Modelling the impact and control of an infectious disease in a plant nursery with infected plant material inputs.

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Abstract

We will model the impact an infectious disease has on a plant nursery under a constant pressure of potentially infected input plant materials like seeds. The nursery owner has two different forms of control: biosecurity (actions to restrict infected inputs) and removal of infected plants within the nursery. The profit-maximising nursery owner will seek to balance the costs from control with the loss of revenue from having infected plants. We explore the disease dynamics within the nursery and the consequences of removal and restriction including their synergies and trade-offs.

Keywords: biosecurity; plant disease; optimal control; trade.

JEL Codes: Q57, Q29, D81

1 Introduction

Increases in the movement of people and traded goods as a consequence of globalisation (Hulme, 2009; Perrings et al, 2010; Dalmazzone and Giaccaria, 2014) have led to growing concerns about the threat posed by invasive species, and in particular invasive pathogens of humans, plants and livestock (Anderson et al, 2004). Recent disease outbreaks in plants, such as the chalara fungus (*Hymenoscyphus pseudoalbidus*) affecting ash trees across Europe (Pautasso et al, 2013) and the oomycete *Phytophthora ramorum* affecting larch in Europe (Brasier and Webber, 2010) and oaks in the US (Rizzo et al, 2002), have focused attention on the optimal policy options available to reduce the risks of similar outbreaks occurring in the future. Management of pest outbreaks includes a series of instruments that can combine inspections and quarantine, chemical or mechanical removal, biological control, pest-risk analysis, exports pre-clearance programmes or even harvested for economic value. The body of the literature that combines invasion ecology with economic analysis has drastically increased in recent years to explore policy tools to reduce the likelihood of an invasion, to allocate survillance, to control and eradicate a newly established population, and to adapt to damages or to restore habitats where invasive species have been removed (e.g. Finnoff et al. 2006, Fenichel et al. 2014, Shogren and Tschirhart, 2005; Hall and Hastings, 2007; Hennessy, 2008; Finnoff et al, 2010; Horan and Lupin, 2010; Carrasco et al, 2012; Horan et al, 2015).

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One of the challenges for developing policy to reduce the risk of outbreaks of invasive plant pathogens is the fact that the potential routes of invasion are not only diverse but also that they are controlled by a mixture of public and private agents. Trading decisions made by private decision-makers may have significant implications for public interest at a regional or national level, but the public costs of an outbreak are likely to far exceed the costs experienced by any one private business, and a privately optimal trading decision is very unlikely to match the publicly optimal one due to potential conflicting interests (Mills et al, 2011, Perrings et al 2005). Effective control of the risk posed by invasive plant pathogens is therefore an example of a weakest-link public good (Perrings et al, 2002; Burnett, 2005) where strategic interactions among public and private actors in trade networks determined the spread and the level of success of control measures. A better understanding of how decisions are made by private businesses, and the implications these have for public risk, is therefore fundamental for informing effective policy development in this area.

In this paper, we develop a simple bioeconomic model of a private nursery owner seeking to maximise profits from growing and selling plants from seeds in the face of the threats posed by an invasive disease. The management options available to the nursery owner are (1) biosecurity to restrict the import of infected seeds and (2) inspection and removal of infected plants within the nursery. We examine the optimal decisions made by the nursery owner under various biosecurity and inspection conditions, and discuss the implications of this private-level analysis for understanding public-level risks.

2 Model derivation

2.1 Disease dynamics within the plant nursery

We consider a plant nursery with a nursery owner who constantly buys plant material, grows it and sells it on when the plant becomes mature. However, there is an disease which is introduced within the plant material bought and which can spread within the nursery. For simplicity and generality, we will assume that this disease splits the plant population into two classes, susceptible plants and infected plants. Infected plants can infect susceptible plants, and once infected a plant remains infected for the rest of its time in the nursery; there is no recovery from the infection once infected. The consequence of infection for the nursery owner is that infection alters (typically reduces) the net price from selling of a mature plant.

To combat the spread of the infection within the nursery, the nursery owner has two different control measures; the owner can invest in biosecurity to reduce the proportion of infected inputs (be it from inspecting and rejecting infected prey or by selecting sources with less infection) and by removing infected plants within the nursery. Both of these controls measures have an associated cost to their implementation (something we come to later).

Schematically, the plant-disease dynamics can be described as (see Figure 1):

Change in S = Input of S - Output of S - Disease Transmission,

Change in I = Input of I - Output of I - Removal of I + Disease Transmission.

For simplicity, we will assume a constant population, which in practical terms means the nursery is assumed to always be full. To do this, set Total Input=Total Output + Removal, where $\text{Output}_S = \delta S$ and $\text{Output}_I = \delta I$, where δ is the rate of plants become mature and sold off (i.e. plants stay for an expected time of $\frac{1}{\delta}$ in the absence of control). This means we have assumed instantaneous replacement of any removed plant; when something is either removed to be sold or removed by control, it is replaced to keep the nursery full. We also set removal control as proportional to the infected plant population i.e. Removal of $I = u_{rem}I$, and we will assume that u_{rem} is bounded between 0 and u_{remmax}, the maximum possible effort spent on removal. Incorporating this, we have:

$$\text{Total Input} = \delta(S+I) + u_{rem}I. \tag{1}$$

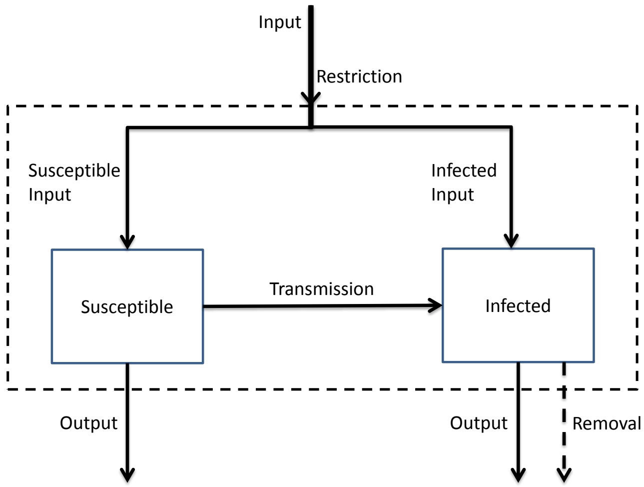


Figure 1: A transfer diagram representing the disease dynamics within the nursery

Now, this input is split between susceptible and infected plants, and suppose that $p(u_{ins})$ is the proportion of input that are infected (as a function of biosecurity control cost per unit time u_{ins}) and thus $(1-p(u_{ins}))$ is the proportion of input that are susceptible.

Armed with all this, and assuming density dependent transmission (βSI), we get:

$$\frac{dS}{dt} = (1-p(u_{ins}))(\delta(S+I)+u_{rem}I) - \delta S - \beta SI, \quad (2)$$

$$\frac{dI}{dt} = p(u_{ins})(\delta(S+I)+u_{rem}I) - \delta I - u_{rem}I + \beta SI. \quad (3)$$

Now, we have a constant population since $\frac{dS}{dt} + \frac{dI}{dt} = 0$, and thus $S+I=N$ is constant, i.e. total population does not change with time, so N is the number of plants in the nursery. This means that we can reduce the system down to one equation, since the number of susceptible plants is known once we have the number of infected plants through $S = N - I$. Also, we can rescale the infected population with the total population by considering disease prevalence, $i = \frac{I}{N}$, the proportion of infected plants in the population. Given it is a proportion, disease prevalence i is always between 0 and 1, inclusive.

Then we get:

$$\frac{di}{dt} = \frac{1}{N}\frac{dI}{dt} = p(u_{ins})(\delta + u_{rem}i) - \delta i - u_{rem}i + \beta N(1-i)i. \quad (4)$$

Furthermore, if we rescale time relative to output such that the rate of output becomes one. This rescaling results in the time unit being the expected time a susceptible plant stays in the nursery, and consequently time τ can be seen as the number of generations. Doing this, we get:

$$\frac{di}{d\tau} = p(u_{ins})(1 + \hat{u_{rem}}i) - i - \hat{u_{rem}}i + R_0(1-i)i, \quad (5)$$

where $\hat{u_{rem}} = \frac{u_{rem}}{\delta}$, the removal effort per plant generation (which is bounded above by $\hat{u_{remmax}} = \frac{u_{remmax}}{\delta}$), and $R_0 = \frac{\beta N}{\delta}$, the basic reproductive number, the expected number of secondary infections from a single infected plant over the lifespan of the infected plant in the nursery in an otherwise wholly susceptible population. The basic reproductive number is fundamental to whether a disease will spread, we will discuss this parameter in detail in the 'perfect biosecurity' subsection of the Results.

We have that some proportion of the plants brought into the nursery are infected. This proportion depends on the cost (per unit time) of the inspection regime u_{ins}; the more money spent on the inspection regime, the proportion of infected plants input is reduced. Consequently, we assume that the proportion of inputting infected plants has the following properties:

- $p(u_{ins})$ is a continuously differentiable function of the inspection cost u_{ins}.
- With no (cost from) inspection of imports, some proportion of infecteds, a, will be inputted, i.e. $p(0) = a$ where $a \in (0,1]$.
- With any finite inspection effort/cost, some proportion of infecteds will be inputted, i.e. $p(u_{ins}) > 0$ for all finite u_{ins}. This means that it is not possible to completely stop infected inputs from arriving no matter how much is spent on biosecurity.
- For all inspection effort/costs, increasing inspection effort/cost reduces the proportion of infecteds being inputted, i.e. $p(u_{ins})$ is a monotonically decreasing function of u_{ins} (equivalently, $\frac{dp}{du_{ins}} \leq 0$ everywhere).

Any function that is (a) continuous, (b) bounded below (by zero in this case) and (c) monotonically decreasing, must converge to some limit as u_{ins} goes to infinity. We denote this limit b, the proportion of inputs that are infected when unlimited biosecurity is used, where $b \in [0,a]$. A simple candidate that satisfies all of these assumptions is $p(u_{ins}) = (a-b)\exp(-du_{ins}) + b$, which we will use later for all numerical solutions and some of the analytics (when the above assumptions for $p(u_{ins})$ are insufficient to proceed).

2.2 Decision model

We are considering a long-term profit-maximising nursery owner. This means that the nursery owner will seek to choose a particular (constant) level of removal and biosecurity such that is maximises profit (per unit time) at the corresponding steady state.

Firstly, the revenue source is from selling plants that are outputted when mature. The net price for an outputted mature susceptible plant is P_{outS}. Likewise, the net price of an outputted mature infected plant is P_{outI}. In most cases, $P_{outI} < P_{outS}$ since the infection would likely decrease the plants value when mature and could incur higher removal and packaging costs; although this is not necessary the case as the disease might be beneficial (noble rot, for example). In particular, P_{outI} might be negative if it has no resale value but has cost for removal.

With our constant population assumption, we need to replace all plants removed from the system be it from being mature or infected plants being removed from control. Each removed plant costs P_{in} to replace. This implies that there is sufficient plant material available in the market to meet this demand and that this demand has a negligible effect on the price.

The cost of removing infected plants is proportional to the number of infected plants and proportional to the control effort in removing infected plants u_{rem}, which is limited by a maximal value of u_{remmax}. We assume that the nursery has a good knowledge of which plants are infected by a regime of within nursery inspections and can act according if desired (we assume this inspection regime is independent of the state of the nursery, i.e. a constant cost and thus ignorable when seeking to optimise). The total cost (per unit time) of the biosecurity regime u_{ins} is a control, the cost of which does not depend on the state within the nursery.

Given all this, the optimising equation is:

$$\text{Maximise Profit} = \overbrace{P_{outS}\delta S}^{\text{Revenue from selling S}} + \overbrace{P_{outI}\delta I}^{\text{Revenue from selling I}} - \overbrace{P_{in}(\delta N + u_{rem}I)}^{\text{Purchase of replacement stock}} - \overbrace{cu_{rem}I}^{\text{Cost of removing}} - \overbrace{u_{ins}}^{\text{Cost of biosecurity}} \tag{6}$$

subject to Equations (2&3) where $u_{rem} \in [0, u_{remmax}]$ and $u_{ins} \geq 0$.

However, we need to do some rescaling so that the optimising equation has the same state variables, parameters and such as the host dynamics, i.e. replacing S, using prevalence i instead of infected populations and scaling time with respect to expected general we arrive at:

$$\text{Maximise Profit} = P_{outS}(1-i) + P_{outI}i - P_{in}(1+\hat{u_{rem}}i) - c\hat{u_{rem}}i - \hat{u_{ins}} \tag{7}$$

subject to Equation (5) where $\hat{u_{rem}} = \frac{u_{rem}}{\delta} \in [0, \hat{u_{remmax}}]$ (as before), $\hat{u_{remmax}} = \frac{u_{remmax}}{\delta}$ and $\hat{u_{ins}} = \frac{u_{ins}}{\delta N}$.

Since u_{ins} has now been rescaled, we need to define the proportion of infected inputs as a function of this rescaled inspection control cost. Consequently, for the case $p(u_{ins}) = (a-b)\exp(-du_{ins}) + b$, define $\hat{p}(\hat{u_{ins}}) = (a-b)\exp(-\hat{d}\hat{u_{ins}}) + b$ where $\hat{d} = d\delta N$ such that $\hat{p}(\hat{u_{ins}}) = p(u_{ins})$.

Given some terms are constant and thus have no influence on the optimised solution, we can simplify slightly and gather terms to arrive at (now as per capita profit which is fine since total population N is constant):

$$\text{Maximise } (\overbrace{P_{outI} - P_{outS}}^{\text{revenue lost from infecteds}} - \overbrace{(P_{in}+c)\hat{u_{rem}}}^{\text{cutting control and replacing infecteds}})i - \overbrace{\hat{u_{ins}}}^{\text{input inspection costs}} \tag{8}$$

$$\longleftrightarrow \quad \text{Maximise } (-L_{out} - C\hat{u_{rem}})i - \hat{u_{ins}} \tag{9}$$

where $L_{out} = P_{outS} - P_{outI}$ and $C = P_{in} + c$. Notice that it does not matter what the values of P_{outS} and P_{outI}, only their difference, L_{out} (the loss incurred from selling a mature infected plant instead of a mature susceptible plant), matters for the optimal control strategy. Also, C is the total cost of removing and replacing an infected plant via the removal control, incorporating both the removal and replacement into one term. Lastly, this equation is solely made of costs from control and losses from infection. This is a consequence of the total revenue from selling susceptible and infected plants being equivalent to the revenue from selling every plant as if it were susceptible (which gives a constant revenue and thus can be ignored for maximisation) minus the loss of revenue from having an infected plant instead of a susceptible.

Consequently, the final decision model is:

$$\text{Maximise } Q := (-L_{out} - C\hat{u_{rem}})i - \hat{u_{ins}} \tag{10}$$

subject to

$$\frac{di}{d\tau} = \hat{p}(\hat{u_{ins}})(1+\hat{u_{rem}}i) - i - \hat{u_{rem}}i + R_0(1-i)i, \tag{11}$$

where $\hat{u_{ins}} \geq 0$ and $\hat{u_{rem}} \in [0, \hat{u_{remmax}}]$.

3 Results

3.1 Long term disease dynamics

In this section, we focus on the disease dynamics for a given control regime. In particular, we will find out what the long term disease dynamics. First, we will focus on the case where all inputs are susceptible (i.e. when $\hat{p}(\hat{u_{ins}}) = 0$) before looking at the more complex case where there are infected inputs (i.e. when $\hat{p}(\hat{u_{ins}}) > 0$).

3.1.1 Perfect biosecurity ($\hat{p}(\hat{u_{ins}}) = 0$)

In this subsection, we focus on the case where we have perfect biosecurity, i.e. all inputs are susceptible. However, we will assume that there exists a small number (say one) of infected plants already in the nursery. Here, we will look to see if the disease will become endemic or not in the nursery without any introduction of new infecteds from outside the nursery.

In the absence of the removal of infected plants (i.e. $\hat{u_{rem}} = 0$), we have two cases: (1) $R_0 < 1$: In this case, a single infected infects less than one susceptible over the lifetime of the infected within and hence the disease will die out from any single introduction. Consequently, the only stable state is the disease-free state and thus the disease can not become endemic ($i^* = 0$) (Figure 2b). (2) $R_0 > 1$: Here, a single infected infects more than one susceptible over the lifetime of the infection and hence the disease will spread out from any single introduction. Hence, the only stable steady state is the endemic steady state $i^* = 1 - \frac{1}{R_0}$ and thus any introduction will result in the disease being endemic (Figure 2a).

In the presence of the removal of infected plants (i.e. $\hat{u_{rem}} > 0$), the results are similar to the absence of removal, except the threshold between a disease-free nursery and an endemic disease in the nursery is based on value of $R_0^{rem} = \frac{R_0}{1+\hat{u_{rem}}}$. For $R_0^{rem} > 1$, for any introduction of disease, the disease will invade and approach the steady state $i^* = 1 - \frac{1}{R_0^{rem}}$ (Figure 2a). For $R_0^{rem} < 1$, the disease will not become endemic from any single introduction (Figure 2b).

Now, for $\hat{u_{rem}} > 0$, we have that $R_0^{rem} < R_0$. What this means is that the disease will find it harder to survive as infected plants have less time in the nursery to infect other plants because of removal. In particular, if $\hat{u_{rem}}$ is sufficiently large, we can reduce R_0^{rem} below 1 and consequently rid the nursery of the disease in the long run.

3.1.2 Imperfect biosecurity ($\hat{p}(\hat{u_{ins}}) = p > 0$)

In this subsection, we will consider the case where biosecurity is no longer perfect; some infected input plant materials will always get through.

With imperfect biosecurity, the disease will always persist in the population to some level (Figure 3). There is always only one steady state that is realistic,

$$i^* = \frac{R_0 - 1 - (1-\hat{p})\hat{u_{rem}} + \sqrt{(R_0 - 1 - (1-p)\hat{u_{rem}})^2 + 4pR_0}}{2R_0}, \tag{12}$$

and it is always stable. The lack of a disease-free steady state is due to the constant inflow of infected into the system. In particular, $\frac{di}{d\tau} = p > 0$ at $i = 0$ and thus disease prevalence will always increase when starting with a disease-free nursery.

Despite the disease always persisting in the nursery, we wish to distinguish between two cases. If $R_0^p = \frac{R_0}{1+\hat{u_{rem}}(1-p)} > 1$ (Figure 3a), the disease spreads through the population like before. Notice that $R_0 > R_0^p > R_0^{rem}$, since the removal control is only effective $(1-p)*100\%$ of the time, since $p*100\%$ of the time in the removing infected is replace by another infected (in particular, if $p = 0$, $R_0^p = R_0^{rem}$, whereas for $p = 1$, $R_0^p = R_0$). Consequently, imperfect biosecurity undermines the removal control. In particular, if $R_0^{rem} > 1$, the disease would persist without any infected inputs (as shown in the previous subsection for perfect biosecurity). If $\frac{R_0}{1+\hat{u_{rem}}(1-p)} < 1$ (Figure 3b); the disease does not spread effectively within the nursery and instead its persistence in the nursery is dependent on constant introduction of infected plants into the nursery.

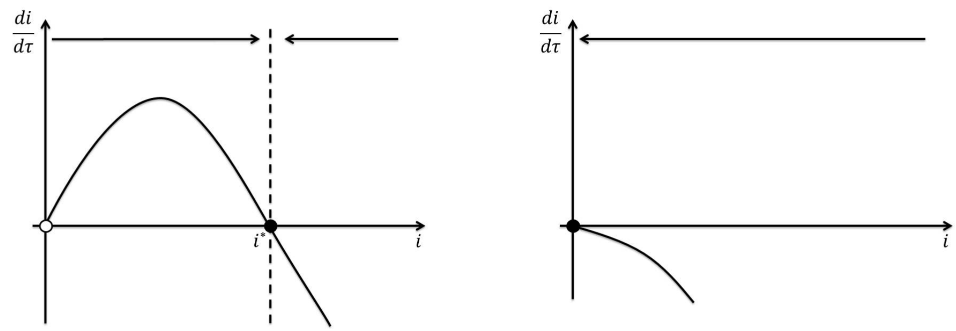
The disease dynamics for the imperfect biosecurity are essentially logistic growth with an addition constant introduction of infected plants. In particular, Figure 3a can be seen as a shifted and transformed version of the logistic growth in Figure 2a, which results in the loss of the disease-free steady state and an increase in the endemic steady state. Likewise, Figure 3b can be seen as a shifted version of the 'negative logistic growth' in Figure 2b, where the disease-free steady state becomes an endemic steady state.

3.2 Optimal control

In this section, we will consider how long-term profit changes with constant removal and biosecurity controls. We will focus on the combination of constant controls that would maximise long-term profit,

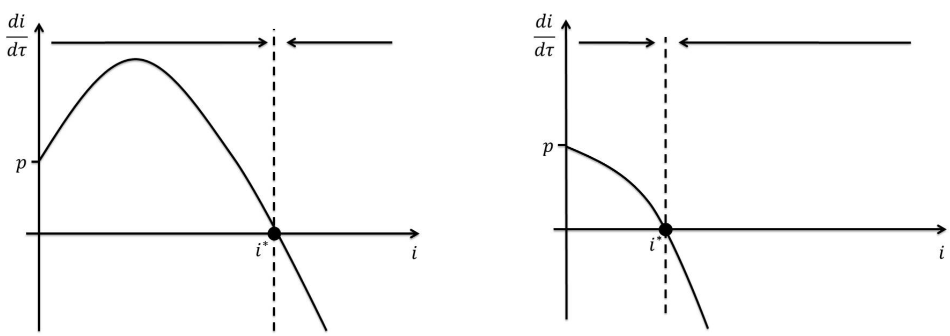
	Endemic	Disease free
Perfect Biosecurity, no removal	$R_0 > 1$	$R_0 < 1$
Perfect Biosecurity with removal	$R_0^{rem} > 1$	$R_0^{rem} < 1$
Imperfect Biosecurity	Always	Never

Table 1: Summary of Constant Control where $R_0^{rem} = \frac{R_0}{1+\hat{u_{rem}}}$ and $R_0^p = \frac{R_0}{1+(1-p)\hat{u_{rem}}}$



(a) (b)

Figure 2: Perfect biosecurity ($p = 0$): (a) If $R_0^{rem} = \frac{R_0}{1+\hat{u_{rem}}} > 1$, then the prevalence equation is a form of Logistic growth. There are two steady states (where $\frac{di}{d\tau}$), $i^* = 0$ and $i^* = 1 - \frac{1}{R_0^{rem}}$. $i = 0$ is unstable and that for the region between $i = 0$ and $i = 1 - \frac{1}{R_0^{rem}}$, $\frac{di}{d\tau} > 0$ and thus disease prevalence will increase over time (represented by the arrow at the top). (b) If $R_0^{rem} < 1$, then the prevalence equation is negative for all positive prevalence. There is one realistic steady state, $i^* = 0$, which is stable. Note that when $\hat{u_{rem}} = 0$, $R_0^{rem} = R_0$.



(a) (b)

Figure 3: Imperfect Biosecurity ($p > 0$): (a) $\frac{R_0}{1+\hat{u_{rem}}(1-p)} > 1$ and (b) $\frac{R_0}{1+\hat{u_{rem}}(1-p)} < 1$. For both figures have only one steady state that is stable; there is no disease-free steady state unlike the case with $p = 0$.

using the equilibrium found in the previous section.

3.2.1 Analytic results

Working with the prevalence steady state, we seek to find the best combination of $u_{\hat{rem}}$ and $u_{\hat{ins}}$ that maximises:

$$Q = -(L+Cu_{\hat{rem}})i^* - u_{\hat{ins}} = -(L+Cu_{\hat{rem}})\frac{M+\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}{2R_0} - u_{\hat{ins}} \tag{13}$$

where $M(u_{\hat{ins}}, u_{\hat{rem}}) = R_0 - 1 - (1-\hat{p}(u_{\hat{ins}}))u_{\hat{rem}}$ and $L = L_{out}$ (for brevity). Note, M is fundamentally linked with R_0^p with equivalent threshold properties: $M = 0$ corresponds with $R_0^p = 1$, $M > 0$ corresponds with $R_0^p > 1$ and $M < 0$ corresponds with $R_0^p < 1$.

To find the combination of $u_{\hat{rem}}$ and $u_{\hat{ins}}$ that maximises Q, we need to consider the partial derivatives of Q to find internal and boundary maxima. For internal maxima, $u_{\hat{rem}}$ and $u_{\hat{ins}}$ must satisfy:

$$\frac{\partial Q}{\partial u_{\hat{rem}}} = -(L+Cu_{\hat{rem}})\frac{\frac{\partial M}{\partial u_{\hat{rem}}} + \frac{2M\frac{\partial M}{\partial u_{\hat{rem}}}}{2\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}}{2R_0} - C\frac{M+\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}{2R_0} \tag{14}$$

$$= \overbrace{\frac{(L+Cu_{\hat{rem}})(1-\hat{p}(u_{\hat{ins}}))}{2R_0}\left(1+\frac{M}{\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}\right)}^{\text{Marginal benefit from removal}} - \overbrace{\frac{C}{2R_0}\left(M+\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}\right)}^{\text{Marginal cost from removal}} = 0 \tag{15}$$

and

$$\frac{\partial Q}{\partial u_{\hat{ins}}} = -(L+Cu_{\hat{rem}})\frac{\frac{\partial M}{\partial u_{\hat{ins}}} + \frac{2M\frac{\partial M}{\partial u_{\hat{ins}}}+4R_0\frac{\partial \hat{p}(u_{\hat{ins}})}{\partial u_{\hat{ins}}}}{2\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}}{2R_0} - 1 \tag{16}$$

$$= \overbrace{-\frac{(L+Cu_{\hat{rem}})\frac{\partial \hat{p}(u_{\hat{ins}})}{\partial u_{\hat{ins}}}}{2R_0}\left(u_{\hat{rem}}+\frac{Mu_{\hat{rem}}+2R_0}{\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}\right)}^{\text{Marginal benefits of biosecurity}} - \overbrace{1}^{\text{Marginal cost of biosecurity}} = 0. \tag{17}$$

The analysis on the properties of local and global maxima for removal (Equation (15)) and biosecurity (Equation (17)), are in Appendices A and B, respectively. For the finding of local and global maxima with respect to biosecurity, we assume that $\hat{p}(u_{\hat{ins}})$ takes the form $\hat{p}(u_{\hat{ins}}) = b + (a-b)\exp(-\hat{d}u_{\hat{ins}})$.

Looking at Equations (15)&(17) and incorporating the results found in Appendix A and B, we have the following:

- With respect to removal, if $\frac{\partial Q}{\partial u_{\hat{rem}}} > 0$ at $u_{\hat{rem}} = 0$ then $\frac{\partial Q}{\partial u_{\hat{rem}}} > 0$ for all $u_{\hat{rem}}$ and thus $u_{\hat{rem}} = u_{\hat{remmax}}$ is the global maximum with respect to $u_{\hat{rem}}$. This means that the marginal benefit of removal is always greater than the marginal cost.
- If $\frac{\partial Q}{\partial u_{\hat{rem}}} < 0$ at $u_{\hat{rem}} = u_{\hat{remmax}}$ then $\frac{\partial Q}{\partial u_{\hat{rem}}} < 0$ for all admissible $u_{\hat{rem}}$ and thus $u_{\hat{rem}} = 0$ is the global maximum with respect to $u_{\hat{rem}}$. This means that the marginal benefit of removal is always less than the marginal cost.
- The only other case with respect to $u_{\hat{rem}}$ is that there exists an internal solution of $\frac{\partial Q}{\partial u_{\hat{rem}}} = 0$. This internal solution is a local minimum. Both $u_{\hat{rem}} = 0$ and $u_{\hat{rem}} = u_{\hat{remmax}}$ are local maxima with respect to $u_{\hat{rem}}$. One of these will be the global maximum with respect to $u_{\hat{rem}}$. This requires comparing their values of Q directly.

- If $\frac{\partial Q}{\partial \hat{u_{ins}}} \leq 0$ at $\hat{u_{ins}} = 0$, then $\frac{\partial Q}{\partial \hat{u_{ins}}} < 0$ for all $\hat{u_{ins}} > 0$ and thus Q is maximised at $\hat{u_{ins}} = 0$, i.e. no biosecurity is optimal. This is equivalent to stating that the marginal benefit from biosecurity is always less than the marginal cost.
- Conversely, if $\frac{\partial Q}{\partial \hat{u_{ins}}} > 0$ for $\hat{u_{ins}} = 0$ (for fixed $\hat{u_{rem}}$), then there is a value of $\hat{u_{ins}} > 0$ such that $\frac{\partial Q}{\partial \hat{u_{ins}}} = 0$ and this value is the global maximum with respect to $\hat{u_{ins}}$, i.e. there is moderate biosecurity is optimal. This occurs at the level of biosecurity where the marginal benefit is equal to the marginal cost.
- If $L < 0$, then infection is beneficial and thus no removal and no biosecurity will always be optimal.
- Increasing L and/or C increases $\frac{\partial Q}{\partial \hat{u_{ins}}}$ and thus general results in higher biosecurity.
- Increasing L alone increases $\frac{\partial Q}{\partial \hat{u_{rem}}}$ and thus makes removal more important.
- Increasing C alone effect on $\frac{\partial Q}{\partial \hat{u_{rem}}}$ depends on the relative size of $(1-\hat{p}(\hat{u_{ins}}))\left(1+\frac{M}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\right)$ and $\left(M+\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}\right)$
- Increasing L and C proportionally results in no change in whether $\hat{u_{rem}} = 0$ or $\hat{u_{rem}} = \hat{u_{remmax}}$ are optimal as doing so increases the marginal benefit and marginal cost of removal proportionally.
- The effects of R_0 and the parameters in $\hat{p}(\hat{u_{ins}})$ are not clear cut, largely due to them being part of M, although the presence of $\frac{\partial \hat{p}(\hat{u_{ins}})}{\partial \hat{u_{ins}}}$ in $\frac{\partial Q}{\partial \hat{u_{ins}}}$ suggests that increasing $\hat{d}$ increases $\frac{\partial Q}{\partial \hat{u_{ins}}}$ around $\hat{u_{ins}} = 0$, making biosecurity more likely.
- As $\hat{u_{rem}}$ gets very large, then M becomes large and negative and thus $\frac{\partial Q}{\partial \hat{u_{rem}}}$ converges to zero.

3.2.2 Numerical solutions

Previously, we have found some analytic solutions to establish patterns on which control strategy is optimal and why. In this subsubsection, we will demonstrate some of these with numerical solutions.

In Figure 4, we look at the case where $R_0 = 5 > 1$, so that the disease will easily invade the nursery in the absence of control. Consequently, for the region of no control ($\hat{u_{ins}} = \hat{u_{rem}} = 0$), we have a very high prevalence of disease within the nursery at equilibrium (over 90%). Increasing either removal or control does reduce disease prevalence. This will always be the case (to varying degrees of effectiveness, biosecurity does not really restrict the disease spreading through the nursery without removal when $R_0 >> 1$ as disease prevalence is around 80% for $\hat{u_{ins}} = 8$ in Figure 4b), however it is not always economical to do so. In particular, by looking at the coloured contour regions, we see that Q does not necessarily follow the contours of disease prevalence.

In Figure 4a, we have several local extrema with respect to Q, represented by various dots. The black dots are local maxima, white dots are local minima and grey dots are saddle-points. As we see, there are two local maxima, one at the origin ($\hat{u_{rem}} = \hat{u_{ins}} = 0$) and one for maximum removal effort and moderate levels of biosecurity, a saddle point for an intermediate level of removal and biosecurity and two local 'minima' at maximum removal effort with no biosecurity ($\hat{u_{rem}} = \hat{u_{remmax}}$ and $\hat{u_{ins}} = 0$) and high biosecurity with low removal effort. The local maxima correspond to either doing nothing and letting a disease take hold, or go with maximal effort in removal with a sufficient amount of biosecurity.

Firstly, the local 'minima'. One local 'minima'[1] suggests the worst case scenarios are to spend too much into biosecurity, especially for low removal. In short, this scenario involves spending more biosecurity than the damage from the disease. Likewise, another local minimum occurs with 'high' removal and no biosecurity. Here, removal is not cost-effective since removed infected plants are often replaced with another infected plant.

[1]This is a local minimum if we restrict spending on biosecurity to that of the figure axis. In the model, we have actually allowed infinite biosecurity in this model, and thus no strict minimum exists. We include this 'minimum' to emphasise this.

Secondly, the local maxima suggest there are two possible best case scenarios for managing the disease. One maximum is either moderate biosecurity with maximum removal, which is to remove the disease quickly to minimise secondary infections with a biosecurity level that is the best compromise between benefit of reducing new infections with the cost of the biosecurity regime. The other local maximum is do nothing at all. Here, the disease will spread of its own accord and biosecurity does not really restrict the disease at steady state when $R_0^p >> 1$ to ignore the disease. Likewise, removal is ineffective compared to the cost, especially with removed infected plants being replaced by another infected plant.

There is one internal point of interest and that is the local saddle point where the nullclines of $\frac{\partial Q}{\partial \hat{u_{ins}}}$ and $\frac{\partial Q}{\partial \hat{u_{rem}}}$ intersect (a minimum with respect to $\hat{u_{rem}}$ and a maximum with respect to $\hat{u_{ins}}$) which separates the local maxima from each other as well as the two local minima.

Globally, in Figure 4a, there is one clear global maximum, indicated by the dark red, and that is no removal and no biosecurity, i.e. do nothing and let the disease take its toll. Contrast this with Figure 4b. In Figure 4b, we have increased the maximum removal effort from $\hat{u_{remmax}} = 2$ to $\hat{u_{remmax}} = 10$ (and increase the biosecurity axis to $\hat{u_{ins}} = 8$). Firstly, we established that the local minimum with zero biosecurity is for moderate removal, and that further increasing removal starts to reduce the overall cost due to it sufficiently reducing disease prevalence, which reduces both the losses from selling infecteds, but also by reducing prevalence so which could reduce overall removal costs.

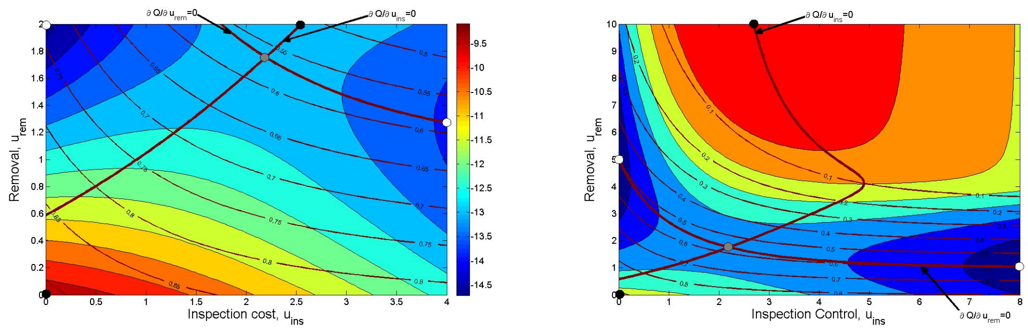
The biggest difference between Figure 4a and Figure 4b is that the global maximum is represented by the black dot with maximum removal and moderate biosecurity in Figure 4b whereas doing nothing is the global maximum in Figure 4a. This is the result of the increase in $\hat{u_{remmax}}$. With this increase, we are now capable at removing infected plants quickly enough that the disease does not persist at large levels. In short, with high enough effort in removal, it is possible to get on top of the disease, and if this is not possible, efforts to restrict the disease are futile. In particular, if we reduced the $\hat{u_{remmax}}$ to less than about 1.75 (the saddle point in Figure 4a), there is no local maximum involving maximum removal.

If we decrease R_0 to 0.5 (Figure 5), we are in the realm where the disease does not spread by itself; instead it only persists because of the constant introduction of infected plants. Here, we will show that biosecurity is much more important in this scenario. Notice that the prevalence contours (the numbered lines) are no where near as horizontal as those in Figure 4 for low removal effort. In particular, for no removal, biosecurity alone can substantially reduce disease prevalence.

Figure 5a has only one maximum, full removal with moderate biosecurity. There is no intersection between the removal and biosecurity nullclines so no internal saddle points can exist. Also, since the inspection nullcline does not intersect the removal axis and instead intersections the inspection axis, 'doing nothing' is not a local maximum. This means is the some biosecurity is better than no biosecurity for any level of removal. Increasing $\hat{u_{remmax}}$ qualitatively does not alter the results, the optimal control is still maximum removal with moderate biosecurity, however quantitatively, we have increased $\hat{u_{rem}}$ with this increase in $\hat{u_{remmax}}$ results in a reduction in the level of biosecurity.

The kink in the biosecurity nullcline found the Figure 4b seems to occur 'close' to where $M = 0$, i.e. $R_0^p \approx 1$. Although this is not proven, several other simulations where $R_0 > 1$ have a similar kink 'around' $M = 0$ in the biosecurity nullcline. If this pattern is general then we can lead to some nice conclusions, because it suggests that while $M \gtrsim 0$ (i.e. $R_0^p \gtrsim 1$) increasing $\hat{u_{rem}}$ means that the optimal level of biosecurity will increase, that removal and biosecurity synergise well each other. Conversely, while $M \lesssim 0$ (i.e. $R_0^p \lesssim 1$) (this is seen in both Figure 4b and Figure 5), then increasing $\hat{u_{rem}}$ results in a decrease in the optimal level of biosecurity, meaning that the increased removal replaces some biosecurity. In practice, this means that the better we can manage a disease through removal, the less worried we are about disease coming into the nursery to start with and thus less biosecurity is necessary.

Figures 4 and 5 highlight several different scenarios found in the analytical analysis. There are two states missing. One case is where there is some biosecurity ($\hat{u_{ins}} > 0$) but no removal control ($\hat{u_{rem}} = 0$) is a local/global maximum. This occurs when the $\frac{\partial Q}{\partial \hat{u_{ins}}}$ nullcline intercepts the x-axis and replaces the zero biosecurity and no removal local/global maximum. This is seen in Figure 6a, which is like Figure 4a except the local/global maximum at zero biosecurity with no removal has been replaced by a local/global



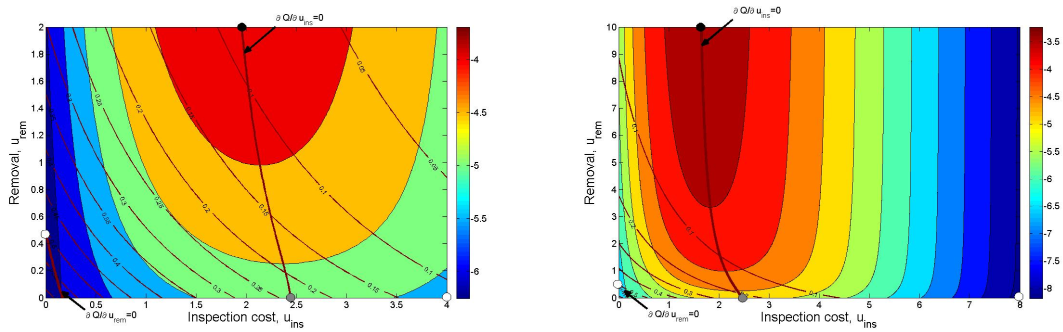
(a) (b)

Figure 4: Constant control $R_0 = 5$: Contour plots of (I) profit function Q (filled) (II) disease prevalence at steady state (numbered contour lines) and (III) the nullclines of Q with respect to inspection and removal controls (lines where $\frac{\partial Q}{\partial \hat{u_{ins}}} = 0$ and $\frac{\partial Q}{\partial \hat{u_{rem}}} = 0$, represented by a thick line) where (a) $u_{rem\hat{m}ax} = 2$ and (b) $u_{rem\hat{m}ax} = 10$. The red regions are where the value of Q (profit) is highest. Black dots represent local maxima, white dots represent local 'minima' and grey dots represent a saddle point with respect to Q. Here we see that there are two local maxima. In (a) the 'do nothing' local maximum is optimal whereas a significant increase in $u_{rem\hat{m}ax}$ has resulted in the 'maximum removal, moderate biosecurity' local maximum being optimal. Other parameter values (ignoring hats): $L_{out} = 10$, $C = 5$, $a = 0.5$, $b = 0$ and $d = 0.5$.

moderate biosecurity with no removal. This difference is the result of improved cost-effectiveness in biosecurity as a result of an increase in $\hat{d}$ from 0.5 to 2. The other case is where there is no biosecurity and maximum removal. This occurs when there is no $\frac{\partial Q}{\partial \hat{u_{ins}}}$ nullcline in the figure and $\frac{\partial Q}{\partial \hat{u_{rem}}} > 0$ at $\hat{u_{rem}} = u_{rem\hat{m}ax}$. This is seen in Figure 6b, which has two local maxima, one is the new state of no biosecurity with maximum removal (the other is the no biosecurity and no removal as seen like Figure 4). In this case, the no biosecurity with maximum removal is the global maximum (although this might change with $u_{rem\hat{m}ax}$). Figure 6b and Figure 5a are only different because $\hat{d}$ has been reduced from 0.5 to 0.1, reducing the cost-effectiveness of biosecurity to the extent that any attempt to improve biosecurity is not worth it.

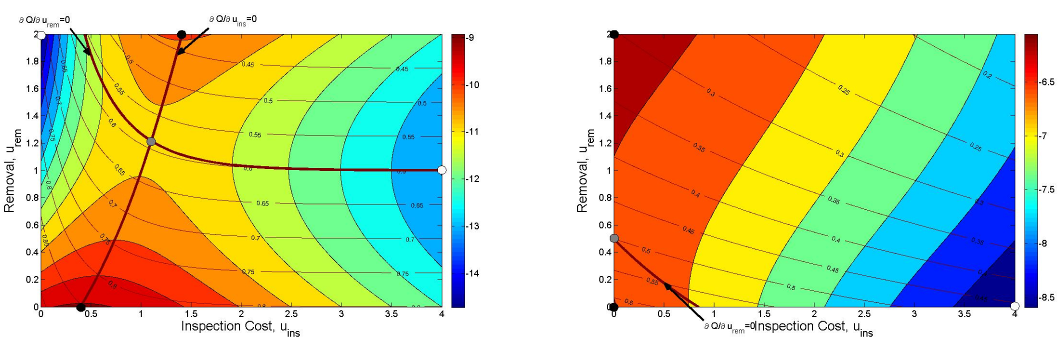
4 Discussion

In this paper, we derived a relatively simple bioeconomic model of a plant nursery that buys, grows and sells materials, where some of the inputted plant material is infected with a disease that spreads within the nursery, reducing the value of plants when mature. The nursery owner will try to manage the infection armed with the ability to restrict the proportion of infected coming into the nursery and the ability to remove infected plants in the nursery. From this, assuming the nursery owner seeks to maximise profits, we find that (a) if infected inputs are always coming into the nursery, the disease will persist, (b) the optimal removal is either maximum removal or no removal whereas the optimal level of biosecurity occurs where the marginal cost of biosecurity equals the marginal benefit (and if this does not occur, the optimal level of biosecurity is zero), (c) since removed infected plants can be replaced by infected plant inputs, increasing biosecurity increases the effectiveness of removal and (d) the optimal level of biosecurity is complementary with removal if the disease is beyond the owner's ability to limit its spread, whereas for biosecurity and removal are substitutes if the owner is able to limit the



(a) (b)

Figure 5: Constant control $R_0 = 0.5$: Contour plots of (I) profit function Q (filled) (II) disease prevalence at steady state (numbered contour lines) and (III) the nullclines of Q with respect to inspection and removal controls (lines where $\frac{\partial Q}{\partial \hat{u_{ins}}} = 0$ and $\frac{\partial Q}{\partial \hat{u_{rem}}} = 0$, represented by a thick line) where (a) $u_{re\hat{m}max} = 2$ and (b) $u_{re\hat{m}max} = 10$. The red regions are where the value of Q (profit) is highest. Black dots represent local maxima, white dots represent local 'minima' and grey dots represent a saddle point with respect to Q. In both (a) and (b), there is only one local maximum, maximum removal with moderate biosecurity. As it is the only local maximum, it is the optimal control. Other parameter values are the same as Figure 4.



(a) (b)

Figure 6: Constant control (a) $R_0 = 5$ and $\hat{d} = 2$ and (b) $R_0 = 0.5$ and $\hat{d} = 0.1$: Contour plots of (I) profit function Q (filled) (II) disease prevalence at steady state (numbered contour lines) and (III) the nullclines of Q with respect to inspection and removal controls (lines where $\frac{\partial Q}{\partial \hat{u_{ins}}} = 0$ and $\frac{\partial Q}{\partial \hat{u_{rem}}} = 0$, represented by a thick line). The red regions are where the value of Q (profit) is highest. Black dots represent local maxima, white dots represent local 'minima' and grey dots represent a saddle point with respect to Q. In (a), we have two local maxima, no removal with some biosecurity and maximum removal with some (other level of) biosecurity. In this case, the darkest red occurs around the no removal with some biosecurity local maximum and thus this is the global maximum. In (b), there are two local maxima, one has no removal with no biosecurity (do nothing) and the other has maximum removal with no biosecurity. In this case, the darkest red occurs around the maximum removal with no biosecurity local maximum and thus this is the optimal control. $u_{re\hat{m}max} = 2$ and the other parameter values are the same as Figure 4.

spread of the disease.

The consequences of the latter two points is stark. What it means is that biosecurity itself does not help much in cases of highly infectious diseases, since some infected plants materials will always get past the biosecurity regime and spread fast within the nursery. However, with increases in removal, the disease becomes more manageable, making biosecurity more viable, especially as it makes removal more effective. Consequently, removal and biosecurity are complementary while the disease can spread in the nursery. This complementary relationship continues as we increase removal until around $R_0^p = 1$. Beyond this point is where the disease no longer spreads through the nursery and instead relies on the constant introduction of infected plant inputs to persist in the nursery. In this case, the disease is now completely manageable and instead the choice changes to whether to remove it once it is in the nursery or prevent it from entering the nursery, i.e. biosecurity and removal have become substitutes, akin to the classic 'prevention vs cure' argument.

This transition from biosecurity and removal being complementary to being substitutes seems to occur close to $R_0^p = 1$. In particular, this phenomena has occured 'near' R_0^p in every simulation where $R_0 = 1$ and biosecurity is viable (biosecurity nullcline is in the figures). However, since we have not mathematically proven this, we do not know if this always true nor do we know a rule on how close 'close' is.

To the best of the authors knowledge, we are not aware of any theoretical work that is equivalent to the disease dynamics found under imperfect restriction, which can be seen as a logistic growth model with constant addition. However, we are sceptical that this is the first time this has been found, given that work on the classic fisheries/harvesting model (which have the same logistic growth but with constant removal instead of addition) have been around since the 1950's (Schaefer, 1954; Gordon, 1954). The result that a disease will persist if constantly introduced is intuitive and quite simple, possibly to extent that it appears trivial.

In this paper, we assume the disease is an SI disease. This was for simplicity and generality. However, many plant diseases have recovery, latency, asymptomatic infection and immunity, as well as free-living pathogens in the environment (i.e. in the soil or water). For environmental diseases, infections can spontaneously occur within the nursery once free-living pathogens enter and persist within the nursery. Likewise, with the existence of latent and asymptomatic infections, it becomes difficult to see how widespread the disease is within the nursery. In particular, with respect to biosecurity, the presence of asymptomatic and latent infected plant inputs would undermine the owner's ability to restrict infected inputs coming into the nursery since identifying infected plants material inputs can become much more complex or even impossible if no symptoms of infection or clear evidence of pathogens are present.

Linking with the existence of environmental diseases for plants, another assumption here is that the disease can only enter the nursery via the inputting of infected plant materials, that the nursery is an otherwise impenetrable fortress, or at least at a time scale smaller than the disease dynamics within the nursery. However, for many different nurseries, pathogens and pests get into the nursery through a number of different pathways. In particular, contaminated water is often the reason for *Phytophthora* and other pathogens getting into plant nurseries (Hong and Moorman, 2005, and references therein).

The level of biosecurity in this paper depends greatly on the choice of the function $p(u_{ins})$, the proportion of infected plant material inputs that are infected. In this paper, when forced to pick a form for $p(u_{ins})$, we proceeded with an exponentially decreasing function. This function has the consequence that the first pound spent on restriction is always the most effective, and that each pound spent has a smaller effect on $p(u_{ins})$ than the previous pound. This would not necessarily be appropriate for many cases. For example, functions where the first few pounds spent on restriction have little effect and that more has to spent for a biosecurity regime to start to have a noticeable effect on the proportion of infected plant materials coming in could be more appropriate if a substantial funds are needed for effective levels of knowledge, labour, machinery and skills to be maintained. An example of a function that satisfies this is $(a-b)\exp^{-du_{ins}^2}+b$ (in which case the most effective pound is at $u_{ins}=(2d)^{-1/2}$).

The analysis in this paper is based on equilibria and thus based on the long term dynamics of the disease and decision models. However, several nurseries work on a shorter term basis. For example, some nurseries are seasonal and only have a generation or two of plants in the nursery for one season before an annual reset of nursery, with new plants stock and possibly new soil and water. In this case, a steady state might not be appropriate analysis as not enough time has occured for a steady state to be reached. However, even in shorter time-scales, equilibrium-based analysis form a strong baseline for understanding optimal decisions.

We assumed that there is only one disease of concern for the nursery owner to control. Generally, a nursery owner has a multitude of diseases to be concerned about. For example, entering *Solanum lycopersicum* into the UK Plant Health Risk Register (FERA, 2015) has 75 pests and pathogens that have the tomato as a host. Likewise, a nursery can have many pathogens present. For example, at least 13 different species of *Phytophthora* were found in the irrigation water at three nurseries in northern Germany in 1995 (Themann et al, 2002; Brasier, 2008) and Bavaria in 2002, there were five different species of *Phytophthora* found in the soil around a single open-planted alder seedling (T.Jung, LWF, D-85354 Freising, personal communication cited in Brasier, 2008). With a multitude of diseases to manage, a common optimal strategy on biosecurity and removal would be needed, a strategy that would likely differ from the strategy of each of the diseases in isolation.

A plant nursery does not exist in a vacuum; it exists within a trade network. This network overlaps with other trade networks, which can include trades related to other hosts and vectors for the disease as well as contaminated equipment and resources. The nursery model in this paper is suitably simple enough, and has clear inputs and outputs, such that it could be form a component in more complex models. Likewise, a nursery has suppliers, costumers, neighbours, stakeholders and various regulatory regimes to work within. The actions, motives and opinions of these groups frame how the nursery can operate. In particular, from a policy point of view, the interactions between a public inspection regime and the disease management strategies of private nurseries could be of great interest.

To conclude, we investigated the management of an infectious disease within a plant nursery with infected plant inputs and found that the disease will always exists and if it spreads greater than the ability to control, removal and biosecurity complement each other whereas if the disease is controllable, removal and biosecurity become substitutes.

Appendix

A Optimal solution with respect to $\hat{u_{rem}}$: all or nothing

Now, to find out what the optimal solutions with respect to $\hat{u_{rem}}$, we need to investigate Equation 15 further. First, we need to manipulate Equation 15 into something more manageable.

$$\frac{\partial Q}{\partial \hat{u_{rem}}} = \frac{(L+C\hat{u_{rem}})(1-\hat{p}(\hat{u_{ins}}))}{2R_0}\left(1+\frac{M}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\right) - \frac{C}{2R_0}\left(M+\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}\right) \tag{18}$$

$$= \frac{C}{2R_0}\left(\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))\left(1+\frac{M}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\right) - \left(M+\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}\right)\right) \tag{19}$$

$$= \frac{C}{2R_0\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\left(\left(\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))-M\right)\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}+M\right)-4R_0\hat{p}(\hat{u_{ins}})\right) \tag{20}$$

Consequently, solutions of $\frac{\partial Q}{\partial \hat{u_{rem}}}=0$ are solutions of $\left(\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))-M\right)\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}+M\right)-4R_0\hat{p}(\hat{u_{ins}})=0$. Now, if such solutions exist and are admissible, we need to find out if this solution is a maximum with respect $\hat{u_{rem}}$. To do so, we need to look at the second derivative.

$$\frac{\partial^2 Q}{\partial \hat{u_{rem}}^2} = \frac{C}{2R_0}\frac{\partial M}{\partial \hat{u_{ins}}}\frac{\partial}{\partial M}\left(\frac{1}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\right)\overbrace{\left(\left(\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))-M\right)\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}+M\right)-4R_0\hat{p}(\hat{u_{ins}})\right)}^{=0} \tag{21}$$

$$+\frac{C}{2R_0\sqrt{M^2+4R_0\hat{p}(u_{ins})}}\left((1-\hat{p}(\hat{u_{ins}}))\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}+M\right)-\frac{\partial M}{\partial \hat{u_{ins}}}\left(1+\frac{M}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\right)+\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))\frac{\partial M}{\partial \hat{u_{ins}}}\frac{\partial}{\partial M}\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}\right)\right) \tag{22}$$

$$=\frac{C}{2R_0\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\left(2(1-\hat{p}(\hat{u_{ins}})\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}+M\right)-(1-\hat{p}(\hat{u_{ins}})\left(\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))-M\right)\left(1+\frac{M}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\right)\right) \tag{23}$$

$$=\frac{C(1-\hat{p}\hat{u_{ins}})}{2R_0(M^2+4R_0\hat{p}(\hat{u_{ins}}))}\left(2\left(M^2+4R_0\hat{p}(\hat{u_{ins}})+M\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}\right)-\left(\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))-M\right)\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}+M\right)\right) \tag{24}$$

$$=\frac{C(1-\hat{p}(\hat{u_{ins}}))}{2R_0(M^2+4R_0\hat{p}(\hat{u_{ins}}))}\left(2\left(M^2+2R_0\hat{p}(\hat{u_{ins}})+M\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}\right)-\overbrace{\left(\left(\left(\left(\frac{L}{C}+\hat{u_{rem}}\right)(1-\hat{p}(\hat{u_{ins}}))-M\right)\left(\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}+M\right)\right)-4R_0\hat{p}(\hat{u_{ins}})\right)}^{=0}\right) \tag{25}$$

$$=\frac{C(1-\hat{p}(\hat{u_{ins}}))}{R_0(M^2+4R_0\hat{p}(\hat{u_{ins}}))}\left(M^2+2R_0\hat{p}(\hat{u_{ins}})+M\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}\right) \tag{26}$$

If $M>0$, then $\frac{\partial^2 Q}{\partial \hat{u_{rem}}^2}>0$ and thus all internal solutions are local minima with respect to $\hat{u_{rem}}$. It is not completely clear if this is the case for $M<0$ so instead look to find the value of M where $M^2+2R_0\hat{p}(\hat{u_{ins}})+M\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}$ has its minimum. So we look at the properties of solutions of $\frac{\partial}{\partial M}\left(M^2+2R_0\hat{p}(u_{\hat{ins}})+M\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}\right)=0$.

$$\frac{\partial}{\partial M}\left(M^2+2R_0\hat{p}(u_{\hat{ins}})+M\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}\right)=2M+\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}+\frac{M^2}{\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}} \quad (27)$$

$$=\frac{2}{\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}\left(M^2+2R_0\hat{p}(u_{\hat{ins}})+M\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}\right)=0 \quad (28)$$

Solutions of this satisfy $M=-\frac{M^2+2R_0\hat{p}(u_{\hat{ins}})}{\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}$. Substituting this into $M^2+2R_0p+M\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}$ gives:

$$\begin{aligned}
&-\frac{M^2+2R_0\hat{p}(u_{\hat{ins}})}{\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}\left(-\frac{M^2+2R_0\hat{p}(u_{\hat{ins}})}{\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}}+\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}\right)+2R_0\hat{p}(u_{\hat{ins}})\\
&=-\frac{M^2+2R_0\hat{p}(u_{\hat{ins}})}{M^2+4R_0\hat{p}(u_{\hat{ins}})}\left(-(M^2+2R_0\hat{p}(u_{\hat{ins}}))+M^2+4R_0\hat{p}(u_{\hat{ins}})\right)+2R_0\hat{p}(u_{\hat{ins}}) \quad (29)\\
&=2R_0\hat{p}(u_{\hat{ins}})\left(1-\frac{M^2+2R_0\hat{p}(u_{\hat{ins}})}{M^2+4R_0\hat{p}(u_{\hat{ins}})}\right)>0
\end{aligned}$$

and thus $M^2+2R_0p+M\sqrt{M^2+4R_0\hat{p}(u_{\hat{ins}})}>0$ always and likewise $\frac{\partial^2 Q}{\partial u_{\hat{rem}}{}^2}>0$ and thus internal solutions are always local minima with respect to $u_{\hat{rem}}$. As there is no internal maxima with respect to $u_{\hat{rem}}$, the global maximum must occur on the boundary, either at $u_{\hat{rem}}=0$ or $u_{\hat{rem}}=u_{re\hat{m}max}$. If $\frac{\partial Q}{\partial u_{\hat{rem}}}>0$ at $u_{\hat{rem}}=0$ then $u_{\hat{rem}}=0$ is a local (global) minimum and $u_{\hat{rem}}=u_{re\hat{m}max}$ is the global maximum. Conversely, if $\frac{\partial Q}{\partial u_{\hat{rem}}}<0$ at $u_{\hat{rem}}=u_{re\hat{m}max}$ then $u_{\hat{rem}}=u_{re\hat{m}max}$ is a local (global) minimum and thus $u_{\hat{rem}}=0$ is a global maximum. If $\frac{\partial Q}{\partial u_{\hat{rem}}}<0$ at $u_{\hat{rem}}=0$ and $\frac{\partial Q}{\partial u_{\hat{rem}}}>0$ at $u_{\hat{rem}}=u_{re\hat{m}max}$, then you have must compare Q for $u_{\hat{rem}}=0$ and $u_{\hat{rem}}=u_{re\hat{m}max}$ since both are local maxima.

B Optimal control with respect to biosecurity $u_{\hat{ins}}$: do something or do nothing

Now, we need to find out the global maximum with respect to biosecurity $u_{\hat{ins}}$ by analysing Equation (17). Firstly, we will look at the second partial derivative to see if $\frac{\partial Q}{\partial u_{\hat{ins}}}$ is a increasing or decreasing function of $u_{\hat{ins}}$:

$$\frac{\partial^2 Q}{\partial \hat{u_{ins}}^2} = -\frac{\partial^2 \hat{p}(\hat{u_{ins}})}{\partial \hat{u_{ins}}^2}\frac{(L+C\hat{u_{rem}})}{2R_0}\left(\hat{u_{rem}} + \frac{M\hat{u_{rem}}+2R_0}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}\right) \tag{30}$$

$$-\left(\frac{\partial \hat{p}(\hat{u_{ins}})}{\partial \hat{u_{ins}}}\right)^2 \frac{(L+C\hat{u_{rem}})}{2R_0}\left(\frac{-2R_0(M\hat{u_{rem}}+2R_0)}{(M^2+4R_0\hat{p}(\hat{u_{ins}}))^{\frac{3}{2}}}\right)$$

$$= -\frac{\partial^2 \hat{p}(\hat{u_{ins}})}{\partial \hat{u_{ins}}^2}\frac{L+C\hat{u_{rem}}}{2R_0}\left(\hat{u_{rem}} + \frac{(M\hat{u_{rem}}+2R_0)(M^2+4R_0\hat{p}(\hat{u_{ins}})) - 2R_0\frac{\left(\frac{\partial \hat{p}}{\partial \hat{u_{ins}}}\right)^2}{\frac{\partial^2 \hat{p}}{\partial \hat{u_{ins}}^2}}(M\hat{u_{rem}}+2R_0)}{(M^2+4R_0\hat{p}(\hat{u_{ins}}))^{\frac{3}{2}}}\right) \tag{31}$$

$$= -\frac{\partial^2 \hat{p}(\hat{u_{ins}})}{\partial \hat{u_{ins}}^2}\frac{L+C\hat{u_{rem}}}{2R_0}\left(\hat{u_{rem}} + \frac{M^2+4R_0\hat{p}(\hat{u_{ins}}) - 2R_0\frac{\left(\frac{\partial \hat{p}}{\partial \hat{u_{ins}}}\right)^2}{\frac{\partial^2 \hat{p}}{\partial \hat{u_{ins}}^2}}}{M^2+4R_0\hat{p}(\hat{u_{ins}})}\underbrace{\frac{M\hat{u_{rem}}+2R_0}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}}_{\text{always } > -\hat{u_{rem}}}\right) \tag{32}$$

Now, since we do not have sufficient knowledge on the properties of $\frac{\partial^2 hatp}{\partial \hat{u_{ins}}^2}$ in general, we will continue with $\hat{p}(\hat{u_{ins}}) = b + (a-b)\exp(-\hat{d}\hat{u_{ins}})$. Thus $\frac{\partial \hat{p}}{\partial \hat{u_{ins}}} = -\hat{d}(a-b)\exp(-\hat{d}\hat{u_{ins}}) = -\hat{d}(\hat{p}(\hat{u_{ins}})-b)$ and $\frac{\partial^2 \hat{p}}{\partial \hat{u_{ins}}^2} = -d\frac{\partial \hat{p}}{\partial \hat{u_{ins}}} = \hat{d}^2(a-b)\exp(-\hat{d}\hat{u_{ins}}) = \hat{d}^2(\hat{p}(\hat{u_{ins}})-b)$. Armed with this, we have:

$$\frac{\partial^2 Q}{\partial \hat{u_{ins}}^2} = -\frac{(L+C\hat{u_{rem}})\hat{d}^2(\hat{p}(\hat{u_{ins}})-b)}{2R_0}\left(\underbrace{\hat{u_{rem}} + \overbrace{\frac{M^2+2R_0(\hat{p}(\hat{u_{ins}})+b)}{M^2+4R_0\hat{p}(\hat{u_{ins}})}}^{\in(0,1)}\overbrace{\frac{M\hat{u_{rem}}+2R_0}{\sqrt{M^2+4R_0\hat{p}(\hat{u_{ins}})}}}^{\text{always } > -\hat{u_{rem}}}}_{>0}\right) \tag{33}$$

$$< 0 \text{ when } L + Cu_{rem} > 0 \tag{34}$$

Firstly, we note that if $L+C\hat{u_{rem}} \leq 0$, there are no internal solutions from possible for Equation (17) internal solutions and we have $\frac{\partial Q}{\partial \hat{u_{ins}}}$ is monotonically increasing to -1. Hence, $\frac{\partial Q}{\partial \hat{u_{ins}}}$¡0 always and thus zero biosecurity is always the best (a disease that is beneficial should not be restricted). For $L+C\hat{u_{rem}} > 0$, we have that $\frac{\partial Q}{\partial \hat{u_{ins}}}$ is monotonically decreasing (to -1 as $\hat{u_{ins}} \to \infty$). In other words, increasing biosecurity has even diminishing returns, reducing the marginal benefit, whereas the marginal cost remains the same. Given we have that $\frac{\partial Q}{\partial \hat{u_{ins}}}$ is monotonically decreasing to -1 (and is continuous), we know that there exists one and only one admissible solution with respect to $\hat{u_{ins}}$ (for fixed $\hat{u_{rem}}$) if $\frac{\partial Q}{\partial \hat{u_{ins}}} > 0$ at $\hat{u_{ins}} = 0$ and that this solution is a global maximum with respect to $\hat{u_{ins}}$, i.e. the optimal control involves some biosecurity. Otherwise, $\frac{\partial Q}{\partial \hat{u_{ins}}} \leq 0$ at $\hat{u_{ins}} = 0$, there is no internal solution and the global maximum with respect to $\hat{u_{ins}}$ is at $\hat{u_{ins}} = 0$, i.e. no biosecurity is optimal.

If such solutions do not exist within admissible controls ($\hat{u_{rem}} \in [0, \hat{u_{remmax}}]$ and $\hat{u_{ins}} \geq 0$), we need to pick the maximising values on the boundary, i.e. if $\frac{\partial Q}{\partial \hat{u_{ins}}} < 0$ at $\hat{u_{ins}} = 0$, then $\hat{u_{ins}} = 0$ and $\hat{u_{ins}} = \infty$, otherwise (which can not occur since $\frac{\partial \hat{p}(\hat{u_{ins}})}{\partial \hat{u_{ins}}} \to 0$ and thus $\frac{\partial Q}{\partial \hat{u_{ins}}} \to -1$ as $\hat{u_{ins}}$ is converging to b, implying an internal maximum as long a $\hat{p}(\hat{u_{ins}})$ is sufficiently smooth). Likewise, if $\frac{\partial Q}{\partial \hat{u_{rem}}} < 0$ at $\hat{u_{rem}} = 0$, then $\hat{u_{rem}} = 0$ and $\hat{u_{rem}} = \hat{u_{remmax}}$, otherwise.

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