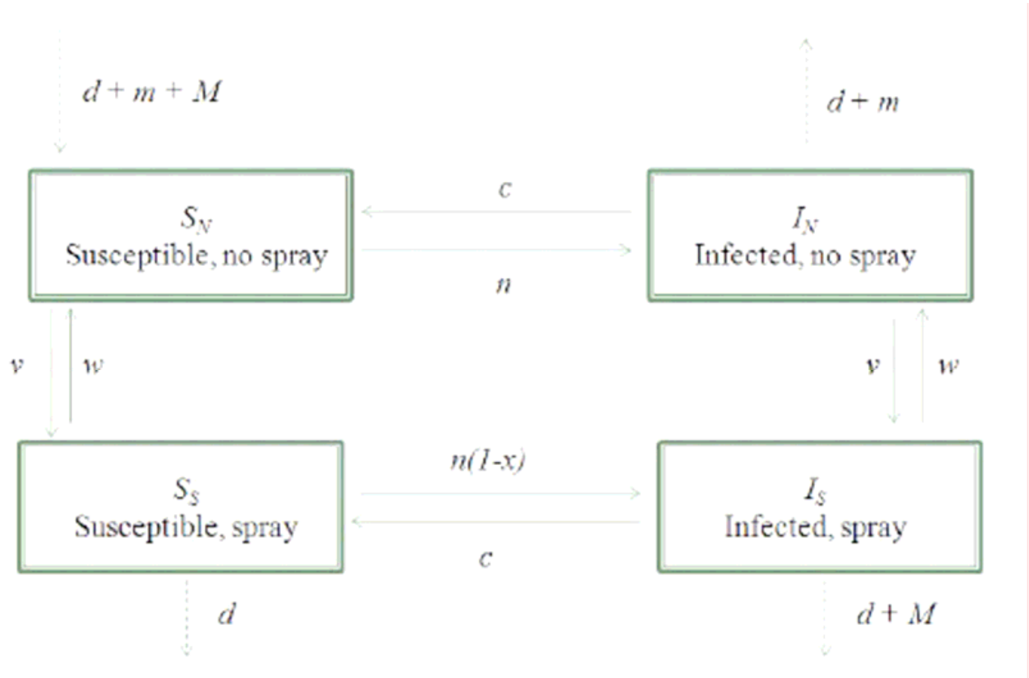

Figure 4. Flow diagram for the CB model.

The disease-free equilibrium for the model is given by

$$(S_N^*, S_S^*, I*_N, I*_S) = \left(\frac{N(w+d)}{w+d+v}, \frac{N(v)}{w+d+v}, 0, 0\right)$$

In order to determine R_0 for this model, we use the next-generation method rather than using the Jacobian method, which has a characteristic that can be solved using the quadratic formula, but yields unwieldly eigenvalues with little biological meaning [13, 15]. Using the next-generation method, we consider only the two classes of infected trees, I_N and I_S. We obtain the matrices F and V , which we evaluate at the disease-free equilibrium, where F includes all terms of new infections and V includes terms describing class transfers, which we evaluate at the disease-free equilibrium:

$$F = \begin{bmatrix} nS_N^* & nS_N^* \\ nS_S^*(1-x) & nS_S^*(1-x) \end{bmatrix}$$

$$V = \begin{bmatrix} v+c+d+m & -w \\ -v & c+w+M+d \end{bmatrix}$$

$$V^{-1} = \frac{1}{(v+c+d+m)(c+w+M+d)-vw} \begin{bmatrix} c+w+M+d & w \\ v & v+c+d+m \end{bmatrix}$$

$$FV^{-1} = \frac{1}{(v+c+d+m)(c+w+M+d)-vw} A$$

where

$$A = \begin{bmatrix} nS_N^*(c+w+M+d+v) & nS_N^*(w+v+c+d+m) \\ nS_S^*(1-x)(c+w+M+d+v) & nS_S^*(1-x)(w+v+c+d+m) \end{bmatrix}.$$

We then have

$$\det(FV^{-1} - \lambda I) = \lambda^2 - \lambda \frac{1}{\det V}(nS_N^*(c+w+M+D+V) + nS_S^*(1-x)(w+v+c+d+m))$$

$$\det(V) = (v+c+d+m)(c+w+M+d) - vw.$$

The largest eigenvalue of $FV^{-1} - \lambda I$ is used to find R_0:

$$R_0 = \frac{nS_N^*(c+w+M+d+v) + nS_S^*(1-x)(w+v+c+d+m)}{(v+c+d+m)(c+w+M+d)-vw}.$$

Figure 5. Sensitivity analysis for R_0 from the CB model.

It follows that the disease-free equilibrium is stable if $R_0 < 1$.

The sensitivity analysis depicted in Figure 5 shows that cutting off branches has the most influence in reducing R_0. The spray efficacy and spray rate both have a moderate effect on R_0. The spray rate and the rate that spray wears off have similar amounts of influence, with the former decreasing R_0 and the latter increasing R_0. The size of the orchard and infection from nature are the most influential terms, both of which result in an increase in R_0.

6. Discussion

The full model for the spread of fire blight in an orchard incorporated a wide variety of biological factors that contribute to the spread of the disease. However, it did not lend itself well to analysis because of the non-linear nature of all of the ODEs. Therefore, two simplified models were constructed, based on additional assumptions that removed some of the complexity. The first model, Constant Spray (CS), allowed us to remove two classes of trees because the sprayed and unsprayed trees were combined. The second model, Constant number of infectious Bees per infected tree (CB), also reduced the model to four equations because the bee classes were removed.

One of the major differences that is observed between the two models is that spray efficacy is much more significant in reducing R_0 in the CS model than in the CB model. This could be because the CS model assumes that spray is present at all times and does not take into account the weather conditions in which bacteria thrive. Conversely, the CB model assumes that the trees are being sprayed during optimal weather conditions when bacterial growth will be greatest. This suggests that the spraying strategy of the CB model may be more effective in reducing the spread of fire blight. Furthermore, the assumption that trees would always be sprayed in the CS model does not hold because spray wears off in 3-5 days and it is too costly and time consuming for farmers to maintain. The other treatment option for the disease - cutting off branches - appears highly significant in both models. This demonstrates that this is a good method of reducing infection, despite the high costs associated with crop loss and labour.

It is difficult to assess whether the assumption about bees made in the CB model is well justified. We compare the results with those of the CS model, which shows that the number of bees and the rate that the bees pick up bacteria have a greater influence in increasing the spread of disease than the infection through nature does. In the construction of the CB model, infection from bees was accounted for in the infection from nature term. This is demonstrated by the sensitivity analysis, which shows that this term is highly influential in increasing R_0, especially when compared to its influence in the CS model.

Both models demonstrate that the size of the orchard is important in the spread of disease and a larger orchard may be more susceptible to the spread of fire blight. In the two models, this may be because there is no spatial consideration, so a larger orchard would have the disease spread much faster. There are many reasons that a larger orchard may actually be more susceptible to an outbreak, such as the decreased spray coverage, the decreased chance of detecting an infected tree before an outbreak occurs and an increased number of pollinators.

The results from the CB and CS models suggest that all of the factors included in the full model are significant and may contribute to a more accurate prediction of the spread and control of fire blight. Neither of the two simplified models seems more accurate than the other; however, they both provide useful insight into fire blight outbreaks and management. The models suggest that the most effective way to control fire blight is through a combination of cutting off branches and spraying. However, both must be done in moderation because spraying is costly and cutting off branches reduces crop yield and increases labour costs. Fire blight cannot be eradicated at a reasonable cost with these methods because spray efficacy is so low

Therefore, greater efforts should be made by pesticide manufacturers towards creating a more efficient spray to target bacteria with less resistance and effectively reduce the spread of infection and chance of an outbreak.

If spraying of sufficient efficacy can be developed, then eradication of Fire Blight may be within reach. However, until then, this disease will continue to wreak environmental and economic devastation upon a crucial worldwide industry.

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