

NUMERICAL SOLUTION OF A DYNAMIC EQUILIBRIUM OF PATHOGEN COHORTS.

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1. INTRODUCTION

In this report, we study a zero-sum feedback game for a system of nonlinear ordinary differential equations describing the one-seasonal dynamics of two biotrophic fungal cohorts within a shared host plant. The first fungus can be understood as the resident, while the second is the mutant. The invasion functional takes the form of the difference between the two marginal fitness criteria and represents the cost in defining the differential game's value. A general dynamic game approach of [1] is explored and discussed. The Cauchy problem for the first-order Hamilton–Jacobi partial differential equation (HJ PDE) created by this situation is numerically solved using the ROC-HJ software [2]. Analysis of the numerical simulation interpretations obtained by this package is further investigated later in this document.

2. STATEMENT OF THE MODEL

Consider the one-seasonal dynamics of two biotrophic fungal cohorts within one host plant. Let us refer to them as to cohorts 1 and 2. For cohort i , let n_i be the lesion density, which is the number of mycelia per unit area of the host. For simplicity, assume n_1 and n_2 to be constant during the entire infection period within the season, which means that new infectious agents do not penetrate the host during the analyzed period. Even though this is typically a substantial restriction for infections in nature, it still allows for drawing significant conclusions with relevant biological interpretations and adhering to standard experimental infection protocols.

Denote the average size of a mycelium in cohort i by M_i . Let S_i be the average quantity of spores produced by a mycelium in cohort i . The infection age t within the season is a time variable. Note that the mycelial sizes M_1 and M_2 are measured in terms of equivalent amounts of infecting spores (for instance, if a mycelium appears from one spore at the beginning of the infection period, the initial mycelial size can be set as one equivalent of an infecting spore or only as one spore).

To determine the nutrient flux by cohort i we use the function, $f_i = f_i(M_1, M_2)$, which is allocated between two different pathogen activities such as within-host multiplication (mycelial growth) and producing asexual spores. For brevity, we do not explicitly show the dependence on the constant parameters n_1, n_2 when writing $f_i = f_i(M_1, M_2)$, $i = 1, 2$. Let $u_i = u_i(t)$ be a related resource allocation (control) function, taking values between zero and one. Suppose that the whole flux goes to mycelial growth when $u_i(t) = 0$ and to spore production when $u_i(t) = 1$, while, for $0 < u_i(t) < 1$, there is an intermediate configuration.

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Let $g = g(M)$ be the rate of mycelial decay for both cohorts. Assume the constant yield of spores, $\delta > 0$, as compared to mycelial growth.

The period of the infections within the season is a fixed interval $[0, T]$.

The following dynamic model can thus be formulated [1]:

$$(1) \quad \begin{cases} \frac{dM_1(t)}{dt} = (1 - u_1(t)) f_1(M_1(t), M_2(t)) - g(M_1(t)), \\ \frac{dM_2(t)}{dt} = (1 - u_2(t)) f_2(M_1(t), M_2(t)) - g(M_2(t)), \\ \frac{dS_1(t)}{dt} = \delta u_1(t) f_1(M_1(t), M_2(t)), \\ \frac{dS_2(t)}{dt} = \delta u_2(t) f_2(M_1(t), M_2(t)), \\ M_1(0) = M_1^0, \quad M_2(0) = M_2^0, \quad S_1(0) = S_1^0, \quad S_2(0) = S_2^0, \\ 0 \leq u_1(t) \leq 1, \quad 0 \leq u_2(t) \leq 1, \quad t \in [0, T]. \end{cases}$$

Since the right-hand sides of the third and fourth equations in (1) do not contain S_1 and S_2 , one does not need to treat S_1 and S_2 explicitly, so that M_1 and M_2 can be considered as the only state variables.

The reproductive success of cohort i is determined by:

$$(2) \quad \int_0^T \frac{dS_i(t)}{dt} e^{-\mu t} dt = \delta \int_0^T u_i(t) f_i(M_1(t), M_2(t)) e^{-\mu t} dt,$$

where $e^{-\mu t}$ describes the exponential extinction of the infections, and μ is a positive constant. Since δ is a positive constant, we can divide (2) by δ and arrive at

$$J_i(u_1(\cdot), u_2(\cdot)) = \int_0^T u_i(t) f_i(M_1(t), M_2(t)) e^{-\mu t} dt.$$

In line with [1, 3], we study one-seasonal competition between the two pathogen cohorts in terms of their average reproductive outputs by seeking the saddle control strategies in the following zero-sum two-player differential game:

$$(3) \quad \begin{cases} \frac{dM_1(t)}{dt} = (1 - u_1(t)) f_1(M_1(t), M_2(t)) - g(M_1(t)), \\ \frac{dM_2(t)}{dt} = (1 - u_2(t)) f_2(M_1(t), M_2(t)) - g(M_2(t)), \\ M_1(0) = M_1^0, \quad M_2(0) = M_2^0, \\ 0 \leq u_1(t) \leq 1, \quad 0 \leq u_2(t) \leq 1, \quad t \in [0, T], \end{cases}$$

$$(4) \quad J(u_1(\cdot), u_2(\cdot)) \longrightarrow \inf_{u_1(\cdot)} \sup_{u_2(\cdot)} \text{ or } \sup_{u_2(\cdot)} \inf_{u_1(\cdot)},$$

$$(5) \quad \begin{aligned} J(u_1(\cdot), u_2(\cdot)) &= J_2(u_1(\cdot), u_2(\cdot)) - J_1(u_1(\cdot), u_2(\cdot)) \\ &= \int_0^T (u_2(t) f_2(M_1(t), M_2(t)) - u_1(t) f_1(M_1(t), M_2(t))) e^{-\mu t} dt. \end{aligned}$$

According to [1], we represent the nutrient fluxes and decay rates as

$$(6) \quad f_i(M_1, M_2) = \nu(n_1 M_1 + n_2 M_2) \cdot \rho(M_i) \quad \forall M_1 \geq 0 \quad \forall M_2 \geq 0, \quad i = 1, 2,$$

$$(7) \quad \rho(M) = \alpha \frac{M}{M + k} \quad \forall M \geq 0,$$

$$(8) \quad \nu(n_1 M_1 + n_2 M_2) = \frac{1}{1 + \beta(n_1 M_1 + n_2 M_2)} \quad \forall M_1 \geq 0 \quad \forall M_2 \geq 0,$$

$$(9) \quad g(M) = \gamma M \quad \forall M \geq 0.$$

Moreover, the following parameter values are useful for the numerical simulations and arise from the analysis of [14]:

$$(10) \quad \begin{aligned} \alpha &= 0.2 \cdot 10^4 \text{ spores/day}, & k &= (1/6) \cdot 10^4 \text{ spores}, \\ \beta &= 10^{-5} \text{ cm}^2/\text{spores}^2, & \gamma &= 0.06 \text{ 1/day}, & \mu &= 0.03 \text{ 1/day}, \\ n_1 &= 9 \text{ spores/cm}^2, & n_2 &= 1 \text{ spore/cm}^2, \\ T &= 60 \text{ days}. \end{aligned}$$

As was shown in [1], the bounded domain

$$G = \{(M_1, M_2) \in \mathbb{R}^2 : 0 < M_1 < \bar{M}_1, 0 < M_2 < \bar{M}_2\}$$

with

$$\bar{M}_1 = \bar{M}_2 > \alpha/\gamma - k$$

is an invariant set in the state space (if a state trajectory starts in G , it cannot leave G). The parameters \bar{M}_1, \bar{M}_2 can be understood as carrying capacity estimates.

3. UNINVADABLE AND EVOLUTIONARILY STABLE STRATEGIES

This section describes our motivation for the game-theoretic statement (3)–(5).

Based on the terminology of Adaptive Dynamics [4], let us interpret cohort 1 as a resident and cohort 2 as a mutant. Denote the corresponding classes of considered strategies as \mathcal{U}_1 and \mathcal{U}_2 . For a pair of methods $(u_1, u_2) \in \mathcal{U}_1 \times \mathcal{U}_2$, the resident is not invaded by the mutant if and only if

$$J(u_1, u_2) = J_2(u_1, u_2) - J_1(u_1, u_2) \leq 0.$$

A strategy $\hat{u}_1 \in \mathcal{U}_1$ is hence uninvadable if and only if

$$J(\hat{u}_1, u_2) \leq 0 \quad \forall u_2 \in \mathcal{U}_2,$$

which is equivalent to

$$\sup_{u_2 \in \mathcal{U}_2} J(\hat{u}_1, u_2) \leq 0.$$

Such a \hat{u}_1 exists if

$$(11) \quad \inf_{u_1 \in \mathcal{U}_1} \sup_{u_2 \in \mathcal{U}_2} J(u_1, u_2) = \min_{u_1 \in \mathcal{U}_1} \sup_{u_2 \in \mathcal{U}_2} J(u_1, u_2) \leq 0$$

or

$$\inf_{u_1 \in \mathcal{U}_1} \sup_{u_2 \in \mathcal{U}_2} J(u_1, u_2) < 0$$

(The latter inequality arises from when the infimum u_1 is not satisfied). Equation (11) motivates our game-theoretic statement (3)–(5), where the first player tries to maximize its resistance to an invasion by the second one, and vice versa.

If $M_1^0 = M_2^0$ and $\mathcal{U}_1 = \mathcal{U}_2 = \mathcal{U}$, then $J(u, u) = 0$ for all $u \in \mathcal{U}$, and (11) is simplified to

$$\min_{u_1 \in \mathcal{U}} \sup_{u_2 \in \mathcal{U}} J(u_1, u_2) = 0.$$

In this case, a strategy

$$\hat{u}_1 \in \operatorname{Arg} \min_{u_1 \in \mathcal{U}} \left(\sup_{u_2 \in \mathcal{U}} J(u_1, u_2) \right)$$

is called evolutionary stable if the related maximum for u_2 is unique:

$$\operatorname{Arg} \max_{u_2 \in \mathcal{U}} J(\hat{u}_1, u_2) = \{\hat{u}_1\}.$$

This approach to defining stable evolutionary strategies was initially proposed in [3] and further developed in [1].

4. HAMILTON–JACOBI–ISAACS EQUATION

Introduce the following function known as Hamiltonian:

$$\begin{aligned} H(t, M_1, M_2, u_1, u_2, p_1, p_2) &= p_1 ((1 - u_1) f_1(M_1, M_2) - g(M_1)) \\ &\quad + p_2 ((1 - u_2) f_2(M_1, M_2) - g(M_2)) \\ &\quad + e^{-\mu t} (u_2 f_2(M_1, M_2) - u_1 f_1(M_1, M_2)) \\ \forall t \in [0, T] \quad \forall (M_1, M_2) \in G \quad \forall (u_1, u_2) \in [0, 1]^2 \quad \forall (p_1, p_2) \in \mathbb{R}^2 \end{aligned}$$

(this is the sum of the dot product of $p = (p_1, p_2)$ with $(dM_1/dt, dM_2/dt)$ and the integrand in $J(u_1(\cdot), u_2(\cdot))$, see (3) and (5)). The Hamiltonian satisfies the saddle point condition concerning the control variables u_1 and u_2 :

$$\begin{aligned} \min_{u_1 \in [0, 1]} \max_{u_2 \in [0, 1]} H(t, M_1, M_2, u_1, u_2, p_1, p_2) \\ = \max_{u_2 \in [0, 1]} \min_{u_1 \in [0, 1]} H(t, M_1, M_2, u_1, u_2, p_1, p_2) = \mathcal{H}(t, M_1, M_2, p_1, p_2) \\ \forall t \in [0, T] \quad \forall (M_1, M_2) \in G \quad \forall (p_1, p_2) \in \mathbb{R}^2 \end{aligned}$$

(here minimax and maximin give the same result). Due to the theoretical results of [5, §XI.6], the value function $V: [0, T] \times G \rightarrow \mathbb{R}$ in the formulated feedback differential game is a unique solution of the following Cauchy problem for the Hamilton–Jacobi–Isaacs partial differential equation (HJI PDE):

$$(12) \quad \begin{cases} \frac{\partial V(t, M_1, M_2)}{\partial t} + \mathcal{H}\left(t, M_1, M_2, \frac{\partial V(t, M_1, M_2)}{\partial M_1}, \frac{\partial V(t, M_1, M_2)}{\partial M_2}\right) = 0, \\ V(T, M_1, M_2) = 0, \\ t \in [0, T], \quad (M_1, M_2) \in G. \end{cases}$$

In general, the solution may be nonsmooth and understood in a generalized (viscosity or minimax) sense [5, 6].

Due to the general properties of value functions of zero-sum feedback differential games [7], the value function V in our problem is Lipschitz continuous in $[0, T] \times G$. Rademacher's theorem, is differentiable almost everywhere in $(0, T) \times G$, except for possibly a subset of Lebesgue measure zero.

```

const int    OPTIM        = MAXMIN;
const int    METHOD       = MFD;
const int    TYPE_SCHEME = ENO2;
const int    TYPE_RK      = RK2;

```

FIGURE 1. A few configuration variables needed to solve the equation using ROC-HJ

For points (t, M_1, M_2) at which the value function is differentiable, one can obtain the saddle feedback control strategies from the relations

$$\begin{aligned}
 u_1(t, M_1, M_2) &\in \operatorname{Arg} \min_{w_1 \in [0,1]} \left\{ \max_{w_2 \in [0,1]} H \left(t, M_1, M_2, w_1, w_2, \frac{\partial V(t, M_1, M_2)}{\partial M_1}, \frac{\partial V(t, M_1, M_2)}{\partial M_2} \right) \right\}, \\
 u_2(t, M_1, M_2) &\in \operatorname{Arg} \max_{w_2 \in [0,1]} \left\{ \min_{w_1 \in [0,1]} H \left(t, M_1, M_2, w_1, w_2, \frac{\partial V(t, M_1, M_2)}{\partial M_1}, \frac{\partial V(t, M_1, M_2)}{\partial M_2} \right) \right\},
 \end{aligned}$$

which reduce to

$$\begin{aligned}
 (13) \quad u_1(t, M_1, M_2) &= \begin{cases} 0, & e^{-\mu t} + \frac{\partial V(t, M_1, M_2)}{\partial M_1} < 0, \\ 1, & e^{-\mu t} + \frac{\partial V(t, M_1, M_2)}{\partial M_1} > 0, \\ \text{arbitrary from } [0, 1], & e^{-\mu t} + \frac{\partial V(t, M_1, M_2)}{\partial M_1} = 0, \end{cases} \\
 u_2(t, M_1, M_2) &= \begin{cases} 0, & e^{-\mu t} - \frac{\partial V(t, M_1, M_2)}{\partial M_2} < 0, \\ 1, & e^{-\mu t} - \frac{\partial V(t, M_1, M_2)}{\partial M_2} > 0, \\ \text{arbitrary from } [0, 1], & e^{-\mu t} - \frac{\partial V(t, M_1, M_2)}{\partial M_2} = 0. \end{cases}
 \end{aligned}$$

These are resource allocation strategies that enable for equilibrium coexistence of the two pathogen cohorts.

5. CODE USED FOR THE NUMERICAL ROC-HJ

As is the case with many differential equations, it is challenging to solve this equation, which means we need to use a numerical solver to do this task. We used ROC-HJ, which is written in C++ and allows for a fast and easy transcription of the functions above into machine code. Most of the preconfigured files and procedures of ROC-HJ allow for a quick transcription of a Hamilton-Jacobi equation.

[2] provides further details of the type of assignments and other variables that need additional configuration in order for ROC-HJ to find a solution. To use ROC-HJ, we must assign a few variables to describe the kind of problem. Fig. 1 contains some of the variables which describe the problem. s

With these as well as many more options that we had to set to correctly assign the type of problem that we needed for the system to function precisely, we also needed to specify both a cost function (fig. 2) and a dynamic equation (fig. 3) to produce the data that we need

```

inline double distributed_cost2(const double* x, C u, C u2, double t) {

    double new_M_1 = x[0],
        new_M_2 = x[1],
        u_1 = u[0],
        u_2 = u2[0];

    if (new_M_1 < 0.0)
        new_M_1 = 0.0;

    if (new_M_2 < 0.0)
        new_M_2 = 0.0;

    double compet_term = 1.0 / (1.0 + new_beta * (n_1 * new_M_1 + n_2 ...
                                * new_M_2));

    return compet_term * new_alpha * exp(-mu_rate * (T - t)) *
        (u_2 * new_M_2 / (new_M_2 + new_k) - u_1 ...
        * new_M_1 / (new_M_1 + new_k));

}

```

FIGURE 2. Function in C++ written for ROC-HJ describing the distributed cost equation.

Within the `data_*.h` file, there is much more information describing the function. One can find more information and details about this project's configuration variables by viewing the data file directly at [15].

6. NUMERICAL SOLUTION

We consider the Cauchy problem (12) for the HJI PDE with the nutrient fluxes (6)–(8), decay rate (9), and parameter values (10). The numerical solution has been obtained via a finite difference method [5, 7–9] using the ROC-HJ software [2].

For practical purposes, it is reasonable to rewrite (12) in reverse time $\tau = T - t$ as

$$(14) \quad \left\{ \begin{array}{l} \frac{\partial V(T - \tau, M_1, M_2)}{\partial \tau} + \max_{u_1 \in [0,1]} \min_{u_2 \in [0,1]} \left(-H \left(T - \tau, M_1, M_2, u_1, u_2, \right. \right. \\ \left. \left. \frac{\partial V(T - \tau, M_1, M_2)}{\partial M_1}, \frac{\partial V(T - \tau, M_1, M_2)}{\partial M_2} \right) \right) = 0, \\ V(T - \tau, M_1, M_2) |_{\tau=0} = 0, \\ \tau \in [0, T], \quad (M_1, M_2) \in G, \end{array} \right.$$

and then to rewrite (14) in the new normalized state variables

$$m_i = M_i \cdot 10^{-4}, \quad i = 1, 2$$

(such changes of the time and state variables lead to an equivalent problem).

```

inline void dynamics2(const double* x, C u, C u2, double t, double* res) {

    double new_M_1 = x[0],
           new_M_2 = x[1],
           u_1 = u[0],
           u_2 = u2[0];

    if (new_M_1 < 0.0)
        new_M_1 = 0.0;

    if (new_M_2 < 0.0)
        new_M_2 = 0.0;

    double compet_term = 1.0 / (1.0 + new_beta * (n_1 * new_M_1...
                                + n_2 * new_M_2));

    res[0] = new_M_1 * ((1.0 - u_1) * compet_term * new_alpha / ...
                        (new_M_1 + new_k) - gamma_rate);
    res[1] = new_M_2 * ((1.0 - u_2) * compet_term * new_alpha / ...
                        (new_M_2 + new_k) - gamma_rate);

}

```

FIGURE 3. A C++ function for use by ROC-HJ to describe the required dynamic equation.

We specify the carrying capacity estimates as $\bar{M}_1 = \bar{M}_2 = \bar{M} = 3.5 \cdot 10^4$, $\bar{m} = \bar{M} \cdot 10^{-4} = 3.5$, and discretize the computational region

$$\{(m_1, m_2, \tau) : 0 \leq m_1 \leq \bar{m}, 0 \leq m_2 \leq \bar{m}, 0 \leq \tau \leq T\}$$

by the spatial step $\Delta m_1 = \Delta m_2 = \Delta m = 2 \cdot 10^{-3}$ and time step $\Delta \tau = 5 \cdot 10^{-3}$.

Monotone finite difference methods (including the classical Lax–Friedrichs scheme) ensure theoretical convergence properties with error estimates, but they are mostly of the first order and may generate so-called numerical diffusion problems on long time intervals. One way to attenuate such practical issues is to use higher-order ENO (essentially non-oscillatory) schemes such as those originally proposed in [8]. They are not necessarily monotone, and there is a lack of associated convergence theorems. However, their relevance is justifiable by various numerical experiments [8, 9].

We have used the second-order ENO scheme (to approximate the partial derivatives concerning the state variables), coupled with the second-order Runge–Kutta time discretization scheme and implemented in [2]. To evaluate the partial derivatives $\partial V/\partial M_i$, $i = 1, 2$, in the saddle feedback control representations (13), we have applied the standard second-order symmetrized approximation [10, §5.7].

Figs. 4 and 5 show the reductions of the approximate value function and corresponding saddle feedback control strategies to the coordinate plane (m_1, m_2) for the time instants $\tau = 0$ ($t = T = 60$), $\tau = 5$ ($t = T - 5 = 55$), $\tau = \tau^{**} \approx 11.175$ ($t = T - \tau^{**} \approx 48.825$), and $\tau = T = 60$ ($t = 0$). Here τ^{**} is a reverse time instant that triggers the appearance of singular

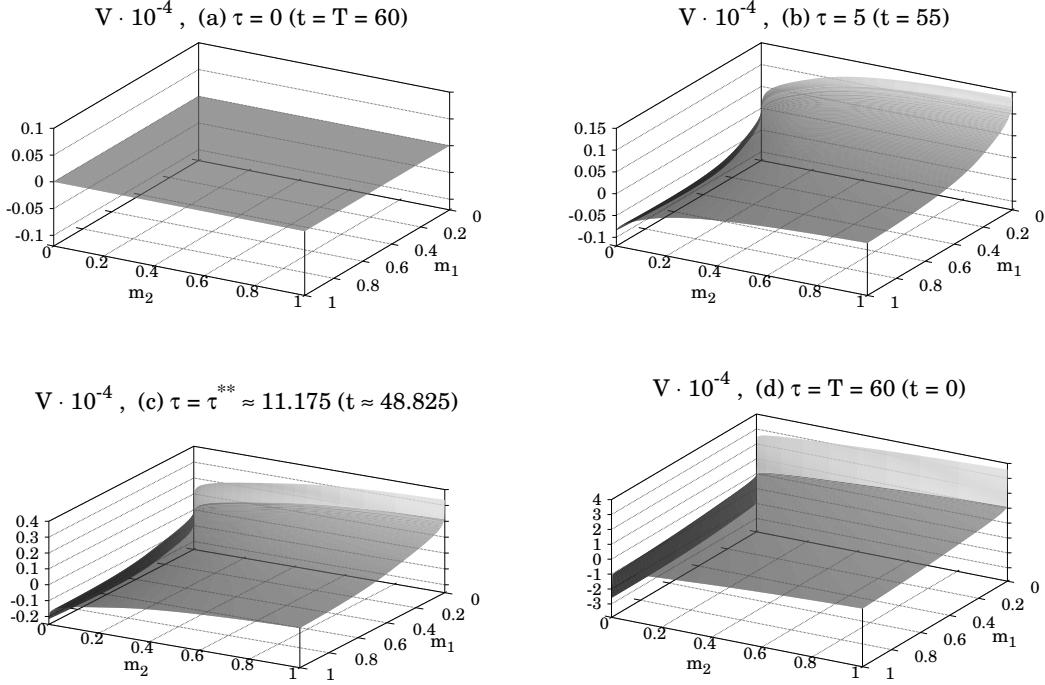


FIGURE 4. *Finite-difference approximation of the value function V at several time instants.*

control regimes and is obtained together with the equilibrium steady state (M^{**}, M^{**}) from the analysis based on Pontryagin's principle [1]. Note that Pontryagin's principle for zero-sum two-player differential games describes necessary conditions for saddle open-loop strategies [11].

Fig. 5 illustrates the appearance and time evolution of four approximate switching curves. For $\tau \geq \tau^{**}$, they intersect at the point $(m^{**}, m^{**}) = 10^{-4} \cdot (M^{**}, M^{**})$. With the further increase of τ , the feedback control portrait approaches a stationary form. Fig. 6 is a three-dimensional portrait of the four control switching surfaces. For $\tau \geq \tau^{**}$, the point (m^{**}, m^{**}) attracts forward-time trajectories and determines a steady-state equilibrium regime for both cohorts, while one can interpret the four surfaces as turnpikes.

From Fig. 4d, one can see that, in the considered domain of initial states, the value $V(0, M_1^0, M_2^0)$ of the zero-sum feedback differential game is negative for $M_1^0 > M_2^0$, zero for $M_1^0 = M_2^0$, and positive for $M_1^0 < M_2^0$. The saddle feedback resource allocation strategy of cohort 1 is uninvadable if $M_1^0 \geq M_2^0$. Similarly, the saddle feedback resource allocation strategy of cohort 2 is uninvadable if $M_1^0 \leq M_2^0$.

7. CONCLUSION

The current report discusses a mathematical development that allows for constructing benchmark pathogenic resource allocation strategies against which we may compare actual infection mechanisms.

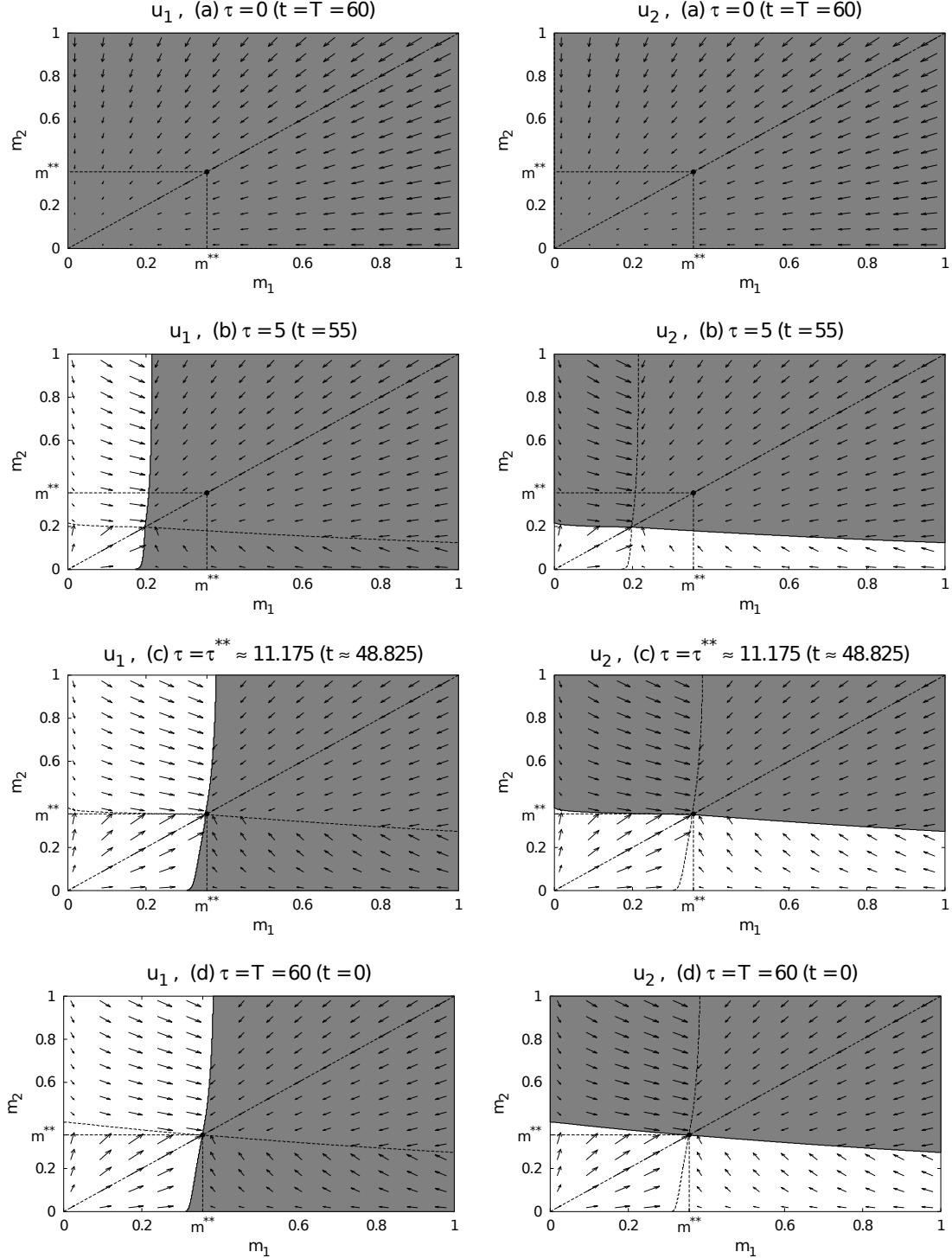


FIGURE 5. Finite-difference approximations of the saddle feedback control strategies at several time instants. White and gray colors show the regions of the control values 0 and 1, respectively. Also illustrated are the fields of the corresponding forward-time velocities.

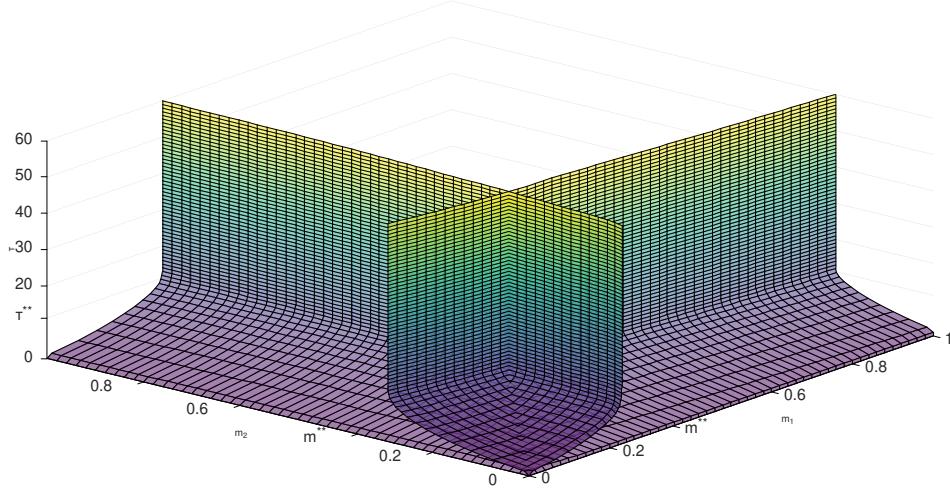


FIGURE 6. *The four control switching surfaces in the three-dimensional space (m_1, m_2, τ) .*

We have studied resource allocation equilibrium for the one-seasonal dynamics of two biotrophic fungal cohorts within a shared host plant. It is also relevant to investigate long-seasonal dynamics and associated evolutionary equilibria of competing pathogen cohorts. One may exploit specific discrete rules to transition from one season to another [12, 13]. Another important research direction is to characterize such equilibria themselves and whether they represent evolutionary attractors or not and how the situation may change through evolution.

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data_user_biotroph_fungi_game.h](https://raw.githubusercontent.com/stevenglasford/Seminar_NDSU_2020/main/ivan_to_2.5/data/data_user_biotroph_fungi_game.h)

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