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Optimal resource allocation for biotrophic plant pathogens^{*}

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Abstract: A significant class of plant pathogens is constituted by biotrophic fungi. They set up long-term feeding relationships with their hosts. This kind of parasitism decreases competitive abilities of plants in natural environments and reduces yields in agricultural systems. Therefore, it is relevant to develop and validate mathematical models which can help to better understand how related disease associated traits evolve. In this paper, one-season dynamics of a within-host cohort of spore-producing biotrophic fungi is considered. Their within-host multiplication and outer transmission are implemented by the mycelial growth and free-living (spore) forms, respectively. We state and investigate a specific dynamic optimization problem in order to determine how the fungi allocate available host resources between mycelial growth and spore production. The pathogen fitness criterion is introduced as maximization of the reproductive output. The constructed optimal feedback strategy can serve as a benchmark to compare actual infection mechanisms. There is a singular control subregime which plays an important role from the biological point of view. It keeps the average mycelium size equal to a particular steady value and represents an intermediate configuration of the resource allocation. We also analyze the asymptotic behavior of this steady state when the lesion density is large.

Keywords: biotrophic pathogen, within-host multiplication, spore production, resource allocation, optimal control, singular control, switching surfaces.

1. INTRODUCTION

A significant class of plant pathogens is constituted by biotrophic fungi (Deacon (1997)) such as rust fungi (*Basidiomycota*) and powdery mildew fungi (*Ascomycota*). They invade only a few cells of their hosts in order to produce nutrient-absorbing structures known as haustoria, and the hosts are disadvantaged but not killed. This kind of parasitism decreases competitive abilities of plants in natural environments and reduces yields in agricultural systems. One can mention leaf rust of willow, poplar (*Melampsora* species), and wheat (*Puccinia* species), as well as powdery mildew of hawthorn (*Podosphaera oxycanthae*), gooseberry (*Sphaerotheca mors-uae*), cereals and grasses (*Erysiphe graminis*), etc. Thus, it is relevant to develop and validate theories which can help to better understand how related disease associated traits evolve, and dynamic mathematical modeling can be useful for that, as indicated, for instance, by Sasaki and Iwasa (1991); Day (2001, 2003); Gilchrist et al. (2006); Akhmetzhanov et al. (2011, 2012).

In this paper, one-season dynamics of a within-host cohort of spore-producing biotrophic fungi is considered. Their within-host multiplication and outer transmission are implemented by inner growth and free-living (spore) forms, respectively. For many plant pathogenic fungi exploiting leaf tissues as hosts, within-host multiplication relies on mycelial growth within foliar lesions, while transmission is achieved by producing and releasing asexual spores. We assume that there is no conversion between these two forms. Then there arises the problem of allocating the available nutrient flux between the two different activities in order to maximize the pathogen fitness.

The aim of the current work is to construct a dynamic mathematical model of the described process together with a suitable fitness criterion so that the corresponding optimal resource allocation strategy could serve as a benchmark to compare actual infection mechanisms.

Note that, for another wide class of fungi such as saprophytes (obtaining nutrients from dead organic matter), optimal resource allocation strategies turn out to be purely bang-bang as shown by Gilchrist et al. (2006). However, long-term feeding sink activity of biotrophic fungi can lead to coexistence of both mycelial growth and spore production (Deacon (1997); Newton et al. (1999); Robert et al. (2004); Bancal et al. (2012)), which corresponds to a regime with an intermediate resource allocation. Such

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a regime indeed appears in the solution to our dynamic optimization problem.

The paper is organized as follows. First, we provide the statement of our problem. Then it is investigated by using necessary optimality conditions. The obtained results together with additional arguments allow us to construct the sought-for optimal feedback control. Next, we analyze the asymptotic behavior of the optimal steady-state infection size for large lesion densities. Finally, the results of numerical simulations are presented and discussed.

2. PROBLEM STATEMENT

Consider a cohort of biotrophic fungi developing during one season within one host plant. Denote the lesion density, i. e., the number of mycelia in the cohort per unit area of the host, by n , and assume that it is constant during the season. Let M be the average size of a mycelium in the cohort, and let S be the average quantity of spores produced by such a mycelium. Time variable t plays the role of the infection age within the season. The mycelia get nutrients from the host. The related flux is determined by a function $f(M)$ and allocated between two different pathogen activities such as within-host multiplication (mycelial growth) and production of asexual spores. Denote a time-dependent resource allocation function taking values from the interval $[0, 1]$ by u . When $u(t) = 0$, the whole flux is spent on within-host multiplication. When $u(t) = 1$, it goes only to spore production. For $0 < u(t) < 1$, an intermediate allocation takes place. Let the rate of mycelial decay be specified by a function $g(M)$. Spores are produced with a constant yield $\delta \in (0, 1]$ in comparison with mycelial growth.

The observed time interval $[0, T]$ is the time-course of the infection within the season. Time horizon $T > 0$ is fixed. It can be finite or infinite. For $T = +\infty$, $[0, T]$ is understood as $[0, +\infty)$. The infinite-horizon case is a reasonable abstraction when the pathogen dynamics is rather fast with respect to season duration.

Thus, we come to the model

$$\begin{cases} \frac{dM(t)}{dt} = (1 - u(t)) \cdot f(M(t)) - g(M(t)), \\ \frac{dS(t)}{dt} = \delta \cdot u(t) \cdot f(M(t)), \\ M(0) = M_0, \quad S(0) = 0, \\ 0 \leq u(t) \leq 1, \quad t \in [0, T]. \end{cases} \quad (1)$$

Let us treat any Lebesgue measurable function $u : [0, T] \rightarrow [0, 1]$ as an admissible (open-loop) control.

Assuming epidemiological equilibrium and the absence of within-host competition between pathogen genotypes (i. e., multiple infections are not allowed), we set the pathogen fitness criterion as maximization of the reproductive output $\int_0^T (dS(t)/dt) \cdot e^{-\mu t} dt$, where $dS(t)/dt$ is the spore production rate at infection age t , and $e^{-\mu t}$ is the term describing exponential extinction of the infection with a constant rate $\mu > 0$ (Sasaki and Iwasa (1991); Day (2001, 2003)). Since δ is a positive constant, the criterion can be written as

$$\int_0^T u(t) \cdot f(M(t)) \cdot e^{-\mu t} dt \longrightarrow \max. \quad (2)$$

This maximization is over all admissible controls.

One can easily see that M is in fact a single state variable in our problem (we do not need to treat S explicitly).

In order to better represent biological aspects of the model, let us write the nutrient flux in the form

$$f(M) = f_1(M) \cdot f_2(nM), \quad (3)$$

where $f_1(M)$ describes the resource flow that can be obtained by a single mycelium, while $f_2(nM)$ determines negative influence of competition between mycelia for host resources. For example, one can choose

$$f_1(M) = \frac{\alpha M}{M + k}, \quad f_2(nM) = \frac{1}{1 + \beta nM}, \quad g(M) = \gamma M, \quad (4)$$

where α, β, γ, k are positive constants. If the lesion density is zero, then $f_2(nM) = 1$, i. e., there is no competition.

Note that, when considering lesion densities, we implicitly suppose that the total observed host area is sufficiently large. However, for biological experiments with a fixed small area, it may be reasonable to introduce parameter n not as the real-valued density but as the total number of mycelia. In such a case, the competition term can be taken as $f_2((n-1)M) = 1/(1+\beta(n-1)M)$ (it equals 1 when there is a single lesion). From the mathematical point of view, this leads merely to some change of constant parameters, and the model essentially remains the same.

Now let us introduce the following technical assumption (further assumptions will be formulated later).

Assumption 1. *Functions f_1, f_2, g are twice continuously differentiable on $[0, +\infty)$ and positive on $(0, +\infty)$, derivative g' is nonnegative on $[0, +\infty)$, $f_1(0) = g(0) = 0$, and, moreover, $f(M_{\text{up}}) - g(M_{\text{up}}) < 0$ for some sufficiently large $M_{\text{up}} > 0$.*

It is clear that functions (4) satisfy this assumption.

From Assumption 1, we obtain that, for any initial state $M_0 \in (0, M_{\text{up}})$ and for any admissible control $u : [0, T] \rightarrow [0, 1]$, there exists a unique trajectory $M : [0, T] \rightarrow \mathbb{R}$ of (1), and $M(t) \in (0, M_{\text{up}})$ for all $t \in [0, T]$. Therefore, $0 < M < M_{\text{up}}$ is a bounded strongly invariant domain in the state space according to the definition of (Clarke et al., 1998, Chapter 4, §3). Similarly to (Yong and Zhou, 1999, Chapter 2, §5.1), one can verify that, for every fixed $M_0 \in (0, M_{\text{up}})$, there exists an optimal open-loop control for problem (1),(2).

Let us consider only admissible state trajectories lying in the strongly invariant domain $0 < M < M_{\text{up}}$.

The key objective of this paper is to find optimal feedback control laws for problem (1),(2) in both of the cases $T < +\infty$ and $T = +\infty$.

3. NECESSARY OPTIMALITY CONDITIONS IN THE FINITE-HORIZON CASE

Consider the finite-horizon case $T < +\infty$.

Necessary optimality conditions for open-loop controls date back to Pontryagin et al. (1964) and are known as

Pontryagin's maximum principle (PMP). For our problem (1),(2), PMP leads to the Hamiltonian

$$H(t, M, u, \psi) = (f(M) - g(M))\psi + uf(M)(e^{-\mu t} - \psi), \quad (5)$$

adjoint system

$$\begin{cases} \frac{d\psi(t)}{dt} = -(f'(M(t)) - g'(M(t))) \cdot \psi(t) - \\ \quad - u(t) \cdot f'(M(t)) \cdot (e^{-\mu t} - \psi(t)), \\ \psi(T) = 0, \end{cases} \quad (6)$$

and ensuing maximum condition

$$u(t) = \begin{cases} 0, & \psi(t) > e^{-\mu t}, \\ 1, & \psi(t) < e^{-\mu t}, \end{cases} \quad (7)$$

which holds necessarily for an optimal open-loop control.

Since $\psi(T) = 0 < e^{-\mu T}$, then an extremal control equals 1 near the final instant $t = T$.

If $\psi(t) = e^{-\mu t}$ on some time subinterval, then a singular regime takes place. General results concerning such regimes were introduced by Gabasov and Kirillova (1982). For describing singular regimes in our problem, let us use equations (1) and (6) so as to write the following expressions for the derivatives of the switching function $e^{-\mu t} - \psi(t)$:

$$\begin{aligned} \frac{d}{dt}(e^{-\mu t} - \psi) &= -\mu e^{-\mu t} + (f'(M) - g'(M))\psi + \\ &\quad + uf'(M)(e^{-\mu t} - \psi), \\ \frac{d}{dt}(e^{-\mu t} - \psi) \Big|_{e^{-\mu t} - \psi = 0} &= e^{-\mu t}(f'(M) - g'(M) - \mu), \\ \frac{d}{dt} \left(\frac{d}{dt}(e^{-\mu t} - \psi) \Big|_{e^{-\mu t} - \psi = 0} \right) &= \\ &= -\mu e^{-\mu t}(f'(M) - g'(M) - \mu) + \\ &\quad + e^{-\mu t}(f''(M) - g''(M))((1-u)f(M) - g(M)). \end{aligned} \quad (8)$$

For verifying Kelley condition (Gabasov and Kirillova (1982)), let us differentiate the last expression with respect to u :

$$\begin{aligned} \frac{\partial}{\partial u} \left(\frac{d}{dt} \left(\frac{d}{dt}(e^{-\mu t} - \psi) \Big|_{e^{-\mu t} - \psi = 0} \right) \right) &= \\ &= -e^{-\mu t} f(M)(f''(M) - g''(M)) \end{aligned}$$

(this partial derivative should be nonnegative along singular subarcs of optimal processes). Based on the obtained representations, we impose the next assumption that guarantees existence of a singular arc as a unique steady state and also fulfillment of Kelley condition in the strict inequality form.

Assumption 2. *There exists a unique solution $M^* \in (0, M_{\text{up}})$ to the equation*

$$\begin{aligned} f'(M^*) - g'(M^*) &= nf_2'(nM^*)f_1(M^*) + \\ &\quad + f_2(nM^*)f_1'(M^*) - g'(M^*) = \mu, \end{aligned} \quad (9)$$

and the following inequality holds:

$$\begin{aligned} f''(M^*) - g''(M^*) &= n^2 f_2''(nM^*)f_1(M^*) + \\ &\quad + 2nf_2'(nM^*)f_1'(M^*) + f_2(nM^*)f_1''(M^*) - \\ &\quad - g''(M^*) < 0. \end{aligned} \quad (10)$$

Thus, direct analysis of the PMP boundary value problem (1),(6),(7) leads to the following theorem.

Theorem 1. *Suppose that $T < +\infty$ and Assumptions 1,2 hold. Singular arcs of optimal state trajectories for prob-*

lem (1),(2) stay at $M = M^$, correspond to the constant control*

$$u^* = 1 - \frac{g(M^*)}{f(M^*)} \in (0, 1), \quad (11)$$

and satisfy strong Kelley condition. Moreover,

$$\begin{aligned} f'(M) - g'(M) &< \mu \quad \forall M > M^*, \\ f'(M) - g'(M) &> \mu \quad \forall M \in (0, M^*), \\ f(M) &> g(M) \quad \forall M \in (0, M^*). \end{aligned} \quad (12)$$

Hence, the singular control indeed keeps the average mycelium size equal to the steady value M^* and represents an intermediate configuration of the resource allocation.

Also note that

$$\begin{aligned} \frac{dM}{dt} \Big|_{u=1} &= -g(M) < 0 \quad \text{if } M > 0, \\ \frac{dM}{dt} \Big|_{u=0} &= f(M) - g(M) > 0 \quad \text{if } M \in (0, M^*). \end{aligned} \quad (13)$$

In order to analyze time subintervals on which the switching function $e^{-\mu t} - \psi(t)$ keeps its sign, let us use representations (8) together with relations (9)–(13). Then the next properties can be verified.

Proposition 1. *Suppose that $T < +\infty$, Assumptions 1,2 hold, $(u(\cdot), M(\cdot), \psi(\cdot))$ is an admissible process, $\tilde{t} \in (0, T]$ is a fixed instant, $M(\tilde{t}) = \tilde{M}$, and $\psi(\tilde{t}) = \tilde{\psi}$. Then the following properties hold:*

- 1) *if $\tilde{M} \geq M^*$, $\tilde{\psi} < e^{-\mu \tilde{t}}$, and process $(u(\cdot), M(\cdot), \psi(\cdot))$ fulfills PMP for all $t \in [0, \tilde{t}]$, then*

$$\begin{aligned} M(t) &> M^* \quad \forall t \in [0, \tilde{t}], \\ \psi(t) &< e^{-\mu t} \quad \text{and } u(t) = 1 \quad \forall t \in [0, \tilde{t}]; \end{aligned}$$
- 2) *if $\tilde{M} \leq M^*$, $\tilde{\psi} > e^{-\mu \tilde{t}}$, and process $(u(\cdot), M(\cdot), \psi(\cdot))$ fulfills PMP for all $t \in [0, \tilde{t}]$, then*

$$\begin{aligned} M(t) &< M^* \quad \forall t \in [0, \tilde{t}], \\ \psi(t) &> e^{-\mu t} \quad \text{and } u(t) = 0 \quad \forall t \in [0, \tilde{t}]; \end{aligned}$$
- 3) *if $\tilde{M} = M^*$, $\tilde{\psi} = e^{-\mu \tilde{t}}$, and $u(t) = 1$ for all $t \in [0, \tilde{t}]$, then*

$$M(t) > M^* \quad \text{and } \psi(t) < e^{-\mu t} \quad \forall t \in [0, \tilde{t}],$$
which implies fulfillment of PMP for all $t \in [0, \tilde{t}]$;
- 4) *if $\tilde{M} = M^*$, $\tilde{\psi} = e^{-\mu \tilde{t}}$, and $u(t) = 0$ for all $t \in [0, \tilde{t}]$, then*

$$M(t) < M^* \quad \text{and } \psi(t) > e^{-\mu t} \quad \forall t \in [0, \tilde{t}],$$
which implies fulfillment of PMP for all $t \in [0, \tilde{t}]$.

Now, based on Theorem 1 and Proposition 1, let us summarize possible qualitative portraits of optimal processes.

Theorem 2. *Under Assumptions 1,2, the following statements hold for optimal processes of problem (1),(2) in case $T < +\infty$:*

- 1) *if $M(T) \geq M^*$, then $u(t) \equiv 1$ for all $t \in [0, T]$ (due to item 1 in Proposition 1);*
- 2) *if $M(T) < M^*$, then there is at most one bang-bang switching, and it may happen only when $M \leq M^*$ (due to items 1,2 in Proposition 1);*
- 3) *if $M(T) < M^*$, then there is at most one singular arc, and it stays at $M = M^*$ (due to Theorem 1 and items 3,4 in Proposition 1);*

- 4) if an optimal control contains a bang-bang switching (note that switchings to or from the singular control are not treated as bang-bang), then it does not contain a singular arc, and vice versa (due to items 2–4 in Proposition 1).

In the next section, we will use the derived results in order to determine the optimal feedback control.

4. OPTIMAL FEEDBACK CONTROL IN THE FINITE-HORIZON CASE

From Theorem 2, we conclude that, for constructing the optimal feedback control, it is necessary to characterize the bang-bang switching set Γ_b in the space (t, M) of the time and state variables. For this purpose, it is convenient to introduce the reverse time variable $\tau = T - t$.

Recall that boundary condition in (6) and maximum condition (7) imply $u = 1$ and $dM/d\tau = g(M)$ for sufficiently small τ . For any $\tilde{\tau} \geq 0$ and $\tilde{M} \in (0, M_{\text{up}})$, let $\eta(\cdot; \tilde{\tau}, \tilde{M})$ be the solution to $dM/d\tau = g(M)$ considered for $\tau \leq \tilde{\tau}$ and reaching $M = \tilde{M}$ at $\tau = \tilde{\tau}$. Due to autonomy of this equation, we have $\eta(\tau; \tilde{\tau}, \tilde{M}) = \eta(-(\tilde{\tau} - \tau); 0, \tilde{M})$ for all $\tau \leq \tilde{\tau}$.

Suppose that $(T - \tilde{\tau}, \tilde{M}) \in \Gamma_b$ and $M|_{\tau=\tilde{\tau}} = \tilde{M}$. From adjoint system (6) rewritten in reverse time on the interval $0 \leq \tau \leq \tilde{\tau}$, we get

$$\psi|_{\tau=\tilde{\tau}} = \int_0^{\tilde{\tau}} \exp \left\{ - \int_{\tau}^{\tilde{\tau}} g'(\eta(-(\tilde{\tau} - \zeta); 0, \tilde{M})) d\zeta \right\} \cdot f'(\eta(-(\tilde{\tau} - \tau); 0, \tilde{M})) e^{-\mu(T-\tau)} d\tau.$$

It remains to recall the switching condition $\psi|_{\tau=\tilde{\tau}} = e^{-\mu(T-\tilde{\tau})}$ in order to obtain the following result.

Proposition 2. *Under Assumptions 1,2, the bang-bang switching surface for problem (1),(2) in case $T < +\infty$ can be represented as*

$$\Gamma_b = \{(t, M) \in [0, T] \times (0, M^*] : \lambda_b(T - t, M) = 0\},$$

where

$$\lambda_b(\tau, M) = - \int_0^{\tau} \exp \left\{ - \int_0^s g'(\eta(-\xi; 0, M)) d\xi - \mu s \right\} \cdot f'(\eta(-s; 0, M)) ds + 1 \quad \forall \tau \geq 0 \quad \forall M \in (0, M_{\text{up}}).$$

Also note that there exists a unique $\tau^* > 0$ for which $\lambda_b(\tau^*, M^*) = 0$.

One can verify that optimal integral trajectories cross $\Gamma_b \setminus \{(T - \tau^*, M^*)\}$ transversally under the next condition (it is in fact related to the subarcs for $u = 0$, because a similar condition on the subarcs for $u = 1$ can be directly obtained by using the previous assumptions).

Assumption 3. *The following property holds:*

$$\frac{\partial \lambda_b(T - t, M)}{\partial \tau} + (g(M) - f(M)) \cdot \frac{\partial \lambda_b(T - t, M)}{\partial M} < 0$$

$$\forall (t, M) \in \Gamma_b.$$

In the particular case (4), we have

$$\lambda_b(\tau, M) = - \int_0^{\tau} e^{-(\gamma+\mu)s} f'(M e^{-\gamma s}) ds + 1,$$

which implies the inequality

$$\begin{aligned} \frac{\partial \lambda_b(\tau, M)}{\partial \tau} + \frac{\partial \lambda_b(\tau, M)}{\partial M} \cdot (g(M) - f(M)) &= \\ &= -e^{-(\gamma+\mu)\tau} f'(M e^{-\gamma\tau}) - (g(M) - f(M)) \cdot \\ &\quad \cdot \int_0^{\tau} e^{-(2\gamma+\mu)s} f''(M e^{-\gamma s}) ds < 0 \end{aligned}$$

for $(M, T - \tau) \in \Gamma_b$, i. e., Assumption 3 indeed holds.

Now, with the help of Theorems 1,2 and Propositions 1,2, we can describe the optimal feedback control strategy (see also Fig. 2 in section 7).

Theorem 3. *Under Assumptions 1–3, the optimal feedback control law for problem (1),(2) in case $T < +\infty$ has the form*

$$u_{\text{opt}}(t, M) = \begin{cases} 1, & 0 < M < M^*, \lambda_b(T - t, M) \geq 0, \\ 0, & 0 < M < M^*, \lambda_b(T - t, M) < 0, \\ u^*, & M = M^*, 0 \leq t < T - \tau^*, \\ 1, & M = M^*, T - \tau^* \leq t \leq T, \\ 1, & M > M^*, \end{cases}$$

$$\forall t \in [0, T] \quad \forall M \in (0, M_{\text{up}}).$$

5. OPTIMAL FEEDBACK CONTROL IN THE INFINITE-HORIZON CASE

Note that the switching surface Γ_b and reverse time instant τ^* are independent from T . Since we consider only state trajectories lying in the bounded strongly invariant domain $0 < M < M_{\text{up}}$, then the contribution to cost (2) on the subinterval $T - \tau^* \leq t \leq T$ uniformly tends to zero as $T \rightarrow +\infty$. Therefore, the optimal feedback control strategy in case $T = +\infty$ can be described as follows (see also Fig. 2 in section 7).

Theorem 4. *Under Assumptions 1–3, the optimal feedback control law for problem (1),(2) in case $T = +\infty$ has the form*

$$u_{\text{opt}}(t, M) = u_{\text{opt}}(M) = \begin{cases} 0, & 0 < M < M^*, \\ u^*, & M = M^*, \\ 1, & M > M^*, \end{cases}$$

$$\forall t \geq 0 \quad \forall M \in (0, M_{\text{up}}).$$

Furthermore, Assumptions 1–3 and, consequently, Theorems 1–4 (together with Propositions 1,2) hold in case (4) if $\alpha > (\gamma + \mu)k$ (this inequality appears from the condition $f'(0) - g'(0) > \mu$ which is required for fulfilling the first part of Assumption 2).

6. ASYMPTOTICS OF THE OPTIMAL STEADY-STATE INFECTION SIZE FOR LARGE LESION DENSITIES

Consider the optimal steady-state infection size

$$\mathcal{M}(n) = n \cdot M^*(n) \quad (14)$$

(i. e., the total mycelial size on a singular arc) as a function of the lesion density $n > 0$. Transform equation (9) into

$$\begin{aligned} \chi(\mathcal{M}(n), n) &= n \cdot f'_2(\mathcal{M}(n)) \cdot f_1\left(\frac{\mathcal{M}(n)}{n}\right) + \\ &+ f_2(\mathcal{M}(n)) \cdot f'_1\left(\frac{\mathcal{M}(n)}{n}\right) - \left(g'\left(\frac{\mathcal{M}(n)}{n}\right) + \mu\right) = 0. \end{aligned} \quad (15)$$

Note that, if nutrient flux (3) does not contain the competition term $f_2(nM)$ or if $f_2(x) \equiv \text{const}$, then M^* does not depend on n and, therefore, the infection size $\mathcal{M}(n) = nM^* \rightarrow +\infty$ as $n \rightarrow \infty$. However, this is impossible from the biological point of view, because host resources are limited and, regardless of the lesion density, the total infection cannot infinitely grow. Thus, the competition term should lead to saturation of $\mathcal{M}(n)$ for large n . Let us formulate sufficient conditions for that.

Assumption 4. For every $n \geq 0$, $M^*(n)$ is a unique solution to equation (9) on the whole interval $(0, +\infty)$ (not only on $(0, M_{\text{up}}(n))$), and inequality (10) also holds. Moreover, f'_1 is bounded on $[0, +\infty)$, f'_2 is nonpositive on $[0, +\infty)$, and $\lim_{x \rightarrow +\infty} f_2(x) = 0$.

Now the sought-for property can be verified by contradiction (if there is a sequence $\{n_i\}_{i=1}^{\infty}$ of positive numbers such that $n_i \rightarrow +\infty$ and $\mathcal{M}(n_i) \rightarrow +\infty$ as $i \rightarrow \infty$, then, due to Assumption 4, $\chi(\mathcal{M}(n_i), n_i)$ has a negative upper limit for $i \rightarrow \infty$ and, therefore, cannot be identical to zero).

Proposition 3. Let Assumptions 1,4 hold for every $n \geq 0$. Then function (14) is bounded for $n \geq 0$.

One more natural property in addition to boundedness of the infection size is its increase with increase of n . The next result can be proved by applying the rule of differentiating implicit functions to an equation which is equivalent to (15).

Proposition 4. Suppose that Assumptions 1,4 hold for every $n \geq 0$, and, moreover, there exists a positive smooth function $\kappa = \kappa(x, n)$ defined for positive arguments and such that the partial derivatives $\partial \tilde{\chi}(x, n)/\partial x$, $\partial \tilde{\chi}(x, n)/\partial n$ of the product $\tilde{\chi}(x, n) = \chi(x, n) \cdot \kappa(x, n)$ are nonzero and have opposite signs for all $x > 0$, $n > 0$. Then function (14) is strictly increasing for $n \geq 0$.

One can directly verify that, for particular functions (4), all the conditions of Propositions 3,4 hold if $\alpha > (\gamma + \mu)k$.

7. NUMERICAL SIMULATIONS

First, note that it is convenient to measure mycelium sizes in terms of equivalent amounts of infecting spores. In particular, if a mycelium appears from one spore at the beginning of the infection period, then the initial mycelium size can be represented as one equivalent of an infecting spore or, roughly speaking, as one spore. Furthermore, let us measure time (infection age) in days and lesion densities in spores/cm².

For numerical simulations, consider functions (4) with the following parameter values: $k = (1/6) \cdot 10^4$ spores, $\alpha = 0.2 \cdot 10^4$ spores/day, $\beta = 10^{-5}$ cm²/spores², $\gamma = 0.06$ 1/day, $\mu = 0.03$ 1/day.

These values are contained in the physically realistic ranges that can be seen, for instance, in the works of Newton et al. (1999); Pei et al. (2003); Robert et al. (2004); Gilchrist et al. (2006). In fact, estimating actual parameter values via experiments with real plant-pathogen interactions (for example, leaf rust of poplar) is a possible subject of future research. Nevertheless, taking exact parameter values for numerical simulations does not seem

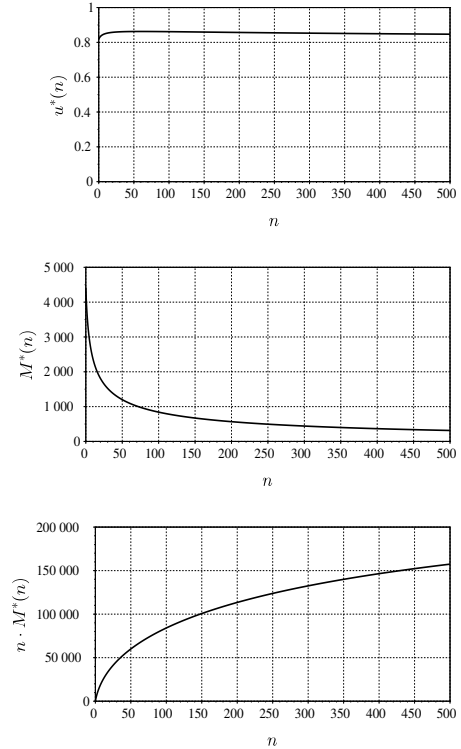


Fig. 1. Functions $u^*(n)$, $M^*(n)$, and $\mathcal{M}(n) = n \cdot M^*(n)$.

to be crucial, since the key objective of our model is to obtain general qualitative results allowing clear biological interpretation.

Fig. 1 indicates how the singular control u^* , steady state M^* , and optimal steady-state infection size $\mathcal{M}(n) = n \cdot M^*(n)$ depend on the lesion density n . As n increases, $u^*(n)$ stays approximately constant, while $M^*(n)$ decreases. One can also see growth and saturation of $\mathcal{M}(n)$ in compliance with Propositions 3,4.

Now fix the lesion density $n = 10$ spores/cm². The global phase portraits of the optimal feedback control strategies together with the corresponding integral trajectories in cases $T = 20$ and $T = +\infty$ are given in Fig. 2. In the infinite-horizon case, the line $M = M^*$ can be characterized as a turnpike regime with an intermediate resource allocation (Zelikin and Borisov (2005)). This line separates the latency ($u = 0$) and pure sporulation ($u = 1$) regimes so that optimal trajectories are attracted to it from both of the opposite sides. Such an attracting manifold is called universal (Melikyan (1998)). A similar description can be applied to the finite-horizon case with the difference that the pure sporulation regime occupies not only the half-plane $M > M^*$ but also some domain lying in $M \leq M^*$ and contiguous to the final instant line $t = T$. The latter property represents the necessity to stop supporting mycelial growth and, consequently, to invest all available nutrient resources in spore production closer to the end of the observed time interval. Thereby, the bang-bang switching surface Γ_b appears, which is specific for finite-horizon optimal resource allocation problems (Yegorov et al. (2015)).

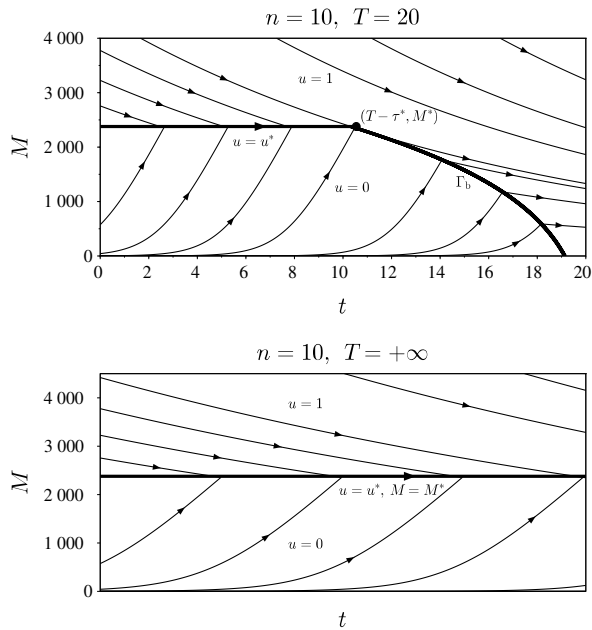


Fig. 2. Optimal feedback control strategies for $n = 10$ in cases $T = 20$ and $T = +\infty$.

8. CONCLUSION

In this paper, we developed a nonlinear model for one-season dynamics of a within-host cohort of spore-producing biotrophic fungi and solved a related optimal resource allocation problem. In addition to the finite-horizon case, such a reasonable abstraction as the infinite-horizon case was also treated.

The constructed optimal feedback strategy can serve as a benchmark to compare actual mechanisms of infections caused by biotrophic plant pathogens. There is a singular control subregime that leads to a steady-state arc and an intermediate resource allocation. This is specific namely for biotrophic fungi (as was noted in the introduction, another fungal class such as saprophytes can be characterized by purely bang-bang resource allocation strategies).

Furthermore, we analyzed asymptotics of the optimal steady-state infection size for large lesion densities. The obtained saturation property was an important argument in favor of our problem statement including competition between pathogens for limited host resources.

Biological implications of this modeling work are manifold. Spore production and mycelium sizes can be practically measured (for instance, through real-time PCR analysis), and our model predictions can thus be challenged with biological experiments. Moreover, the latent period (i.e., the time between inoculation at $t = 0$ and the onset of sporulation with $u = u^*$) is a key trait for most pathogens and accounts for both epidemiological dynamics and parasite virulence. A better understanding of how resource allocation strategies rule the evolution of this trait is a strong prerequisite for the development of sustainable crop protection techniques.

Another promising direction of future theoretical research is application of the differential game framework

to models describing resident-mutant type interactions (Akhmetzhanov et al. (2012)) between different cohorts of biotrophic fungi within one host.

REFERENCES

- Akhmetzhanov, A.R., Grogard, F., and Mailleret, L. Optimal life-history strategies in seasonal consumer-resource dynamics. *Evolution* 2011; **65**(11): 3113–3125.
- Akhmetzhanov, A.R., Grogard, F., Mailleret, L., and Bernhard, P. Join forces or cheat: Evolutionary analysis of a consumer-resource system. In *Advances in Dynamic Games, Volume 12 of the series Annals of the International Society of Dynamic Games*, 73–95. Springer: New York, 2012.
- Bancal, M.O., Hansart, A., Sache, I., and Bancal, P. Modelling fungal sink competitiveness with grains for assimilates in wheat infected by a biotrophic pathogen. *Ann. Bot.* 2012; **110**(1): 113–123.
- Clarke, F.H., Ledyev, Yu.S., Stern, R.J., and Wolenski, P.R. *Nonsmooth Analysis and Control Theory*. Springer-Verlag: New York, 1998.
- Day, T. Parasite transmission modes and the evolution of virulence. *Evolution* 2001; **55**: 2389–2400.
- Day, T. Virulence evolution and the timing of disease life-history events. *Trends Ecol. Evol.* 2003; **18**: 113–118.
- Deacon, J.W. *Modern Mycology*. Blackwell Scientific: Oxford, 1997.
- Gabasov, R. and Kirillova, F.M. *Singular Optimal Control*. Plenum Press: New York, 1982.
- Gilchrist, M.A., Sulsky, D.L., and Pringle, A. Identifying fitness and optimal life-history strategies for an asexual filamentous fungus. *Evolution* 2006; **60**: 970–979.
- Melikyan, A.A. *Generalized Characteristics of First Order PDEs: Application in Optimal Control and Differential Games*. Birkhauser: Boston, 1998.
- Newton, M.R., Wright, A.S., Kinkel, L.L., and Leonard, K.J. Competition alters temporal dynamics of sporulation in the wheat stem rust fungus. *J. Phytopathol.* 1999; **147**: 527–534.
- Pei, M.H., Ruiz, C., Harris, J., and Hunter, T. Quantitative inoculations of poplars with *Melampsora larici-populina*. *Eur. J. Plant Pathol.* 2003; **109**: 269–276.
- Pontryagin, L.S., Boltyansky, V.G., Gamkrelidze, R.V., and Mishchenko, E.F. *The Mathematical Theory of Optimal Processes*. Macmillan: New York, 1964.
- Robert C., Bancal M.O., and Lannou C. Wheat leaf rust uredospore production on adult plants: Influence of leaf nitrogen content and septoria tritici blotch. *Phytopathology* 2004; **94**(7): 712–721.
- Sasaki, A. and Iwasa, Y. Optimal-growth schedule of pathogens within a host: switching between lytic and latent cycles. *Theor. Popul. Biol.* 1991; **39**: 201–239.
- Yegorov, I., Bratus, A., and Todorov, Y. Synthesis of optimal control in a mathematical model of economic growth under R&D investments. *Appl. Math. Sci.* 2015; **9**(91): 4523–4564.
- Yong, J. and Zhou, X. Yu. *Stochastic Controls: Hamiltonian Systems and HJB Equations*. Springer-Verlag: New York, 1999.
- Zelikin, M.I. and Borisov, V.F. Singular optimal regimes in problems of mathematical economics. *J. Math. Sci.* 2005; **130**(1): 4409–4570.