Modelling Cellular Kinematics in Self-Similar Plant Growth

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1 Introduction

The diffusion-advection-reaction equation is

$$\frac{\partial U}{\partial t} + as\frac{\partial U}{\partial s} = D\nabla^2 U + p - gU \tag{1.1}$$

where $U = U(\mathbf{s}, t)$ is the concentration, which varies with the position $\mathbf{s}$ and time t; a is the velocity coefficient; D is the diffusion coefficient; p is the source; and g is the degradation rate.

The parabolic map $f : \mathbb{R}^2 \to \mathbb{R}^2$ is written as

$$\begin{aligned} s \mapsto & x = sr \\ r \mapsto & y = \frac{1}{2}(r^2 - s^2) \end{aligned} \tag{1.2}$$

the Jacobian of which is

$$J = \begin{pmatrix} \frac{\partial x}{\partial r} & \frac{\partial x}{\partial s} \\ \frac{\partial y}{\partial r} & \frac{\partial y}{\partial s} \end{pmatrix} = \begin{pmatrix} s & r \\ r & -s \end{pmatrix} . \tag{1.3}$$

The metric is then

$$g = J^T J = \begin{pmatrix} s^2 + r^2 & 0 \\ 0 & s^2 + r^2 \end{pmatrix} . \tag{1.4}$$

The Laplacian is then

$$\begin{aligned} \nabla^2 U &= \frac{1}{\sqrt{g}} \partial_i (\sqrt{g} g^{ij} \partial_j U) \\ &= \frac{1}{s^2 + r^2} (\partial_s^2 + \partial_r^2) U \quad \because \ \sqrt{\det g} = s^2 + r^2 . \end{aligned} \tag{1.5}$$

In general if $g_{ij} = h_j^2 \delta_{ij}$ we have $\sqrt{\det g} = \prod_j h_j$. So the Laplacian in 2D is now

$$\nabla^2 U = \frac{1}{h_1 h_2} \left(\partial_1 \left(\frac{h_2}{h_1} \partial_1 U \right) + \partial_2 \left(\frac{h_1}{h_2} \partial_2 U \right) \right) \tag{1.6}$$

To make the calculation easier we can immediately move to a frame of reference that follows the growth of the plant with the change of variables

$$s = \xi e^{at} \tag{1.7}$$

motivated from the velocity relation $\dot{s} = as$. We will then be interested in transforming the equation from $U(s, r, t)$ to $V(\xi, r, t)$. Using the chain rule

$$\begin{aligned} \frac{\partial U}{\partial t} =& \frac{\partial x^j}{\partial t} \partial_j V = \partial_t V - a\xi \partial_\xi V \\ \frac{\partial U}{\partial s} =& e^{-at} \frac{\partial V}{\partial \xi} \\ \frac{\partial^2 U}{\partial s^2} =& e^{-2at} \frac{\partial^2 V}{\partial \xi^2} \end{aligned} \tag{1.8}$$

So Equation (1.1) becomes

$$\frac{\partial V}{\partial t} = \frac{D}{h_s h_r} \left(e^{-2at} \partial_\xi \left(\frac{h_r}{h_s} \partial_\xi V \right) + \partial_r \left(\frac{h_s}{h_r} \partial_r V \right) \right) + p - gV . \tag{1.9}$$

2 1D

In 1D we have

$$\frac{\partial V}{\partial t} = \frac{D}{h^2(\xi)} e^{-2at} \partial_\xi^2 V + p - gV \,. \tag{2.1}$$

If we assume that $h(\xi)$ takes the form $h(\xi) = s = \xi e^{at}$ then we have

$$\frac{\partial V}{\partial t} = \frac{D}{\xi^2} e^{-4at} \partial_\xi^2 V + p - gV \,. \tag{2.2}$$

Looking at the homogeneous part and assuming the $V(\xi, t)$ is separable we can write $V(\xi, t) = \Xi(\xi) T(t)$ and find

$$e^{4at} \Big(\frac{\partial_t T}{T} + g \Big) = \frac{D}{\xi^2} \frac{\partial_\xi^2 \Xi}{\Xi} = \lambda \,, \tag{2.3}$$

where λ is some constant. The $T(t)$ part becomes

$$\begin{aligned} \int_{T_0}^{T} \frac{dT}{T} &= \int_{t_0}^{t} dt \, (\lambda e^{-4at} - g) \\ \ln \frac{T}{T_0} &= -\frac{\lambda}{4a} \big(e^{-4at} - e^{-4at_0} \big) - g(t - t_0) \\ T(t) &= T_0 e^{-\lambda \phi(t) - g(t - t_0)} \qquad ; \; \phi(t) := \frac{e^{-4at_0} - e^{-4at}}{4a} \,. \end{aligned} \tag{2.4}$$

Then for $\Xi(\xi)$ we have

$$\partial_\xi^2 \Xi = \frac{\lambda}{D} \xi^2 \Xi \,, \tag{2.5}$$

which is solvable in terms of the parabolic cylinder function $D_v(z)$ as

$$\Xi(\xi) = c_1 D_{-\frac{1}{2}} \left(x\sqrt{2} \sqrt[4]{\frac{\lambda}{D}} \right) + c_2 D_{-\frac{1}{2}} \left(ix\sqrt{2} \sqrt[4]{\frac{\lambda}{D}} \right) . \tag{2.6}$$

Combining $\Xi(\xi)$ and $T(t)$ with the trivally obtained particular solution $V_p(\xi, t) = \frac{p}{g}$ we obtain

$$V(\xi, t) = \left(c_1 D_{-\frac{1}{2}} \left(x\sqrt{2} \sqrt[4]{\frac{\lambda}{D}} \right) + c_2 D_{-\frac{1}{2}} \left(ix\sqrt{2} \sqrt[4]{\frac{\lambda}{D}} \right) \right) e^{-\lambda \phi(t) - g(t - t_0)} + \frac{p}{g} \,, \tag{2.7}$$

where c_1 and c_2 have been redefined to absorb the factor of T_0.

3 2D

3.1 Constant Metric

Suppose that h_i are constants. The transformed expression Equation (1.9) becomes

$$\frac{\partial V}{\partial t} = D \left(\frac{1}{h_s^2} e^{-2at} \partial_\xi^2 V + \frac{1}{h_r^2} \partial_r^2 V \right) + p - gV \,. \tag{3.1}$$

This can be solved analytically using Fourier transforms and working in the Fourier space spanned by $\mathbf{k} = (k_\xi, k_r)^T$. We will use the convention that the Fourier transforms of the function between the two spaces are

$$\begin{aligned}\tilde{V}(\mathbf{k},t) &= \int_{-\infty}^{\infty} d\xi \int_{-\infty}^{\infty} dr\, V(\xi,r,t) e^{-i(\mathbf{k}_\xi \xi + \mathbf{k}_\mathbf{r} r)}\,, \\ V(\mathbf{k},t) &= \iint_{\mathbb{R}^2} d\!\!{}^-{}^2\mathbf{k}\, \tilde{V}(\mathbf{k},t) e^{i(\mathbf{k}_\xi \xi + \mathbf{k}_\mathbf{r} r)}\,.\end{aligned} \tag{3.2}$$

Moving Equation (3.1) to Fourier space and examining the homogeneous part ($p = 0$) we have

$$\partial_t \tilde{V} = -\Big(\frac{D}{h_s^2} e^{-2at} k_\xi^2 + \frac{D}{h_r^2} k_r^2 + g\Big)\tilde{V}\,. \tag{3.3}$$

Integrating the homogeneous equation

$$\begin{aligned}\int_{\tilde{V}_0}^{\tilde{V}} \frac{d\tilde{V}}{\tilde{V}} &= -\int_{t_0}^{t} dt\,\Big(\frac{D}{h_s^2} e^{-2at} k_\xi^2 + \frac{D}{h_r^2} k_r^2 + g\Big) \\ \ln\Big(\frac{\tilde{V}}{\tilde{V}_0}\Big) &= -\frac{D}{h_s^2} k_\xi^2 \phi(t) - \Big(\frac{D}{h_r^2} k_r^2 + g\Big)(t - t_0) \qquad ;\ \phi(t) := \frac{e^{-2at_0} - e^{-2at}}{2a} \\ \tilde{V}_c(\mathbf{k},t) &= \tilde{V}_0(\mathbf{k},0) \exp\Big(-\frac{D}{h_s^2} k_\xi^2 \phi(t) - \Big(\frac{D}{h_r^2} k_r^2 + g\Big)(t - t_0)\Big)\,.\end{aligned} \tag{3.4}$$

When also including the inhomogeneous source Equation (3.1) in Fourier space becomes

$$\partial_t \tilde{V} = -\Big(\frac{D}{h_s^2} e^{-2at} k_\xi^2 + \frac{D}{h_r^2} k_r^2 + g\Big)\tilde{V} + p\delta\!\!\!{}^-{}^2(\mathbf{k})\,, \tag{3.5}$$

which using the complementary function results in the integrating factor

$$\begin{aligned}\tilde{V}(\mathbf{k},t) &= \tilde{V}_c(\mathbf{k},t) + p\delta\!\!\!{}^-{}^2(\mathbf{k}) \int_{t_0}^{t} d\tilde{t}\, e^{-g(\tilde{t} - t_0)} \\ \tilde{V}(\mathbf{k},t) &= \tilde{V}_0(\mathbf{k},0) \exp\Big(-\frac{D}{h_s^2} k_\xi^2 \phi(t) - \Big(\frac{D}{h_r^2} k_r^2 + g\Big)(t - t_0)\Big) + \frac{p}{g}\delta\!\!\!{}^-{}^2(\mathbf{k})\big(1 - e^{-g(t-t_0)}\big)\,,\end{aligned} \tag{3.6}$$

having already used $\mathbf{k} = 0$ in the second term.

Suppose we have a Gaussian packet as our initial condition

$$V(\xi, r, 0) = V_0 \exp\Big(-\frac{\xi^2}{4\sigma_\xi^2} - \frac{r^2}{4\sigma_r^2}\Big)\,, \tag{3.7}$$

which in Fourier space is

$$\tilde{V}(\mathbf{k},0) = V_0 \int_{-\infty}^{\infty} d\xi \int_{-\infty}^{\infty} dr\, \exp\Big(-\frac{\xi^2}{4\sigma_\xi^2} - ik_\xi \xi\Big) \exp\Big(-\frac{r^2}{4\sigma_r^2} - ik_r r\Big)\,, \tag{3.8}$$

then using the Gaussian integral

$$\int_{-\infty}^{\infty} dx\ \exp(-ax^2+bx) = e^{\frac{b^2}{4a}}\sqrt{\frac{\pi}{a}} \tag{3.9}$$

this initial condition in Fourier space becomes

$$\tilde{V}(\mathbf{k},0) = V_0 e^{-\sigma_\xi^2 k_\xi^2} e^{-\sigma_r^2 k_r^2}\,. \tag{3.10}$$

Combining this with the general solution in Equation (3.6) (and only focusing on the complementary solution for convenience) we obtain

$$\tilde{V}_c(\mathbf{k},t) = V_0 e^{-g(t-t_0)} \exp\left(-k_\xi^2\Big(\frac{D}{h_s^2}\phi(t)+\sigma_\xi^2\Big)\right)\exp\left(-k_r^2\Big(\frac{D}{h_r^2}(t-t_0)+\sigma_r^2\Big)\right). \tag{3.11}$$

To move back to position space we use the Fourier transform in Equation (3.2) and the Gaussian integral to obtain

$$\begin{aligned} V(\xi,r,t) =& V_0\tau^{-2}e^{-g(t-t_0)}\int_{-\infty}^{\infty} dk_\xi\ \exp\left(-k_\xi^2\Big(\frac{D}{h_s^2}\phi(t)+\sigma_\xi^2\Big)+ik_\xi\xi\right) \\ &\cdot\int_{-\infty}^{\infty} dk_r\ \exp\left(-k_r^2\Big(\frac{D}{h_r^2}(t-t_0)+\sigma_r^2\Big)+ik_r r\right) \\ &+\frac{p}{g}\iint_{\mathbb{R}^2} đ^2\mathbf{k}\,\delta̸^2(\mathbf{k})\big(1-e^{-g(t-t_0)}\big) \\ =& \frac{V_0 e^{-g(t-t_0)}}{2\tau\sqrt{\Big(\frac{D}{h_s^2}\phi(t)+\sigma_\xi^2\Big)\Big(\frac{D}{h_r^2}(t-t_0)+\sigma_r^2\Big)}} \\ &\cdot\exp\left(-\frac{\xi^2}{4\Big(\frac{D}{h_s^2}\phi(t)+\sigma_\xi^2\Big)}\right)\exp\left(-\frac{r^2}{4\Big(\frac{D}{h_r^2}(t-t_0)+\sigma_r^2\Big)}\right)+\frac{p}{g}(1-e^{-g(t-t_0)})\,. \end{aligned} \tag{3.12}$$

3.2 Small a

For the parabolic map Equation (1.9) becomes

$$\partial_t V = \frac{D}{\rho^2}\Big(e^{-2at}\partial_\xi^2 V + \partial_r^2 V\Big)\,, \tag{3.13}$$

where $\rho := \sqrt{s^2+r^2} = \sqrt{\xi^2 e^{2at}+r^2}$. To use perturbation theory we say that $a \ll 1$ and $V(\xi,r,t) = V_0(\xi,r,t)+aV_1(\xi,r,t)$. Expanding in a first of all we obtain

$$\begin{gathered} \partial_t V = \frac{D}{\xi^2+r^2+2at\xi^2}\Big((1-2at)\partial_\xi^2 V+\partial_r^2 V\Big)+p-gV \\ \Big((\xi^2+r^2)(\partial_t+g)-D(\partial_\xi^2+\partial_r^2)+a(2Dt\partial_\xi^2+\partial_t+g)\Big)V = (\xi^2+r^2+2at\xi^2)p\,. \end{gathered} \tag{3.14}$$

3.2.1 $\mathcal{O}(a^0)$

At $\mathcal{O}(a^0)$ we are examining a system without growth so both the ξ and r directions are treated on equal footing, that is we have an O(2) symmetry group. The resulting expression is

$$\Big((\xi^2 + r^2)(\partial_t + g) - D(\partial_\xi^2 + \partial_r^2)\Big)V_0 = (\xi^2 + r^2)p\,. \tag{3.15}$$

Due to the symmetry now present it is natural to use polar coordinates (λ, θ) with $\lambda^2 \equiv \xi^2 + r^2$. Using the Cartesian Laplacian in polar coordinates

$$\partial_\xi^2 + \partial_r^2 = \partial_\lambda^2 + \frac{1}{\lambda}\partial_\lambda + \frac{1}{\lambda^2}\partial_\theta^2 \tag{3.16}$$

we arrive at

$$\Big(\lambda^2(\partial_t + g) - D(\partial_\lambda^2 + \frac{1}{\lambda}\partial_\lambda + \frac{1}{\lambda^2}\partial_\theta^2)\Big)V_0 = \lambda^2 p\,. \tag{3.17}$$

Then focusing on the homogeneous LHS and using the separation of variables $V_0(\lambda, \theta, t) = T(t)\Lambda(\lambda)\Theta(\theta)$ we obtain

$$\lambda^2\frac{\partial_t T}{T} + \lambda^2 g - D\bigg(\frac{\partial_\lambda^2\Lambda}{\Lambda} + \frac{\partial_\lambda\Lambda}{\lambda\Lambda} + \frac{\partial_\theta^2\Theta}{\lambda^2\Theta}\bigg) = 0\,. \tag{3.18}$$

There is only one term that depends on Θ and so all the θ dependence must be a constant. We choose

$$\partial_\theta^2\Theta = -m^2\Theta \tag{3.19}$$

where m is some constant. This possesses oscillatory solutions of the form $\Theta(\theta) = A_\pm e^{\pm im\theta}$. One can do the same with the time dependence, although in this case we can include the degradation term to and select

$$\frac{\partial_t T}{T} + g = -\mu\,, \tag{3.20}$$

for some arbitrary constant μ. This can be integrated to find

$$T(t) = Be^{-(g+\mu)t}\,. \tag{3.21}$$

Substituting the constants into Equation (3.18) we obtain

$$\lambda^2\frac{\mu}{D} + \frac{\partial_\lambda^2\Lambda}{\Lambda} + \frac{\partial_\lambda\Lambda}{\lambda\Lambda} - \frac{m^2}{\lambda^2} = 0\,, \tag{3.22}$$

which has solutions in terms of Bessel functions of the first kind $J_n(z)$ and gamma functions $\Gamma(x)$ as

$$\Lambda(\lambda) = c_- J_{-\frac{m}{2}}\bigg(\frac{\lambda^2}{2}\sqrt{\frac{\mu}{D}}\bigg)\Gamma\Big(1 - \frac{m}{2}\Big) + c_+ J_{\frac{m}{2}}\bigg(\frac{\lambda^2}{2}\sqrt{\frac{\mu}{D}}\bigg)\Gamma\Big(1 + \frac{m}{2}\Big)\,. \tag{3.23}$$

Combining everything we obtain

$$\begin{aligned} V_0^c(\lambda, \theta, t) =& e^{-(g+\mu)t}(e^{im\theta} + Ae^{-im\theta}) \\ &\cdot \bigg(c_- J_{-\frac{m}{2}}\bigg(\frac{\lambda^2}{2}\sqrt{\frac{\mu}{D}}\bigg)\Gamma\Big(1 - \frac{m}{2}\Big) + c_+ J_{\frac{m}{2}}\bigg(\frac{\lambda^2}{2}\sqrt{\frac{\mu}{D}}\bigg)\Gamma\Big(1 + \frac{m}{2}\Big)\bigg) \end{aligned} \tag{3.24}$$

for the complementary solution, having rescaled constants set by boundary conditions.

Including the inhomogeneous term $\lambda^2 p$ we form the ansatz for the particular solution $V_0^p = \alpha\lambda^2 + \beta\lambda + \gamma$. Substituting this into Equation (3.17) we obtain

$$\lambda^2 g(\alpha\lambda^2 + \beta\lambda + \gamma) - D\Big(2\alpha + 2\alpha + \frac{\beta}{\lambda}\Big) = \lambda^2 p\,, \tag{3.25}$$

which implies $\alpha = 0$, $\beta = 0$, $\gamma = \frac{p}{g}$. Therefore the full $\mathcal{O}(a^0)$ solution is

$$\begin{aligned} V_0(\lambda,\theta,t) =& e^{-(g+\mu)t}(e^{im\theta} + Ae^{-im\theta}) \\ &\cdot \Big(c_- J_{-\frac{m}{2}}\Big(\frac{\lambda^2}{2}\sqrt{\frac{\mu}{D}}\Big)\Gamma\Big(1-\frac{m}{2}\Big) + c_+ J_{\frac{m}{2}}\Big(\frac{\lambda^2}{2}\sqrt{\frac{\mu}{D}}\Big)\Gamma\Big(1+\frac{m}{2}\Big)\Big) + \frac{p}{g}\,. \end{aligned} \tag{3.26}$$

3.2.2 $\mathcal{O}(a^1)$

If we say that the $\mathcal{O}(a^0)$ homogeneous dynamics are encapsulated by $\mathcal{L} = (\xi^2 + r^2)(\partial_t + g) - D(\partial_\xi^2 + \partial_r^2)$ then the $\mathcal{O}(a^1)$ expression is

$$\mathcal{L}V_1 = 2t\xi^2 p - (2Dt\partial_\xi^2 + \partial_t + g)V_0\,, \tag{3.27}$$

where the RHS inhomogeneous part is responsible for the breaking of the O(2) symmetry. Clearly, $\partial_t V_0 = -(g+\mu)V_0^c$. Furthermore, using the Jacobian from Cartesian to Polar coordinates

$$J_{\xi r}^{\lambda\theta} = \begin{pmatrix} \frac{\xi}{\lambda} & \frac{r}{\lambda} \\ -\frac{r}{\lambda^2} & \frac{\xi}{\lambda^2} \end{pmatrix} \tag{3.28}$$

and the fact that the derivative of the Bessel function of the first kind with respect to its argument can be expressed as

$$\partial_z J_n(z) = \frac{1}{2}(J_{n-1}(z) - J_{n+1}(z)) \tag{3.29}$$

we can find

$$\begin{aligned} \partial_\xi e^{im\theta} =& \frac{\partial\theta}{\partial\xi} ime^{im\theta} = -\frac{imr}{\lambda^2}e^{im\theta} \\ \partial_\xi^2 e^{im\theta} =& -\frac{m^2r^2}{\lambda^4}e^{im\theta} + 2imr\lambda^{-3}\frac{\partial\lambda}{\partial\xi}e^{im\theta} = \frac{2imr\xi - m^2r^2}{\lambda^4}e^{im\theta} \\ \partial_\xi J_n\big(L\lambda^2\big) =& \big(J_{n-1}\big(L\lambda^2\big) - J_{n+1}\big(L\lambda^2\big)\big)\lambda L\frac{\partial\lambda}{\partial\xi} \\ =& \big(J_{n-1}\big(L\lambda^2\big) - J_{n+1}\big(L\lambda^2\big)\big)\xi L \\ \partial_\xi^2 J_n\big(L\lambda^2\big) =& \Big(\big(J_{n-2}\big(L\lambda^2\big) - 2J_n\big(L\lambda^2\big)\big) + J_{n+2}\big(L\lambda^2\big)\Big)\xi^2 L^2 \\ &+ \big(J_{n-1}\big(L\lambda^2\big) - J_{n+1}\big(L\lambda^2\big)\big)L\,, \end{aligned} \tag{3.30}$$

where $L := \frac{1}{2}\sqrt{\frac{\mu}{D}}$. So we then have

$$\begin{aligned}
e^{(g+\mu)t}\partial_\xi^2 V_0 =& \lambda^{-4}\big((2imr\xi - m^2r^2)e^{im\theta} + A(-2imr\xi - m^2r^2)e^{-im\theta}\big) \\
&\cdot \left(c_- J_{-\frac{m}{2}}(L\lambda^2)\Gamma\Big(1-\frac{m}{2}\Big) + c_+ J_{\frac{m}{2}}(L\lambda^2)\Gamma\Big(1+\frac{m}{2}\Big)\right) \\
&+ (e^{im\theta} + Ae^{-im\theta})\Bigg(c_-\bigg[\Big(\big(J_{-\frac{m}{2}-2}\big(L\lambda^2\big) - 2J_{-\frac{m}{2}}\big(L\lambda^2\big)\big) + J_{-\frac{m}{2}+2}\big(L\lambda^2\big)\Big)\xi^2L^2 \\
&+ \big(J_{-\frac{m}{2}-1}\big(L\lambda^2\big) - J_{-\frac{m}{2}+1}\big(L\lambda^2\big)\big)L\bigg]\Gamma\Big(1-\frac{m}{2}\Big) \\
&+ c_+\bigg[\Big(\big(J_{\frac{m}{2}-2}\big(L\lambda^2\big) - 2J_{\frac{m}{2}}\big(L\lambda^2\big)\big) + J_{\frac{m}{2}+2}\big(L\lambda^2\big)\Big)\xi^2L^2 \\
&+ \big(J_{\frac{m}{2}-1}\big(L\lambda^2\big) - J_{\frac{m}{2}+1}\big(L\lambda^2\big)\big)L\bigg]\Gamma\Big(1+\frac{m}{2}\Big)\Bigg).
\end{aligned} \tag{3.31}$$

The full expression now takes the form

$$\mathcal{L}V_1 = 2t\xi^2 p + \mu V_0^c - p - 2Dt\partial_\xi^2 V_0\,. \tag{3.32}$$