

Phyllotaxis in a Keller-Segel model

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Plants often exhibit regular arrangements of seeds or leaves, known as phyllotaxis, and can famously exhibit Fibonacci spirals, as in sunflower heads or on pine cones. While there are many models which can reproduce a spiral formation, the actual mechanism of arrangement remains unclear. Here, we test a more general class of model, based on the Keller-Segel model, in which a diffusing chemical signal produces its own transport signal and can form local instabilities. By modeling the plant as a disk with a signal source at the center and radial growth, we show that we can reproduce both Fibonacci spirals and alternating patterns, depending on a balance between growth and source. Finally, using linear stability analysis, we show how the pattern arises due to a balance between the growth of instabilities and the growth of the plant. Overall, this work demonstrates how the Keller-Segel model can reproduce a wide range of observed patterns, and may act as a phenomenological description of a number of processes in plants.

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I. INTRODUCTION

The arrangement of leaves and branches in plants, known as phyllotaxis, can result in a variety of patterns [1,2], the most famous of which are the Fibonacci spirals. The elements are often arranged with i parallel spirals going one way and j spirals going the other, where (i, j) are the parastichy numbers. Often these are found to be a pair of Fibonacci numbers, such as 34 spirals one way and 55 the other on sunflower heads, or 8 and 13 for pine cones. In this case, the divergence ϕ , being the difference in angle between an element and the next furthest element from the center, is approximately equal to the golden angle $\Phi = 180(3 - \sqrt{5})^\circ \approx 137.5^\circ$. Alternatively, leaves may be whorled, where several leaves form at the same level along the stem and can form alternating pairs, as in the basil plant, or in groups of three leaves separated by 120° . Three main theoretical approaches have been used to model the phenomenon, geometric, mechanical, and biochemical, though the exact way leaves are arranged remains unclear [2,3].

The earliest approaches to modeling phyllotaxis consisted of geometric studies following Hofmeister's model, which suggest that new leaves form at the least crowded part of the stem [4]. Airy tested this theory by gluing spheres onto a stretched elastic band, which, when allowed to relax, packed into a cylindrical Fibonacci spiral [5]. Van Iterson developed this idea further by considering the packing of hard disks

around a cylinder and showed that it has an optimal packing that forms a regular lattice, with the angle between successive disks being determined by the ratio of disk and cylinder sizes [6].

Later models considered self-organization due to mechanical interactions between new leaves. Instead of using hard disks, Douady and Couder [7] considered the interaction of repulsive particles. In their experiments, ferrofluid droplets were added to the center of a disk at regular intervals, and were radially advected from the center. Due to the repulsive interactions between nearby droplets, they found that the divergence angle between successive drops was 180° when the advection speed was high and converged to the golden angle as the advection speed was decreased. Theoretically, it was shown that any repulsive particles arranged on a cylinder should form Fibonacci spirals [8], as was demonstrated by the construction of a "mechanical cactus" consisting of magnetic rods attached to a column that could freely rotate [9]. Alternatively, one could consider mechanical interactions from growth of the plant. Since the primordia grow faster than the surrounding tissue, the surface may buckle [10] and can theoretically give Fibonacci spirals through mechanics alone [11].

Recent models have been more biologically informed, by considering the role of the plant hormone auxin in specifying the location of new leaves [12–14]. Auxin undergoes active polar transport by the PIN1 proteins, with regions of high auxin concentration specifying the location of the primordia which grow into the new leaves or branches [15]. By including positive feedback between auxin and PIN1 polarization [16,17] either directly [18], or indirectly through growth-driven stress [19,20] or some biochemical signal such as calcium ions [21], models can form stable phyllotactic patterns where PIN1 polarizes towards regions of high auxin concentration. However, the exact mechanism of alignment

remains unclear, in particular since the precursors of primordia appear much earlier than the differential growth becomes apparent.

Here, we consider a simplified description of morphogen-driven self-organization, in the form of the Keller-Segel model [22–24]. Originally describing chemotaxis in bacteria, we can reinterpret the model in terms of cell signaling with two counterdiffusing signals. One signal represents auxin, which produces a transport signal such as mechanical stress or a chemical signal. Auxin is then transported up the gradient of the transport signal in a similar manner to PIN1 transport. Thus, we agnostically replace polarization with local secretion and diffusion. Since it is long range and locally produced, it is the simplest model of the types considering auxin-PIN1 or stress-PIN1 alignment [18,20]. Using this model, we are able to obtain a range of phyllotactic patterns including Fibonacci spirals or whorls, with the type determined by both growth speed and rate of auxin production. Using a simple linear stability analysis, we can understand how growth and auxin source work together to determine the pattern.

II. MODELING PLANT MORPHOGENESIS

The classical Keller-Segel model for chemotaxis [22] considers the concentration of bacteria which produces its own chemoattractant. The cells execute a run-and-tumble style random walk, with a bias towards regions of higher chemoattractant concentration. In the continuum limit, we write a as the concentration of bacteria, and c as the concentration of chemoattractant, which obey

$$\dot{a} = D_a \nabla^2 a - \alpha \nabla \cdot (a \nabla c), \quad (1)$$

$$\dot{c} = D_c \nabla^2 c + \beta a - \gamma c, \quad (2)$$

such that a is conserved while c is produced by a and decays over time. The bacteria produces the chemoattractant with rate β , which in turn degrades at rate γ . Both bacteria and the chemoattractant diffuse, with coefficients D_a and D_c , respectively. However, the bacteria also swims up the concentration gradient of the chemoattractant which with speed α . At high enough concentrations of bacteria, the positive feedback can outcompete the diffusion and lead to instabilities which grow over time, concentrating the bacteria into local maxima which even diverges in finite time [23].

In this work, we reinterpret the Keller-Segel model in terms of auxin a and a transport signal c , which could represent mechanical stress [20] or a biochemical signal [21] [Fig. 1(a)]. Auxin diffuses and is actively transported up the gradient of the transport signal, representing PIN1 polarization. We use a saturating rate of transport, with saturation parameter c_0 , to prevent singularities in the Keller-Segel model [23] and more accurately model real systems which have limited transport rates. We work in dimensionless units by rescaling time by the degradation rate $1/\gamma$, and space by the diffusion rate $\gamma \sqrt{D_u}$. To model plant growth, we include a source of a in the center, $S(r, t)$, and a radial velocity field representing plant growth, $\mathbf{v}$,

$$\dot{a} + \nabla \cdot (a \mathbf{v}) = \nabla^2 a - \alpha \nabla \cdot \left(a \nabla \frac{c}{c + c_0} \right) + S, \quad (3)$$

$$\dot{c} + \nabla \cdot (c \mathbf{v}) = D \nabla^2 c + \beta a - c, \quad (4)$$

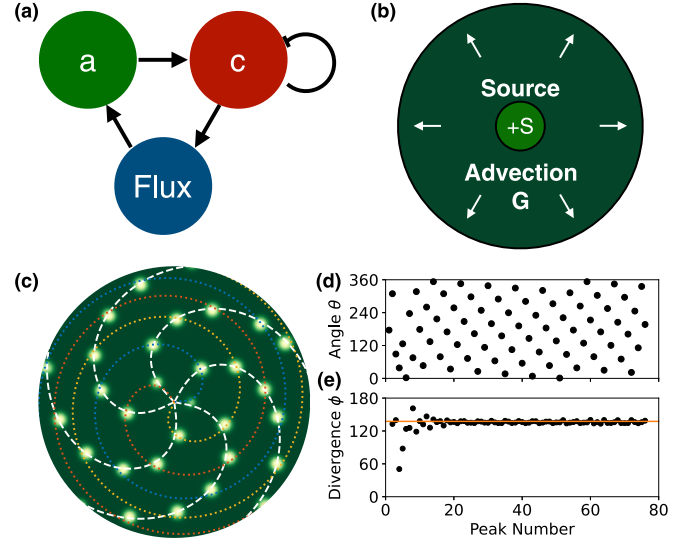


FIG. 1. A Keller-Segel model of plant morphogenesis produces spirals. (a) Schematic of the saturating Keller-Segel model. (b) Schematic of the system geometry. A source of auxin is added within the central region with a flux of S . A radial velocity advects material outward, controlled by the growth parameter G . (c) Simulation output with $S = 1$ and $G = 1.2$, with parastichy numbers (3, 5). The white lines show the five major spirals while the colored lines show the three minor spirals. (d) Polar angle of each auxin peak against peak number, which counts the order in which they appeared. The first peaks appear in disorganized manner, but eventually are arranged with a regular spacing between successive peaks. (e) Divergence angle between successive peaks. The golden line indicates the golden angle Φ .

where α controls the transport rate of auxin, S is a source of auxin which potentially varies in space and time, D is the diffusion coefficient for the transport signal c , and β is the rate of the transport signal production by auxin. While this represents a phenomenological model, we will call the field a auxin, since peaks of auxin indicate the location for new primordia to grow, and will call c the transport signal.

As in the Keller-Segel model for chemotaxis, positive feedback between auxin and its the transport signal through attractive fluxes can lead to pattern formation. In comparison to the ferromagnetic droplets used by Douady and Couder [7], auxin peaks are repulsive at long range, but attractive at short ranges. Since peaks produce their own diffusing chemoattractant, when two peaks are close the chemoattractant fields produced by each peak overlap and add together to create a gradient toward one another and causing peaks to merge. An estimation for this distance is given in the Appendix.

We simulate the formation of patterns on a circular disk with radius $r_d = 50$, and initially zero a and c concentration. We use an outlet boundary condition, allowing auxin and the chemoattractant to be advected off the boundary due to growth but preventing diffusion or transport flux across it. Within a central region of radius r_s , we add a at rate S per unit time and area. The source rate S starts at zero flux but increases over time to its maximum rate S_0 , which helps patterns to form

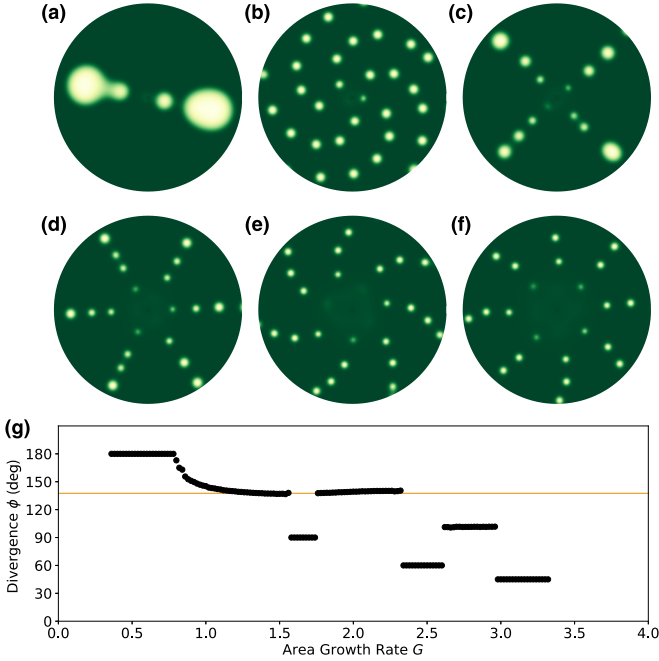


FIG. 2. The pattern depends on the growth rate. (a) A (1, 2) pattern, $S_0 = 1$, $G = 0.5$. (b) A Fibonacci spiral (3, 5) pattern, $S_0 = 1$, $G = 1.2$. (c) An alternating (2, 4) pattern, $S_0 = 1$, $G = 1.6$. (d) A (3, 6) pattern, $S_0 = 1$, $G = 2.5$. (e) A (4, 7) pattern, $S_0 = 1$, $G = 2.9$. (f) A (4, 8) pattern, $S_0 = 1$, $G = 3.1$. (g) Divergence against area growth rate G . The golden line shows the golden angle, $\Phi \approx 137^\circ$.

more stably:

$$S(r, t) = \begin{cases} S_0(1 - e^{-t/\tau}), & \text{if } r < r_s, \\ 0, & \text{otherwise.} \end{cases} \quad (5)$$

Material is then advected away from the center with velocity

$$\mathbf{v} = \frac{G}{r} \hat{\mathbf{r}} \quad (6)$$

representing growth of the plant, where G is the area growth rate. The simulation is run until $t = 2000$, by which point a stable pattern has emerged, integrating the equations numerically using the finite-volume package *fipy* [25].

Using the parameters $S_0 = 1.0$ and $G = 1.2$, we integrate the equations over time and observe the evolution of the pattern. The source of a increases the concentration in the system. At high enough concentration the system breaks symmetry and splits into several high concentration peaks which are advected away radially. New peaks are added sequentially between the gaps, eventually being added at a regular rate with a stable angle between successive peaks, or divergence. The resulting pattern is a Fibonacci spiral, with parastichy numbers (3, 5) as we see five major spirals going one way and three minor spirals the other [Fig. 1(c)]. We can measure the divergence by first tracking the angle of each peak when they are produced [Fig. 1(d)] and taking the difference in angles between successive peaks [Fig. 1(e)]. For these parameters, the mean divergence is $\bar{\phi} = 136^\circ$, close to the golden angle, $\Phi = 180(3 - \sqrt{5}) \approx 137^\circ$.

Different patterns are observed depending on the value of the growth rate, G [Fig. 2(g)]. For very low growth velocity,

TABLE I. Default simulation parameters.

Parameter	Symbol	Default value
Area growth rate	G	1
Auxin transport rate	α	10
Saturating c	c_0	5
c Production rate	β	2
Auxin flux rate	S_0	1
Source timescale	τ	100
Source radius	r_s	2
Disk radius	r_d	50

the auxin from the source is able to attract auxin faster than advection, trapping auxin in a large peak around the center of the disk. The default parameters used throughout the simulations are listed in Table I. Only the growth rate G and auxin flux rate S_0 are varied. For low growth rate, around $G = 0.5$, auxin can escape the center and new peaks are added with a 180° divergence, giving a (1, 2) pattern [Fig. 2(a)]. Note that since peaks are attractive and the radial velocity decreases with distance, peaks eventually merge. While this is a problem in the model, within the plant the pattern is set within only a small distance from the center, after which peaks would stabilize and grow into primordia. As the velocity increases further to around $G = 0.8$, the peaks are added with a slight twist [Fig. 2(b)]. Further increases to the growth rate decrease the divergence, which stabilizes around the golden angle Fibonacci spiral (3, 5) patterns [Fig. 2(c)]. At around $G = 1.5$ the Fibonacci spirals again become unstable, and instead we find alternating (2, 4) patterns, with pairs of peaks added at a time with a 90° divergence [Fig. 2(d)], as seen in plants such as basil. At around $G = 1.7$ Fibonacci spirals become stable. Continuing this trend, as the growth velocity keeps increasing the patterns successively increase in parastichy number, seeing (3, 6) patterns around $G = 2.4$, (4, 7) patterns around $G = 2.6$, and (4, 8) patterns around $G = 3.0$, beyond which the auxin is too dilute to form patterns and we obtain a uniform state.

Similarly, the rate of auxin addition at the center, S_0 , can be varied. We find that increasing the auxin flux has the opposite effect to increasing the growth rate, with increases in S_0 leading to decreases in the parastichy number. For example, starting from $S_0 = 1$ and $G = 2$, the system has a Fibonacci pattern. Increasing S_0 eventually changes the pattern to an alternating (2, 4), while decreasing it can give (3, 6) and higher patterns before the concentration is too low for patterns to form. Such a trend exists for all values for S_0 and G [Figs. 3(a) and 3(b)], thus we next develop a simple model that predicts which patterns are expected using linear stability analysis.

To understand these results, we construct a dimensionless number using the growth rate G and the dominant wave number $k(G, S_0)$, and its corresponding growth rate $\lambda(G, S_0)$ from linear stability analysis (see the Appendix), of the form

$$\text{Ro} = \frac{Gk^2}{\lambda}, \quad (7)$$

which we call the Rosette number, as it aims to predict the arrangement of the peaks or leaves around the disk. Since λ

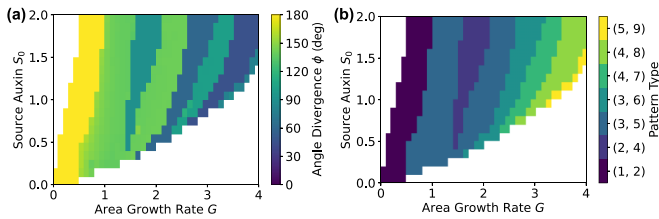


FIG. 3. Auxin flux and area growth rate control the pattern. (a) Angle divergence ϕ , and (b) pattern type, against source auxin S_0 and area growth rate G . The unshaded regions indicate regions where patterns do not form, in the bottom right, or auxin cannot escape the center, in the top left.

is the growth rate of the instability and has units of inverse dimensionless time, $1/\lambda$ scales with the period between successive peaks, thus G/λ represents the amount of area added to the shoot as the peaks form. Since k is the wave number with units of inverse dimensionless length, $1/k$ scales with the distance between peaks, and so $1/k^2$ the area closest to each peak. Thus the Rosette number can be thought of as representing the relative spacing of the peaks, equal to the ideal area between successive peaks over the area added to the shoot from growth. When Ro is high, then the peaks are relatively sparse, and we might expect alternating patterns, as new peaks only interact with the last added peak, as in the case of high growth rates in the Douady and Couder experiments [7]. When Ro is low, then the peaks are relatively dense and we would expect new peaks to interact with many of the existing peaks, and so form complex spirals.

Calculating the Rosette number for each pair of auxin flux S_0 and area growth rate G , we observe a similar trend to the divergence, where increasing the area growth rate increases the Rosette number, while increasing the source decreases it [Fig. 4(a)]. Notably, lines of constant Rosette number follow a similar upwards curve to the boundaries of different pattern types [Fig. 4(b)]. Additionally, there are two regions which are stable against pattern formation, and so have an undefined Rosette number. As the area growth rate G increases, the Rosette number increases and eventually diverges, suggesting that the pattern type would continue to increase up until the border of stability. From simulations, we observe that the distance at which peaks form increases with G , and so larger and larger simulation areas would be needed to capture this trend. In contrast, for a low G or high auxin source there

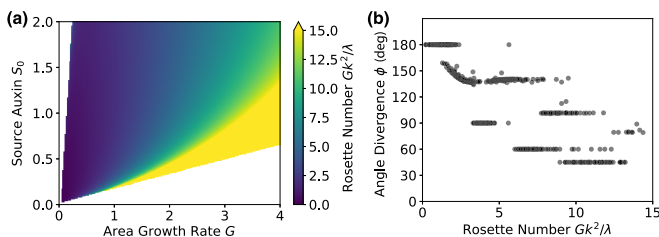


FIG. 4. Linear stability analysis can predict pattern type. (a) Rosette number $\frac{Gk^2}{\lambda}$ against auxin source and growth rates. (b) The divergence against the Rosette number, for all values of S_0 and G in Fig. 3. Points are transparent so darker regions show more overlapping points.

is also a region without pattern forming, since saturation of auxin transport eventually stabilizes when concentrations are very high.

Comparing our calculated Rosette number against the divergence, we observe a fairly strong dependence between the two [Fig. 4(b)]. Across all S_0 and G , increasing the Rosette number changes the divergence, and eventually the pattern type. While this is not a perfect fit, as the actual pattern observed does not fully depend on the Rosette number, such a simplified model considering only linear stability works remarkably well for most cases.

III. DISCUSSION

As the molecular mechanisms which control phyllotaxis remains unclear, we demonstrate how a more general class of model, the Keller-Segel model, can reproduce various patterns observed in nature. Similar to the PIN1 models of phyllotaxis [18–20], the Keller-Segel model is a self-organized patterning that has polarized transport of auxin, but the mechanism is through a signaling intermediate. There could be many mechanisms which produce this kind of instability leading to localized high concentrations of auxin, with mechanical interactions with polarization being one of many. Thus, this model is similar but more general in that it demonstrates that the instability leading to auxin aggregation does not require mechanical interactions. Expanding upon previous work, our model also demonstrates how Fibonacci patterns may spontaneously form, without needing a pattern preseeded on the boundary [20], and shows how other patterns may be obtained depending on the growth rate and source of auxin.

By modeling the shoot apical meristem as a disk with a source of auxin at the center and radial advection due to growth, we show how the observed pattern depends on both that growth rate and the source at the center. In addition to forming alternating patterns which then twist into Fibonacci spirals, as in the Douady and Couder experiments [7], this system can also form whorled patterns, where two or more or more peaks form at the same distance from the center. In contrast to previous mechanical and biochemical models by Newell and collaborators [17], our model spontaneously forms phyllotactic patterns from inside out, rather than initiating the system with a Fibonacci spiral on the outside to form a pattern outside in. Finally, we develop a simple value, the Rosette number, formed using linear stability analysis which can explain most of the patterns observed. This model is theoretical and uses an unidentified transport signal c , it acts to direct transport of auxin and could, for example, represent some hormone which directs PIN1 polarization.

One aspect of the model that is not investigated in detail here is the role of the growth profile and the geometry of the surface. Within our model we have modeled growth as occurring only at the center, which leads to zero dilution in the auxin profile. In reality, the plant cells will continue growing away from the center, as in the exponential growth rate used by Douady and Couder [7], which would dilute the auxin profile with distance. This would both change the growth rate of any instabilities and cause them to be potentially transient, meaning waves which do not grow fast enough are diluted and become stable, potentially limiting the range of pattern

types observed. Similarly, the geometry of the system can also control the dilution rate. Here, we have assumed a flat surface, which may be appropriate for a sunflower, but other plants such as tree branches or cacti may be curved at the tip and cylindrical around the stem, which would initially dilute any auxin before preserving concentrations around the stem. In this case, nonlinear effects would be important for maintaining the arrangement of primordia. Moreover, these would grow and potentially act as their own source of auxin, which may change the interaction strength with nearby peaks.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [26].

APPENDIX: LINEAR STABILITY ANALYSIS

We consider a low advection limit for simplicity, either due to low growth rate or being far from the source, and so neglect the growth rate term in the following analysis, aside from determining the initial concentration. At steady state, we have a constant flux

$$\nabla \cdot (av) = 0. \quad (\text{A1})$$

Solving for a we get

$$a(r) = \bar{a} = \frac{\pi r_s^2 S_0}{2\pi G}. \quad (\text{A2})$$

Since the disk has a uniform auxin concentration, and the advection conserves concentrations, we perform a linear stability analysis to a system of uniform auxin concentration a_0 and transport signal concentration βa_0 :

$$\dot{a} = \nabla^2 a - \alpha \nabla \cdot \left(a \nabla \frac{c}{c + c_0} \right), \quad (\text{A3})$$

$$\dot{c} = D \nabla^2 c + \beta a - c. \quad (\text{A4})$$

We apply a small perturbation about this such that $a = a_0 + \tilde{a}$ and $c = \beta a_0 + \tilde{c}$. These evolve, to leading order, as

$$\dot{\tilde{a}} = \nabla^2 \tilde{a} - \alpha \frac{a_0 c_0}{(\beta a_0 + c_0)^2} \nabla^2 \tilde{c} \quad (\text{A5})$$

and

$$\dot{\tilde{c}} = D \nabla^2 \tilde{c} + \beta \tilde{a} - \tilde{c}. \quad (\text{A6})$$

Working in Fourier space we have

$$\partial_t \hat{a} = -k^2 \hat{a} + k^2 \frac{\alpha a_0 c_0}{(\beta a_0 + c_0)^2} \hat{c}, \quad (\text{A7})$$

$$\partial_t \hat{c} = \beta \hat{a} - (Dk^2 + 1) \hat{c}. \quad (\text{A8})$$

This system of equations has eigenvalues

$$\lambda_{\pm} = -\frac{1}{2}[(1 + D)k^2 + 1] \pm \frac{1}{2}\sqrt{[(D + 1)k^2 + 1]^2 + 4k^2[\alpha' - (Dk^2 + 1)]}, \quad (\text{A9})$$

where $\alpha' = \frac{\alpha \beta a_0 c_0}{(\beta a_0 + c_0)^2}$ is the effective transport rate due to saturation. The eigenvalue for a given k will be positive when $\frac{\alpha \beta a_0 c_0}{(\beta a_0 + c_0)^2} > (Dk^2 + 1)$ and so we always have an instability when $\alpha \beta a_0 c_0 > (\beta a_0 + c_0)^2$. From this, one can find the fastest growing wave length, with growth rate λ^* and corresponding wave number k^* , which are found to be

$$\lambda^* = \frac{1}{(D - 1)^2} (\sqrt{\alpha' D} - \sqrt{\alpha' + D - 1})^2 \quad (\text{A10})$$

and

$$k^* = \sqrt{\frac{\sqrt{D(D + 1)^2(\alpha'^2 + a(D - 1))} + D(1 - D - 2\alpha')}{D(D - 1)^2}}. \quad (\text{A11})$$

Additionally, we can use the eigenvalues to estimate the distance at which peaks transition from being repulsive to attractive. Assuming that the system is unstable, then as the frequency increases the eigenvalue will transition from positive, meaning unstable and growing waves, to negative, meaning decaying waves. The eigenvalues are negative when

$$k^2 > \frac{\alpha' - 1}{D} \quad (\text{A12})$$

or when the distance satisfies

$$d < 2\pi \sqrt{\frac{D}{\alpha' - 1}}. \quad (\text{A13})$$

Intuitively this occurs because auxin is transported up the chemoattractant gradient. When two peaks are close enough their self-produced chemoattractant fields overlap enough to create a gradient towards the other.

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