Modeling a Fungal Competition on a Plant.

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Pathogens are costly.

Pathogens make living things sick.

COVID-19 is a significant pathogen.

Pathogens can end up costing gigantically.

2016 alone saw $540 billion in agricultural damages from plant pathogens.

What is fungal competition?

We will be looking at parasitic pathogenic fungi, such as leaf rust. When you can see the rust it is in the spore producing phase.

Limited resources, fighting for resources, not each other.

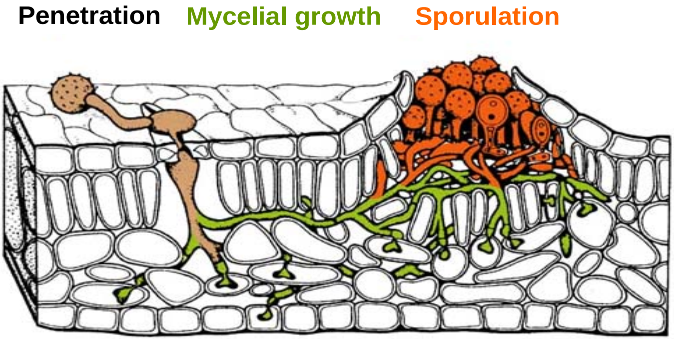
The host has finite resources and fungus does not want to kill plant (loses all of its food).

Closer inspection of Fungi

The pathogens we will be investigating exploit leaf tissue.

Mycelia expand into the current leaf. Latency period as it makes investment in growth

Spore production gets to more leaves.



Matthias Hahn, 2000

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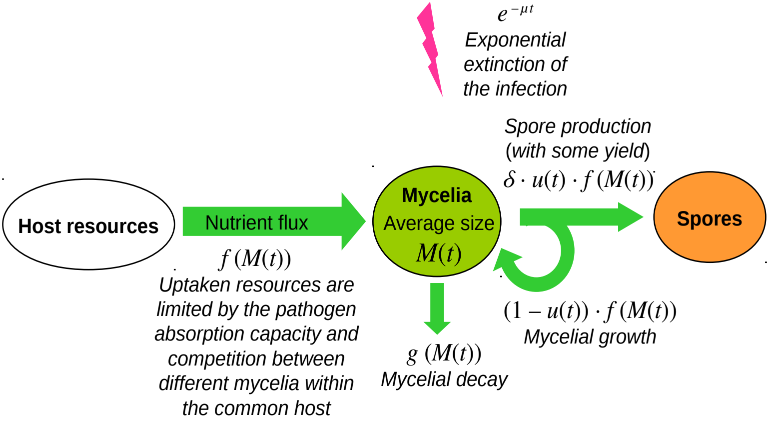
Description of fungal equations.

We focus on a single season, on a single plant, without evolution.

Unrealistic in the wild (wild is complicated), we can still get useful results, especially in laboratory conditions.



Convert to equations

Using the information from the previous slide, we can get:

$$
\begin{cases}
\dfrac{dM_1(t)}{dt} \;=\; (1 - u_1(t))\, f_1(M_1(t), M_2(t)) \;-\; g(M_1(t)), \\
\dfrac{dM_2(t)}{dt} \;=\; (1 - u_2(t))\, f_2(M_1(t), M_2(t)) \;-\; g(M_2(t)), \\
f_i(M_1, M_2) \;\stackrel{\text{def}}{=}\; \nu(n_1 M_1 \;+\; n_2 M_2)\, \rho(M_i), \quad i = 1, 2, \\
0 \leqslant u_i(t) \leqslant 1, \quad i = 1, 2, \quad t \in I_T, \\
M_1(0) = M_1^0, \quad M_2(0) = M_2^0.
\end{cases}
$$

These are the resource allocation strategies.

When $u = 0$ mycelial production, $u = 1$ spore production. A little of both when in between between 1 and 0.

Assumptions

n is the lesion density and is assumed to be constant for simplicity.

$$f(M) \stackrel{\mathrm{def}}{=} \nu(nM)\,\rho(M),$$

is the nutrient flux.

$\rho(M)$ is amount of resources flowing through a single mycelium.
$\nu(nM)$ describes the negative influence of competing mycelia.

We assume the resident is cohort 1, and the mutant is cohort 2.

Uninvadable strategies

The cohorts are not fighting each other. They are fighting for limited resources.

The competition forms a zero-sum feedback game: the resident defends, the mutant is offensive.

We assume that the cohorts use an uninvadable strategy. Each cohort tries its best and tries to ensure the other cohort does not fully invade.

An uninvadable strategy is also known as an evolutionary stable strategy.

Uninvadable equations

Let J_i be the marginal fitness (the amount of success of cohort i)

$$J_i(u_1, u_2) = \int\limits_{I_T} u_i(t) f_i(M_1(t), M_2(t))\, \delta\, e^{-\mu t}\, dt$$

of cohort i.

We can then say that the resident is not invaded if:

$$J(u_1, u_2) \stackrel{\text{def}}{=} J_2(u_1, u_2) - J_1(u_1, u_2) \leqslant 0.$$

We are most interested in modeling when J forms a saddle point (i.e., $J = 0$).

Further derivation and analysis of J can be found in [2]

Differential Game

The previous slides give us the following:

$$J(u_1(\cdot), u_2(\cdot)) \;=\; J_2(u_1(\cdot), u_2(\cdot)) \;-\; J_1(u_1(\cdot), u_2(\cdot)) \;=$$

$$= \int\limits_{I_T} (u_2(t)\, f_2(M_1(t), M_2(t)) \;-\; u_1(t)\, f_1(M_1(t), M_2(t)))\, \delta\, e^{-\mu t}\, dt$$

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

this describes how the first cohort tries to maximize its resistance to the second, and vice versa.

inf is the infimum (greatest) sup is the supremum (least).

$\inf\sup = \sup\inf$ describes a saddle point (unstable equilibrium).

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Numerical Analysis

The equations we are working with are nonsmooth, and nonlinear making them difficult to solve exactly. Numerical analysis is essential

We use computers to simulate this system.

We can convert our equations into Hamilton–Jacobi–Isaacs equation (HJI).

We can then solve the HJI with ROC-HJ (Reachability, Optimal Control, and Hamilton-Jacobi equations).

Hamilton–Jacobi–Isaacs equation

For brevity, we exclude the reasoning behind converting to a Hamiltonian. [2] contain further information

H is the Hamiltonian, describes the minimax/maximin (saddle point) of J.

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

Resource Control Strategy

The Hamiltonian minimax (maximin) condition reduces to the following:

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

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

Where u_1 corresponds to the resource allocation strategy for cohort 1 (resident), and u_2 fits cohort 2 (mutant).

Reverse Time

ROC-HJ works backward (enables the user to start with an outcome and see how it started).

We must rewrite our equations in reverse.

$$\begin{cases} \dfrac{\partial V(T-\tau, M_1, M_2)}{\partial \tau} + \max\limits_{u_1 \in [0,1]} \min\limits_{u_2 \in [0,1]} \Big(-H\Big(T-\tau,\ M_1,\ M_2,\ u_1, \\ \qquad u_2,\ \dfrac{\partial V(T-\tau, M_1, M_2)}{\partial M_1}, \dfrac{\partial V(T-\tau, M_1, M_2)}{\partial M_2}\Big)\Big) \quad = \quad 0, \\ V(T-\tau, M_1, M_2)\,|_{\tau=0} \ = \ 0, \\ \tau \in [0,\ T], \quad (M_1, M_2) \ \in \ G, \end{cases}$$

Example and Basic Parameters

We use the Finite Difference Method,
Second-order time discretization,
Find the saddle strategies.

ROC-HJ [1].

```
const int      OPTIM            = MAXMIN;
const int      METHOD           = MFD;
const int      TYPE_SCHEME      = ENO2;
```

Figure: Configurations of descriptive variables

Output

ROC-HJ produces a large amount of data in .dat files.

0	0	0.000000000000
1	0	-0.012507240463
2	0	-0.017873483512
3	0	-0.021359387034
4	0	-0.023993289170

Figure: The first five lines from when $\tau = 20$ produced from ROC-HJ.

describes a point on a plane and the direction of the vector.
It needs to be graphed to produce meaningful results.

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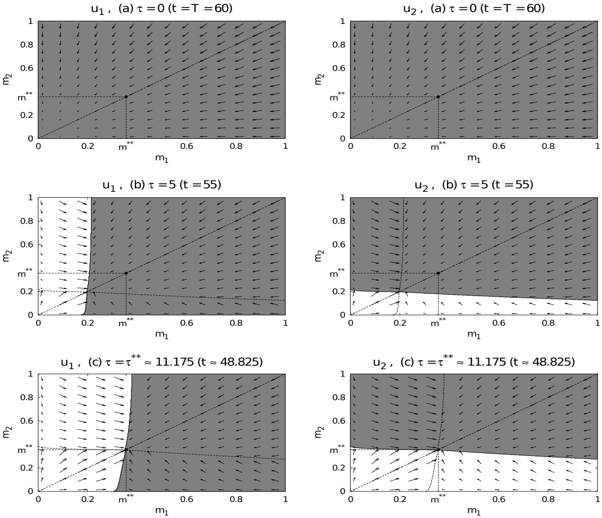
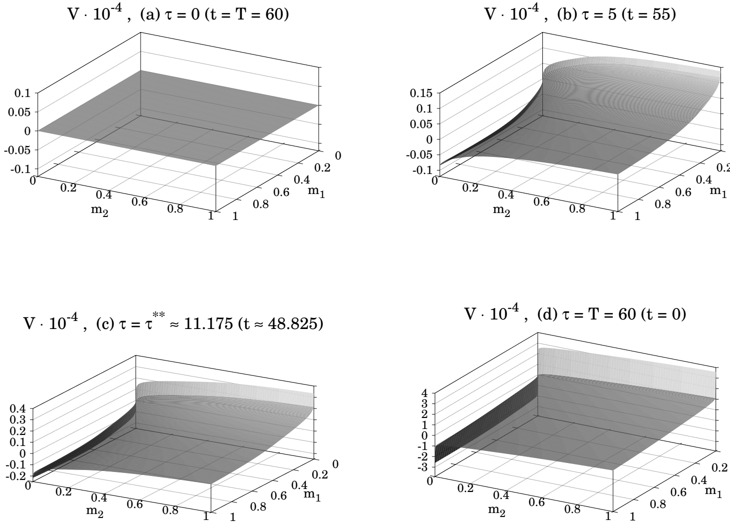
Graphs 1/3



White is mycelial growth, gray is spore production.

Graphs 2/3


V · 10^-4 , (a) τ = 0 (t = T = 60)
0.1
0.05
0
-0.05
-0.1
0
0.2
0.4
0.6
0.8
1
m2
0
0.2
0.4
0.6
0.8
1
m1
V · 10^-4 , (b) τ = 5 (t = 55)
0.15
0.1
0.05
0
-0.05
-0.1
m2
m1
V · 10^-4 , (c) τ = τ** ≈ 11.175 (t ≈ 48.825)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
m2
m1
V · 10^-4 , (d) τ = T = 60 (t = 0)
4
3
2
1
0
-1
-2
-3
m2
m1

Graphs 3/3

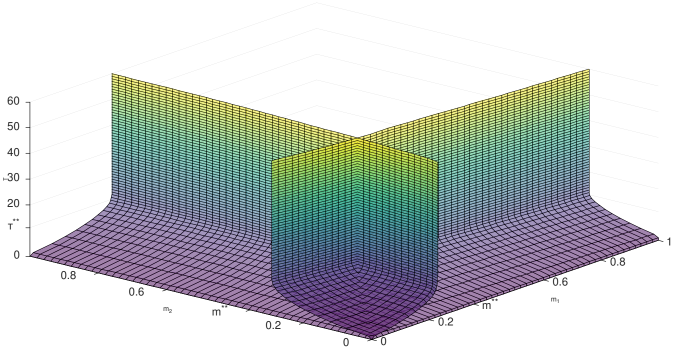


Figure: *The four control turnpike switching surfaces in the three-dimensional space* (m_1, m_2, τ)*. A turnpike is the most efficient route in order to reach the steady-state equilibrium.*

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Model Limitations

- Our model is not super general.
- One-seasonal
- No evolution (plant or fungal)
- Single plant
- Ignores plant diversity
- Ignores plant regrowth and other tolerances
- Ignores actual fighting between fungi (some fungi produce toxins to kill opponents)

More research is needed to investigate more dynamic systems.

Still very useful, sets a benchmark to test against in future analysis.

End statements

Future analysis will include further analysis and inclusion of previously stated limitations.

We looked at strategies for nearly equivalent fungi competing with each other, fighting for resources.

Thank you, Dr. Ivan Yegorov!

References

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https://uma.ensta-paristech.fr/soft/ROC-HJ, 2019-01-21.

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Dynamic Games and Applications, 10(1):257–296, Mar 2020.