

## Optimal resource allocation for biotrophic plant pathogens<sup>\*</sup>

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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.

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**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).

<sup>\*</sup> This work was supported in part by the project FunFit ANR-13-BSV7-0011

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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

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  $\delta$  is a positive constant, the criterion can be written as

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

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  $\alpha, \beta, \gamma, k$  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

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