Alan Turing's chemical theory of phyllotaxis

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Alan Turing's seminal 1952 work on morphogenesis [1] is widely known and recognised in the field of mathematical biology. Less known is his work on the problem of phyllotaxis, which was never published at his time but is included in Turing's collected works [2]. It consists on three parts: the first is a detailed mathematical description of the arrangements of leaves on the stem of plants; the second is an application of the reaction-diffusion equation to the problem, and the third part is a solution of these equation for the case of spherical symmetry. It is the purpose of this work to present Turing's results contained in the second part in a comprehensive and detailed way. This is motivated by the fact that these researches have remained obscure and ill-understood. In particular, we focus on the morphogen equations for an assembly of cells since this discrete case may be useful in many circumstances where the continuum limit is not adequate or applicable.

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1. Introduction

The aim of Turing's "The Chemical Basis of Morphogenesis" [1] (hereafter referred to as CBM) is to show that, by a combination of diffusion and chemical reactions, patterns can arise in an originally homogeneous tissue. This highly cited work became a master piece of the mathematical modeling in biology and the best known model to explain biological pattern formation [3].

Alan Turing was vividly interested in the phenomenon of Fibonacci phyllotaxis, and his work on this problem is less known since it remained unpublished for many years. After publishing the CBM, between 1952 and 1954, Turing wrote unpublished manuscripts and notes of his later research in his chemical theory of morphogenesis. These were studied by Turing's colleagues N.E. Hoskin and B. Richards [4], pieced together, and published under the title "Morphogen Theory of Phyllotaxis" (hereafter referred to as MTP) in 1992 Turing's collected works book [2].

Before describing MTP, we should add some words concerning phyllotaxis. The arrangement of plant organs, also called phyllotaxis, has fascinated scientists and naturalists for centuries. The study of phyllotaxis can be traced back to the 4th century B.C. in the ancient Greece, so it can be considered as the oldest branch of mathematical biology. Ancient naturalists as Theophrastus (370-285 B.C.) and Pliny (23-79 A.D.) recognized and reported distinct patterns of leaf arrangements and proposed them as a tool for plant classification. It was by the time of Leonardo Fibonacci of Pisa (1175-1240) that the relation between phyllotactic patterns, the Fibonacci sequence, and the golden mean was realized. A Fibonacci sequence $1, 1, 2, 3, 5, 8, 13, 21, \dots$ is obtained by the rule $F_{n+1} = F_n + F_{n-1}$, where $F_0 = F_1 = 1$ and the golden mean is defined by the limit

$$\tau = \lim_{n\to\infty} \frac{F_{n+1}}{F_n} = \left(1+\sqrt{5}\right)/2.$$

The golden angle φ is defined as $\varphi = 2\pi\tau$. There are many different types of plat organs arrangements, among which the spiral or helical pattern, as in sunflowers, is the most widespread and complex [5]. In this case families of spirals, called parastichies, are observed and counting spirals in each family results in numbers that follow a Fibonacci sequence (for a didactic description see Ref. 3). Evenmore, the divergence angle between two consecutive plant organs in a spiral is always approximately φ. The first formal study of leaf arrangement was made by Charles Bonnet (1720-1793), who was able to distinguish four different phyllotactic patterns and describe the so called genetic spiral. Phyllotaxis began to be studied in a scientific way in the 1830's, by a combinations of observations, experiments and theoretical hypotheses. Schimper (1830) [7] was the first one to describe the phyllotactic spirals and its relation with the Fibonacci sequence. In 1837 Louis and Auguste Bravais [8] represented the phyllotactic patterns as point-lattices on a cylinder; this idea was retaken by Turing in MTP and was useful to state some mathematical features of phyllotactic spirals. Mechanical and physiological explanations of this phenomenon began until the 1880's [9]. Later in 1982 the hypothesis of efficient packing in phyllotaxis was developed by Ridley and Airy, obtaining the Fibonacci phyllotaxis [10, 11]. After the works of Airy [11] and Hofmeister [12], who established the famous hypothesis of inhibition (which states that the youngest incipient leaf primordium forms in the largest available space left by the previous primordia) the study of phyllotaxis turned its attention to the shoot apical meristem, where these primordia emerge, instead of the organ arrangement on the mature stem. Chemical theories about phyllotaxis appeared at the same time and Turing contributions on the basis of his rectiondiffusion theory of morphogenesis was a pioneering work. Meinhardt and Richards [13, 14] also adopted the chemical approach, obtaining phyllotactic-like patterns. On the other hand, some experiments were performed on the basis of physical hypotheses which could explain the emergence of phyllotactic arrangements. A very illustrative example is found in the experiments performed by Douady and Couder [15], who obtained phyllotactic spirals by adding droplets of a ferromagnetic material in a magnetic field at regular time intervals. The discovery of the plant hormone auxin and its influence on phyllotaxis [16] opened an interdisciplinary way to approach phyllotaxis by modelling an active and polar auxin transport in a growing meristem [17, 18], obtaining phyllotactic-like patterns on the basis of a more realistic set of hypothesis that incorporate the main biological facts involved in plant morphogenesis.

The manuscript MTP is divided into three parts. The first one deals with geometrical and descriptive phyllotaxis; the second part presents a chemical theory of morphogenesis and the third part gives a solution of the morphogenetical equation for systems with spherical symmetry. Here we will be concerned with the second part and, in particular, with the discrete approach, that is, the formulation for an assembly of cells. It is worth to mention that in the CBM, in Sec. 6, Turing studies the discrete case of a ring of cells, but the approach in the MTP is even more general. In the first case, the discreteness is introduced via a discretization of the second derivative (see, for instance, Ref. 3) but in the MTP, Turing considers the general problem of diffusion of reaction of morphogens in an assembly of N cells; "the state of the organism at any time t may be described by $M \times N$ numbers Γ_{mn} ($m = 1, 2, \ldots, M$; $n = 1, 2, \ldots, N$), where Γ_{mn} is the concentration of the mth morphogen in the nth cell" [2]. Albeit Turing eventually considered the limiting case of a continuous tissue, the discrete case is interesting by itself and may be useful under many circumstances. For instance, contrary to the discrete case in the CTM, besides the diffusion constant of each morphogen, the rate of flow from one cell to another is taken into account. This rate of flow not only depends on differences of concentration of the morphogens implicated but it is thought to be dependent on the geometry of the cell wall separating the cells. Albeit basic linear algebra is involved, very soon Truing's calculations become hard to follow. This is in part due to the notation used and also because his approach is based on his great intuition of the problem. It is then the purpose of this work to describe in detail the discrete case following a didactic point of view.

This work is organized as follows: In Sec. 2, the equations that describe morphogens reactions and diffusion in a discrete set of cells are established and simplified, so that solutions can be found by elementary linear algebra. This is done by first considering only diffusion of the morphogens and setting a linear system of equations in terms of a *diffusion matrix*, which contains all the information about the cell assembly, its shape and geometry. Kinetics is then added to the system, following a linear approximation. This procedure allows to express the system as three independent sets of two linear equations, and a solution of each set is found by classical ODE methods. If the assembly consist of n cells, then n different sets of two equations are obtained by this approach. In Sec. 2.3., the solutions found in Sec. 2. are refined by discarding the eigenvalues which do not lead to instability. That is, only terms which grow faster are kept in the solutions found. Finally, in Sec. 2.4. Turing's nonlinear approach (quadratic) is presented.

2. Morphogen equations for an assembly of three cells

In Part II of MTP (page 88) entitled "Chemical Theory of Morphogenesis" , Turing states the morphogen equations for an assembly of cells; first for linear reaction rate functions in Sec. 2.1, and then going beyond the linear case in Sec. 2.2. Even more, Turing's approach surpasses the restriction to a ring of cells worked out in CBM by considering arbitrary arrangements of cells.

As already mentioned, Turing's formulation of the problem very soon becomes cumbersome and hard to follow, so it is the purpose of this part to state the equations in a didactic, easy to follow way. For this, only two morphogens u and w and three cells with volumes v_1, v_2, v_3 are considered. Once the procedure is clarified and mathematical details unveiled, one can easily go back and reproduce calculations for any number of cells in any configuration.

Let u_n and w_n, $n = 1, 2, 3$, be the concentration of the morphogens in the nth cell. That is, u_1 is the concentration of morphogen u in the cell number one, and so on. Then, the flow of the morphogen u from cell r to cell s is proportional to $g_{rs}\,(u_r - u_s)$, where g_{rs} depends on the geometry of the cell wall separation between these cells. For example, it is well known that plant tissues are anisotropic by virtue of the structure of their cell walls [19]. The anisotropic nature of the cell wall is in turn related to the differential flux of plant morphogens like auxin [20], so the terms g_{rs} might be used to model this effect or some other geometrical features that modify the diffusion of substances, such as the surface curvature [21], or the permeability of the complex plasma-membrane-cell-wall [17, 22].

Let μ_u and μ_w be the diffusion coefficients of the morphogens u and w respectively, and establish the same relations for morphogen w, that is, the flow of w between cells r and s is proportional to $g_{rs}\,(w_r - w_s)$. With these assumptions and relations in mind we can go to the next section and establish the equations for morphogen diffusion.

2.1. Morphogen diffusion

If we consider diffusion only, the equations that describe the concentrations of the morphogens in each cell are given by

$$v_r \frac{du_r}{dt} = \mu_u \sum_{s \neq r} g_{rs}\left(u_r - u_s\right),$$

$$v_r \frac{dw_r}{dt} = \mu_w \sum_{s \neq r} g_{rs}\left(w_r - w_s\right), \qquad (1)$$

where v_r is the volume of the rth cell. (Notice a typo on the right side of Eq. II.1.1 in MTP; Γ_{rs} should be Γ_{mr}). Since $r = 1, 2, 3$, what we actually have are six equations of the form

$$v_1 \frac{du_1}{dt} = \mu_u \sum_{s \neq 1} g_{1s}(u_1 - u_s),$$

$$= \mu_u \left(g_{12}\left(u_1 - u_2\right) + g_{13}\left(u_1 - u_3\right)\right), \qquad (2)$$

and similar expressions for u_2 ,u_3, w_1, w_2 and w_3. The right hand side of (2) can be rewritten as $-\mu_u\left(-\left(g_{12} + g_{13}\right)u_1 + g_{12}u_2 + g_{13}u_3\right)$ so, in general we define $g_{rr} = -\sum_{s \neq r} g_{rs}$, and write the equations for u_r and w_r as:

$$v_r \frac{du_r}{dt} {=} {-}\mu_u \sum_s g_{rs}u_s, \quad v_r \frac{dw_r}{dt} {=} {-}\mu_w \sum_s g_{rs}w_s\,. \qquad (3)$$

Now, let us introduce the new variables

$$u_r^{(1)} = \sqrt{v_r}u_r \quad \text{and} \quad w_r^{(1)} = \sqrt{v_r}w_r. \qquad (4)$$

By replacing them into (3), we obtain

$$\frac{du_r^{(1)}}{dt} = -\mu_u \sum_s \frac{g_{rs}}{\sqrt{v_r v_s}} u_s^{(1)},$$

$$\frac{dw_r^{(1)}}{dt} = -\mu_w \sum_s \frac{g_{rs}}{\sqrt{v_r v_s}} w_s^{(1)}, \qquad (5)$$

or in matrix notation

$$\begin{pmatrix} \dot{u}_1^{(1)} & \dot{w}_1^{(1)} \\ \dot{u}_2^{(1)} & \dot{w}_2^{(1)} \\ \dot{u}_3^{(1)} & \dot{w}_3^{(1)} \end{pmatrix} = \begin{pmatrix} \frac{g_{11}}{v_1} & \frac{g_{12}}{\sqrt{v_1 v_2}} & \frac{g_{13}}{\sqrt{v_1 v_3}} \\ \frac{g_{21}}{\sqrt{v_2 v_1}} & \frac{g_{22}}{v_2} & \frac{g_{23}}{\sqrt{v_2 v_3}} \\ \frac{g_{31}}{\sqrt{v_3 v_1}} & \frac{g_{32}}{\sqrt{v_3 v_2}} & \frac{g_{33}}{v_3} \end{pmatrix}$$

$$\times \begin{pmatrix} u_1^{(1)} & w_1^{(1)} \\ u_2^{(1)} & w_2^{(1)} \\ u_3^{(1)} & w_3^{(1)} \end{pmatrix} \begin{pmatrix} -\mu_u & 0 \\ 0 & -\mu_w \end{pmatrix}.$$

The array $G = \left[g_{rs}/\sqrt{v_r v_s}\right]$ is called the *diffusion matrix* and it contains all the spatial information of the cell assembly. Notice that G is always symmetric, independently of the way the cells are arranged, so it is possible to diagonalize it by means of a change of coordinates TGT^{-1}, where T consists of the eigenvectors of G. By Gram-Schmidt process we can find a set of orthonormal eigenvectors, so that $T^{-1} = T^t$.

Let $\alpha_1, \alpha_2, \alpha_3$ be the (real) eigenvalues of G and $\beta_j = (\beta_{j1}, \beta_{j2}, \beta_{j3})$ its associated orthonormal eigenvectors, so that

$$G = \begin{pmatrix} \beta_{11} & \beta_{12} & \beta_{13} \\ \beta_{21} & \beta_{22} & \beta_{23} \\ \beta_{31} & \beta_{32} & \beta_{33} \end{pmatrix} \begin{pmatrix} \alpha_1 & 0 & 0 \\ 0 & \alpha_2 & 0 \\ 0 & 0 & \alpha_3 \end{pmatrix}$$

$$\times \begin{pmatrix} \beta_{11} & \beta_{21} & \beta_{31} \\ \beta_{12} & \beta_{22} & \beta_{32} \\ \beta_{13} & \beta_{23} & \beta_{33} \end{pmatrix}.$$

By performing the matrix product, the entries of the resulting matrix can be written as

$$\frac{g_{rs}}{\sqrt{v_r v_s}} = \sum_k \alpha_k \beta_{rk} \beta_{sk}, \qquad (6)$$

and by using Einstein's summation convention[i], we have

$$\frac{g_{rs}}{\sqrt{v_r v_s}} = \alpha_k \beta_{rk} \beta_{sk}.$$

In order to express the system (5) in terms of a diagonal matrix, we define the new variables $u_r^{(2)}$ and $w_r^{(2)}$ as follows

$$\begin{pmatrix} u_1^{(2)} & w_1^{(2)} \\ u_2^{(2)} & w_2^{(2)} \\ u_3^{(2)} & w_3^{(2)} \end{pmatrix} = T \begin{pmatrix} u_1^{(1)} & w_1^{(1)} \\ u_2^{(1)} & w_2^{(1)} \\ u_3^{(1)} & w_3^{(1)} \end{pmatrix}$$

$$= \begin{pmatrix} \beta_{11} & \beta_{21} & \beta_{31} \\ \beta_{12} & \beta_{22} & \beta_{32} \\ \beta_{13} & \beta_{23} & \beta_{33} \end{pmatrix} \begin{pmatrix} u_1^{(1)} & w_1^{(1)} \\ u_2^{(1)} & w_2^{(1)} \\ u_3^{(1)} & w_3^{(1)} \end{pmatrix},$$

that is

$$u_j^{(2)} = \sum_r u_r^{(1)} \beta_{rj} \quad \text{and} \quad w_j^{(2)} = \sum_r w_r^{(1)} \beta_{rj}. \qquad (7)$$

Notice that the old variables $u_r^{(1)}$ and $w_r^{(1)}$ can be recovered by using T^t, the transpose of T:

$$u_r^{(1)} = \sum_j u_j^{(2)} \beta_{rj}, \quad w_r^{(1)} = \sum_j w_j^{(2)} \beta_{rj}. \qquad (8)$$

Using the summation convention, all these back and forth transformations can be written as

$$u_k^{(2)} = u_r^{(1)} \beta_{rk}, \quad w_k^{(2)} = w_r^{(1)} \beta_{rk}, \qquad (9)$$

$$u_r^{(1)} = u_j^{(2)} \beta_{rj}, \quad w_r^{(2)} = w_j^{(1)} \beta_{rj}. \qquad (10)$$

Since β_j is an orthonormal set, the inner product satisfies

$$\beta_r \cdot \beta_s = \sum_k \beta_{rk} \beta_{sk} = \beta_{rk} \beta_{sk} = \delta_{rs}, \qquad (11)$$

where δ_{rs} is the Kronecker delta. By using these properties we can write the system (5), in terms of $u_j^{(2)}$ and $w_j^{(2)}$. First

$$\frac{du_k^{(2)}}{dt} = \frac{du_r^{(1)}}{dt} \beta_{rk} = -\mu_u \frac{g_{rs}}{\sqrt{v_r v_s}} u_s^{(1)} \beta_{rk}.$$

We also know that $\frac{g_{rs}}{\sqrt{v_r v_s}} = \alpha_k \beta_{rk} \beta_{sk}$, so we write

$$\frac{du_k^{(2)}}{dt} = -\mu_u \alpha_k \beta_{rk} \beta_{sk} u_s^{(1)} \beta_{rk}.$$

From (9) we have that $\beta_{sk} u_s^{(1)} = u_k^{(2)}$, so

$$\begin{aligned}\frac{du_k^{(2)}}{dt} &= -\mu_u \alpha_k \beta_{rk} u_k^{(2)} \beta_{rk} \\ &= -\mu_u \alpha_k \beta_{rk} \beta_{rk} u_k^{(2)}.\end{aligned}$$

Finally, from (11), $\beta_{rk}\beta_{rk} = 1$, thus

$$\frac{du_k^{(2)}}{dt} = -\mu_u \alpha_k u_k^{(2)}.$$

By applying the same procedure to $w_k^{(2)}$, the system (5) is expressed in terms of $u_j^{(2)}$ and $w_j^{(2)}$:

$$\frac{du_k^{(2)}}{dt} = -\mu_u \alpha_k u_k^{(2)} \quad \text{and} \quad \frac{dw_k^{(2)}}{dt} = -\mu_w \alpha_k w_k^{(2)}, \tag{12}$$

which corresponds to Equation (II.1.7) in MTP. This changes of variables will allow us to find a solution for the full system of six equations easily, as we will see in the next Section. In matrix form, the previous equation reads:

$$\begin{pmatrix} \dot{u}_1^{(2)} & \dot{w}_1^{(2)} \\ \dot{u}_2^{(2)} & \dot{w}_2^{(2)} \\ \dot{u}_3^{(2)} & \dot{w}_3^{(2)} \end{pmatrix} = \begin{pmatrix} \alpha_1 & 0 & 0 \\ 0 & \alpha_2 & 0 \\ 0 & 0 & \alpha_3 \end{pmatrix}$$
$$\times \begin{pmatrix} u_1^{(2)} & w_1^{(2)} \\ u_2^{(2)} & w_2^{(2)} \\ u_3^{(2)} & w_3^{(2)} \end{pmatrix} \begin{pmatrix} -\mu_u & 0 \\ 0 & -\mu_w \end{pmatrix}.$$

Since G is symmetric $\alpha_k \in \mathbb{R}$. Moreover, these eigenvalues are positive[ii], since a negative value would mean that diferences in morphogen concentration increase in time, which has no physical meaning. We will see that the solutions of the morphogen equations depend entirely on the eigenvalues α_r, and these eigenvalues impose some conditions on the morphogen diffusibility.

In the next Section, not only diffusion of the two morphogens between cells will be considered, but also the chemical reactions between them. That is, the full reaction-diffusion system for plant morphogenesis will be studied.

2.2. Morphogen kinetics. The linear case

The following discussion concerns the details that lead to solve (II.1.8) in the case of a linear chemical kinetics f_m. The solution for this case is given by Eq. (II.2.6) in MTP. Since only two morphogens are considered here, let $f(u, w)$ and $g(u, w)$ be the rates of change of u and w, respectively. Then we write the full reaction-diffusion (RD) system as follows

$$v_r \frac{du_r}{dt} = \mu_u \sum_{s \neq r} g_{rs} \left(u_r - u_s\right) + v_r f\left(u, w\right), \tag{13}$$

$$v_r \frac{dw_r}{dt} = \mu_w \sum_{s \neq r} g_{rs} \left(w_r - w_s\right) + v_r g\left(u, w\right). \tag{14}$$

Using the change of variables (4) and (7), the RD system (13) can be written as

$$\begin{aligned}\frac{du_r^{(2)}}{dt} &= -\mu_u \alpha_r u_r^{(2)} + f(u, w), \quad \text{and} \\ \frac{dw_r^{(2)}}{dt} &= -\mu_w \alpha_r w_r^{(2)} + g(u, w).\end{aligned}$$

In what follows we carry out a linear local analysis of (13) around an equilibrium point (u^*, w^*) (that is, $f\left(u^*, w^*\right) = 0$ and $g\left(u^*, w^*\right) = 0$), by following a standard approach (see for instance [23]). In absence of spatial variation the system is

$$\frac{du_r^{(2)}}{dt} = f(u, w), \qquad \frac{dw_r^{(2)}}{dt} = g(u, w). \tag{15}$$

Define

$$u_r^{(3)} = \left(u_r^{(2)} - u_r^*\right) \quad \text{and} \quad w_r^{(3)} = \left(w_r^{(2)} - w_r^*\right), \tag{16}$$

where $|u_r^{(3)}|$ and $|w_r^{(3)}|$ are small. Thus, near the equilibrium point the system becomes

$$\frac{du_r^{(3)}}{dt} = a_u u_r^{(3)} + a_w w_r^{(3)} \quad \text{and} \quad \frac{dw_r^{(3)}}{dt} = b_u u_r^{(3)} + b_w w_r^{(3)},$$

where

$$\begin{aligned} a_u &= \frac{\partial f}{\partial u}|_{(u^*, w^*)}, \quad a_w = \frac{\partial f}{\partial w}|_{(u^*, w^*)}, \\ b_u &= \frac{\partial g}{\partial u}|_{(u^*, w^*)}, \quad \text{and} \quad b_w = \frac{\partial g}{\partial w}|_{(u^*, w^*)}.\end{aligned}$$

By incorporating the diffusion terms into the previous equations, we have the linearized RD system (13):

$$\frac{du_r^{(3)}}{dt} = -\mu_u \alpha_r u_r^{(3)} + a_u u_r^{(3)} + a_w w_r^{(3)}, \tag{17}$$

$$\frac{dw_r^{(3)}}{dt} = -\mu_w \alpha_r w_r^{(3)} + b_u u_r^{(3)} + b_w w_r^{(3)}. \tag{18}$$

This system can be separated into three independent sets of two coupled linear equations which can be solved by standard methods. Here we have these three sets:

$$\begin{aligned}\frac{du_1^{(3)}}{dt} &= \left(-\alpha_1 \mu_u + a_u\right) u_1^{(3)} + a_w w_1^{(3)}, \\ \frac{dw_1^{(3)}}{dt} &= \left(-\alpha_1 \mu_w + b_w\right) w_1^{(3)} + b_u u_1^{(3)}, \\ \frac{du_2^{(3)}}{dt} &= \left(-\alpha_2 \mu_u + a_u\right) u_2^{(3)} + a_w w_2^{(3)}, \\ \frac{dw_2^{(3)}}{dt} &= \left(-\alpha_2 \mu_w + b_w\right) w_2^{(3)} + b_u u_2^{(3)},\end{aligned}$$

and

$$\begin{aligned}\frac{du_3^{(3)}}{dt} &= \left(-\alpha_3 \mu_u + a_u\right) u_3^{(3)} + a_w w_3^{(3)}, \\ \frac{dw_3^{(3)}}{dt} &= \left(-\alpha_3 \mu_w + b_w\right) w_3^{(3)} + b_u u_3^{(3)}.\end{aligned}$$

For an arbitrary number of cells n, there will be n sets of such equations. These sets can be expressed in matrix form as

$$\begin{pmatrix} \frac{du_r^{(3)}}{dt} \\ \frac{dw_r^{(3)}}{dt} \end{pmatrix} = \begin{pmatrix} -\alpha_r\mu_u + a_u & a_w \\ b_u & -\alpha_r\mu_w + b_w \end{pmatrix} \times \begin{pmatrix} u_r^{(3)} \\ w_r^{(3)} \end{pmatrix}, \quad r = 1, \ldots, n. \tag{19}$$

Or, even in a more compact notation

$$\dot{U}_r^{(3)} = B_r U_r^{(3)}. \tag{20}$$

Note that since the eigenvalues α_1, α_2 and α_3 may be all distinct, it is necessary to distinguish each matrix B_r, which defines the system of equations for $u_r^{(3)}$ and $w_r^{(3)}$. As in the previous Section, it is possible to find a solution of (20) by means of a change of coordinates R_r that diagonalizes the matrix B_r. Let $p_r(\alpha_r)$ and $p_r'(\alpha_r)$ be the eigenvalues of B_r; from (19) we have that p_r and p_r' satisfy

$$(p + \alpha_r\mu_u - a_u)(p + \alpha_r\mu_w - b_w) = a_w b_u.$$

The solutions of (20) can be expressed in terms of p_r and p_r', and the corresponding eigenvectors of B_r. If these eigenvectors are written as $S_r = (S_{1r1}, S_{2r1})$ and $T_r = (S_{1r2}, S_{2r2})$ then, the coordinates transformation R_r^{-1} is

$$R_r^{-1} = \begin{pmatrix} S_{1r1} & S_{1r2} \\ S_{2r1} & S_{2r2} \end{pmatrix},$$

which has the inverse

$$R_r = \frac{1}{q_r}\begin{pmatrix} S_{2r2} & -S_{1r2} \\ -S_{2r1} & S_{1r1} \end{pmatrix},$$

where $q_r = \det\left(R_r^{-1}\right)$.

Now we are ready to find the solution of (20), which turns out to be:

$$U_r^{(3)}(t) = \begin{pmatrix} c_{r_1} & c_{r_2} \end{pmatrix} R_r \begin{pmatrix} e^{p_r t} & 0 \\ 0 & e^{p_r' t} \end{pmatrix} R_r^{-1}, \tag{21}$$

where, $c_{r_1} = u_r^{(3)}(0)$ and $c_{r_2} = w_r^{(3)}(0)$ are initial conditions.

By introducing the components of $U_r^{(3)}$ in the last equality and performing the matrix product we have the solutions

$$u_r^{(3)}(t) = \frac{1}{q_r}(c_{r_1}S_{2r2} - c_{r_2}S_{2r1})e^{p_r t}S_{1r1} + (c_{r_2}S_{1r1} - c_{r_1}S_{1r2})e^{p_r' t}S_{2r1}, \tag{22}$$

$$w_r^{(3)}(t) = \frac{1}{q_r}(c_{r_1}S_{2r2} - c_{r_2}S_{2r1})e^{p_r t}S_{1r2} + (c_{r_2}S_{1r1} - c_{r_1}S_{1r2})e^{p_r' t}S_{2r2}. \tag{23}$$

These solutions correspond to Eqs. (II.1.10a), (II.1.10b) and (II.1.11) in MPT, page 91.

The roots p_r and p_r' are, explicitly

$$p_r, p_r' = \frac{1}{2}\Bigg(a_u + b_w - \alpha_r(\mu_u + \mu_w) \pm \sqrt{\left[\alpha_r(\mu_u + \mu_w) - (a_u + b_w)\right]^2 - 4h(\alpha_r)}\Bigg), \tag{24}$$

where

$$h(\alpha_r) = \alpha_r^2\mu_u\mu_w - \alpha_r(\mu_u b_w + \mu_w a_u) + a_u b_w - a_w b_u.$$

It is at this point that one of the main Turing's observations arose: he noticed that the terms of major importance in (22) and (23) are those for which Re(p_r) is greatest, because they are the ones which grow faster (this is often called exponential drift); the roots p_r can be either real or complex, and there are many different possibilities for the solutions (22) and (23), but the only case of interest is when p_r is real and maximum and $\alpha_r \neq 0$ is finite. This is described in Turing's CTM as the *case of stationary waves* [1]. As the organisms are finite in number of cells and/or volume, there can only be a finite number of characteristic values α_r for which Re(p_r) has its greatest value (See Appendix).

In the next subsection we refine the solutions (22) and (23), according to the roots p_r that are of main interest. We also express these solutions in terms of the original variables u_r and w_r, which are the morphogen concentrations in each cell.

2.3. Turing instability for morphogen equations of phyllotaxis

Concerning phyllotaxis, in page 93 of MTP, Turing states its main assumptions, that can be summarised as follows:

(a) There is a homogeneous equilibrium in the reaction system, in absence of diffusion, and small deviations from this equilibrium satisfy the conditions for stationary waves [1].

(b) Deviations from equilibrium are small, so that the influence of quadratic terms can be considered as perturbations. Nevertheless, these deviations are sufficiently large for the linear approach to be inapplicable[iii].

(c) The significant wavelengths α_r are those for which the real part of the roots p_r, p_r' is greatest.

In the Appendix we obtain exactly the significant values α_r, which are the *optimum wavelengths*. According to these assumptions, we now look for suitable solutions for the morphogen equations. First, we should establish an algebraic relationship between p_r, p_r' and α_r, as stated in Eqs. (II.1.11) and (II.2.2) in MPT, pages 91 and 95.

An eigenvector $S_r = (S_{1r1}, S_{2r1})$ of B_r must satisfy the equality $(p_r I - B_r)\, S_r = (0,0)$, and the same for p'_r, so we have

$$(p_r + \alpha_r \mu_u - a_u)\, S_{1r1} = a_w S_{2r1} \quad \text{and}$$
$$(p_r + \alpha_r \mu_w - b_w)\, S_{2r1} = b_u S_{1r1}.$$

If we perform the same calculations for the second eigenvector, $T_r = (S_{1r2}, S_{2r2})$, all the relationships between p_r, p'_r and α_r can be known, which turn out to be

$$\begin{aligned} (p_r + \alpha_r \mu_u)\, S_{1r1} &= a_u S_{1r1} + a_w S_{2r1}, \\ (p'_r + \alpha_r \mu_u)\, S_{1r2} &= a_u S_{1r2} + a_w S_{2r2}, \end{aligned} \tag{25}$$

$$\begin{aligned} (p_r + \alpha_r \mu_w)\, S_{2r1} &= b_u S_{1r1} + b_w S_{2r1}, \\ (p'_r + \alpha_r \mu_w)\, S_{2r2} &= b_u S_{1r2} + b_w S_{2r2}. \end{aligned} \tag{26}$$

In matrix notation these are

$$\begin{pmatrix} p_r + \alpha_r \mu_u & p'_r + \alpha_r \mu_u \end{pmatrix} \begin{pmatrix} S_{1r1} & 0 \\ 0 & S_{1r2} \end{pmatrix} = \begin{pmatrix} a_u & a_w \end{pmatrix} \begin{pmatrix} S_{1r1} & S_{1r2} \\ S_{2r1} & S_{2r2} \end{pmatrix}.$$

Define $[S_{irj}] = W(\alpha_r)$, so the previous expression become

$$\begin{pmatrix} p_r + \alpha_r \mu_u & p'_r + \alpha_r \mu_u \end{pmatrix} \begin{pmatrix} S_{1r1} & 0 \\ 0 & S_{1r2} \end{pmatrix} = \begin{pmatrix} a_u & a_w \end{pmatrix} W(\alpha_r), \tag{27}$$

and similarly

$$\begin{pmatrix} p_r + \alpha_r \mu_w & p'_r + \alpha_r \mu_w \end{pmatrix} \begin{pmatrix} S_{1r2} & 0 \\ 0 & S_{2r2} \end{pmatrix} = \begin{pmatrix} b_u & b_w \end{pmatrix} W(\alpha_r). \tag{28}$$

The matrix $W(\alpha_r)$ is non-singular provided that $p_r \neq p'_r$, so we write the solution of (20) as

$$\begin{pmatrix} u_r^{(3)}(t) & w_r^{(3)}(t) \end{pmatrix} = \frac{1}{q_r} \begin{pmatrix} X_{1r}(t) & X_{2r}(t) \end{pmatrix} W(\alpha_r), \tag{29}$$

where

$$X_{1r}(t) = (c_{r_1} S_{2r2} - c_{r_2} S_{2r1})\, e^{p_r t},$$
$$X_{2r}(t) = (c_{r_2} S_{1r1} - c_{r_1} S_{1r2})\, e^{p'_r t}.$$

Notice that at this point we have solved (20), thus solutions are expressed in terms of the variables $u_r^{(3)}$ and $w_r^{(3)}$. Since the problem (13) involves the variables u_r and w_r, we should re-write the solutions in terms of the original variables. We defined $u_r^{(3)}$ and $w_r^{(3)}$ to be $u_r^{(2)}$ and $w_r^{(2)}$, except that they refer to differences from the equilibrium u_r^* and w_r^* (See Eq. 16). Also, $u_r^{(2)}$ and $u_r^{(2)}$ were obtained by means of the orthonormal set of eigenvectors β_j of the diffusion matrix G (See Eq. 7). Therefore, $u_r^{(1)}$ and $u_r^{(1)}$ should be obtained by means of the transpose of the matrix of eigenvectors as follows:

$$\begin{pmatrix} u_1^{(1)} & w_1^{(1)} \\ u_2^{(1)} & w_2^{(1)} \\ u_3^{(1)} & w_3^{(1)} \end{pmatrix} = \begin{pmatrix} \beta_{11} & \beta_{12} & \beta_{13} \\ \beta_{21} & \beta_{22} & \beta_{23} \\ \beta_{31} & \beta_{32} & \beta_{33} \end{pmatrix} \times \begin{pmatrix} u_1^{(3)} & w_1^{(3)} \\ u_2^{(3)} & w_2^{(3)} \\ u_3^{(3)} & w_3^{(3)} \end{pmatrix} + \begin{pmatrix} u_1^* & w_1^* \\ u_2^* & w_2^* \\ u_3^* & w_3^* \end{pmatrix}.$$

Now, Eq. (4) states $u_r^{(1)} = \sqrt{v_r}\, u_r$ and $w_r^{(1)} = \sqrt{v_r}\, w_r$, so:

$$\begin{pmatrix} u_1 & w_1 \\ u_2 & w_2 \\ u_3 & w_3 \end{pmatrix} = \begin{pmatrix} \frac{1}{\sqrt{v_1}} & 0 & 0 \\ 0 & \frac{1}{\sqrt{v_2}} & 0 \\ 0 & 0 & \frac{1}{\sqrt{v_3}} \end{pmatrix} \times \begin{pmatrix} \beta_{11} & \beta_{12} & \beta_{13} \\ \beta_{21} & \beta_{22} & \beta_{23} \\ \beta_{31} & \beta_{32} & \beta_{33} \end{pmatrix} \begin{pmatrix} u_1^{(3)} & w_1^{(3)} \\ u_2^{(3)} & w_2^{(3)} \\ u_3^{(3)} & w_3^{(3)} \end{pmatrix} + \begin{pmatrix} u_1^* & w_1^* \\ u_2^* & w_2^* \\ u_3^* & w_3^* \end{pmatrix}.$$

Then, the relations between variables $u_k^{(3)}$ and $w_k^{(3)}$ and variables u_r and w_r, can be written as follows:

$$\begin{aligned} u_k - u_k^* &= \frac{1}{\sqrt{v_k}} \sum_r u_r^{(3)} \beta_{kr}, \\ w_k - w_k^* &= \frac{1}{\sqrt{v_k}} \sum_r w_r^{(3)} \beta_{kr}. \end{aligned} \tag{30}$$

From (29) we obtain the solution for $u_k^{(3)}$ and $w_k^{(3)}$:

$$\begin{pmatrix} u_r^{(3)}(t) & w_r^{(3)}(t) \end{pmatrix} = \frac{1}{q_r} \begin{pmatrix} X_{1r}(t) & X_{2r}(t) \end{pmatrix} W(\alpha_r).$$

Replacing in (30):

$$\begin{aligned} u_k - u_k^* &= \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} (X_{1r}(t)\, W_{11}(\alpha_r) \\ &\quad + X_{2r}(t)\, W_{21}(\alpha_r)) \beta_{kr}, \\ w_k - w_k^* &= \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} (X_{1r}(t)\, W_{12}(\alpha_r) \\ &\quad + X_{2r}(t)\, W_{22}(\alpha_r)) \beta_{kr}, \end{aligned}$$

which can be rewritten as

$$u_k - u_k^* = \frac{1}{\sqrt{v_k}} \sum_r \sum_l \frac{1}{q_r} X_{lr}(t)\, W_{l1}(\alpha_r)\, \beta_{kr}, \tag{31}$$

$$w_k - w_k^* = \frac{1}{\sqrt{v_k}} \sum_r \sum_l \frac{1}{q_r} X_{lr}(t)\, W_{l2}(\alpha_r)\, \beta_{kr}. \tag{32}$$

This is then the solution of the RD system (13) under the linear approximation, and corresponds to Equation (II.2.4) in MTP. Note that these solutions depend on the functions $X_{lr}(t)$, which are exponential, and the numbers W_{ml} that come from the eigenvectors of the diffusion matrix.

Now, from assumption (c) above, the only terms in (31) and (32) that should be considered are those which arise from the largest real parts of p_r and p'_r, or the ones containing those eigenvalues α_r that are near to zero. Those α_r that yield the greatest Re (p_r) and Re (p'_r) are obtained in the Appendix, by means of a dispersion relation [23]. Some remarks about p_r and p'_r should be made.

If p_r and p'_r are complex, then we have the oscillatory case [1], which is not of interest for the morphogenesis phenomenon. Thus, we assume that p_r and p'_r are real an positive. In order to find solutions (29), it is necessary that $p_r \neq p'_r$, so from (24):

$$[\alpha_r(\mu_u + \mu_w) - (a_u + b_w)]^2 - 4h(\alpha_r) > 0.$$

As the square root of a positive number is always positive, we see that p_r is always larger than p'_r; thus we can drop all the terms that include $X_{2r}(t)$ and write (31) and (32) simply as:

$$u_k - u_k^* = \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} X_{1r}(t)\, W_{11}(\alpha_r)\, \beta_{kr},$$

$$w_k - w_k^* = \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} X_{1r}(t)\, W_{12}(\alpha_r)\, \beta_{kr},$$

where we only choose the terms for which α_r is near to zero or the optimum (See Appendix). We call these terms $X_{1r}(t)^{(0)}, W_{1r}^{(0)}$ and $X_{1r}(t)^{(1)}, W_{1r}^{(1)}$, respectively and write

$$\begin{aligned} u_k - u_k^* &= \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} X_{1r}^{(0)}(t)\, W_{11}^{(0)}(\alpha_r)\, \beta_{kr} \\ &+ \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} X_{1r}^{(1)}(t)\, W_{11}^{(1)}(\alpha_r)\, \beta_{kr}, \\ w_k - w_k^* &= \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} X_{1r}^{(0)}(t)\, W_{12}^{(0)}(\alpha_r)\, \beta_{kr} \\ &+ \frac{1}{\sqrt{v_k}} \sum_r \frac{1}{q_r} X_{1r}^{(1)}(t)\, W_{12}^{(1)}(\alpha_r)\, \beta_{kr}. \end{aligned}$$

Finally, we can assume that, in the two main ranges of values of α_r (near zero and the optimum), the functions $W_{1r}^{(0)}$ and $W_{1r}^{(1)}$ are constant, so we write

$$\begin{aligned} u_k - u_k^* &= W_{11}^{(0)} \sum_r \frac{1}{q_r \sqrt{v_k}} X_{1r}^{(0)}(t)\, \beta_{kr} \\ &+ W_{11}^{(1)} \sum_r \frac{1}{q_r \sqrt{v_k}} X_{1r}^{(1)}(t)\, \beta_{kr} \qquad (33) \\ &= W_{11}^{(0)} V_k + W_{11}^{(1)} U_k, \qquad (34) \\ w_k - w_k^* &= W_{12}^{(0)} \sum_r \frac{1}{q_r \sqrt{v_k}} X_{1r}^{(0)}(t)\, \beta_{kr} \\ &+ W_{12}^{(1)} \sum_r \frac{1}{q_r \sqrt{v_k}} X_{1r}^{(1)}(t)\, \beta_{kr} \qquad (35) \\ &= W_{12}^{(0)} V_k + W_{12}^{(1)} U_k. \qquad (36) \end{aligned}$$

Thus, the solutions of (13), under the linear approximation, depend entirely on the possible values of p_r, which in turn depend on the values of α_r, μ_u and μ_w, and the values of the *stability matrix*

$$\begin{pmatrix} a_u & a_w \\ b_u & b_w \end{pmatrix}.$$

Some restrictions for the stability matrix and the diffusion coefficients μ_u, μ_w are also established in the Appendix, through the analysis of the conditions for Turing instability.

2.4. Morphogen kinetics. The quadratic case

We now consider the case when the reaction rates are quadratic functions of the morphogen concentrations. The quadratic approach is necessary for two reasons. First, the linear analysis is not sufficient for pattern formation, because it only determines a stable state of the system. Second, if some eigenvalue α_r is zero, the linear approximation is not applicable. Thus, it becomes necessary to analyse the quadratic case.

Recall that the full reaction-diffusion system (3) is

$$\frac{du_r}{dt} = \frac{-\mu_u}{v_r} \sum_s g_{rs} u_s + f(u, w),$$

$$\frac{dw_r}{dt} = \frac{-\mu_w}{v_r} \sum_s g_{rs} w_s + g(u, w).$$

Assuming that f and g are quadratic, the system can then be written as

$$\begin{aligned} \frac{du_r}{dt} &= -\frac{\mu_u}{v_r} \sum g_{rs} u_s + a_u (u_r - u_r^*) + a_w (w_r - w_r^*) \\ &+ K_{11} (u_r - u^*)^2 + K_{12} (u_r - u^*)(w_r - w^*) \\ &+ K_{22} (u_r - u^*)^2 \\ \frac{dw_r}{dt} &= -\frac{\mu_w}{v_r} \sum g_{rs} w_s + b_u (u_r - u_r^*) + b_w (w_r - w_r^*) \\ &+ L_{11} (u_r - u^*)^2 + L_{12} (u_r - u^*)(w_r - w^*) \\ &+ L_{22} (u_r - u^*)^2, \end{aligned}$$

where K_{ij}, $L_{ij} \in \mathbb{R}$. These correspond to Eq. (II.2.7) in MPT, page 96. We aim to express these equations in terms of the variables $X_{lr}\,(t)$. By using (29), we can obtain these variables in terms of the inverse of $W_r\,(\alpha)$ as

$$\begin{pmatrix} X_{1r}(t) & X_{2r}(t) \end{pmatrix} = q_r \begin{pmatrix} u_r^{(3)}(t) & w_r^{(3)}(t) \end{pmatrix} W_r(\alpha)^{-1}.$$

Then, X_{lr} can be written in terms of $W_{ml}\,(\alpha_r)$ as follows

$$X_{1r}\,(t) = q_r \left(u_r^{(3)} W_{11}^{-1}\,(\alpha_r) + w_r^{(3)} W_{21}^{-1}\,(\alpha_r) \right), \qquad (37)$$

$$X_{2r}\,(t) = q_r \left(u_r^{(3)} W_{12}^{-1}\,(\alpha_r) + w_r^{(3)} W_{22}^{-1}\,(\alpha_r) \right). \qquad (38)$$

Notice that the last equalities are expressed in terms of the variables $u_r^{(3)}, w_r^{(3)}$, so it is necessary to obtain these in terms of the original variables u_r, w_r. Since

$$\begin{pmatrix} u_1^{(3)} & w_1^{(3)} \\ u_2^{(3)} & w_2^{(3)} \\ u_3^{(3)} & w_3^{(3)} \end{pmatrix} = \begin{pmatrix} \beta_{11} & \beta_{21} & \beta_{31} \\ \beta_{12} & \beta_{22} & \beta_{32} \\ \beta_{13} & \beta_{23} & \beta_{33} \end{pmatrix}$$

$$\times \begin{pmatrix} \sqrt{v_1} & 0 & 0 \\ 0 & \sqrt{v_2} & 0 \\ 0 & 0 & \sqrt{v_3} \end{pmatrix} \begin{pmatrix} u_1 - u_1^* & w_1 - w_1^* \\ u_2 - u_2^* & w_2 - w_2^* \\ u_3 - u_3^* & w_3 - w_3^* \end{pmatrix},$$

we can rewrite (37) as

$$X_{1r}\,(t) = q_r \Bigg(\sum_k \sqrt{v_k}\,(u_k - u_k^*)\,\beta_{kr} W_{11}^{-1}\,(\alpha_r)$$
$$+ \sum_k \sqrt{v_k} (w_k - w_k^*) \beta_{kr} W_{21}^{-1}\,(\alpha_r) \Bigg),$$

$$X_{2r}\,(t) = q_r \Bigg(\sum_k \sqrt{v_k}\,(u_k - u_k^*)\,\beta_{kr} W_{12}^{-1}\,(\alpha_r)$$
$$+ \sum_k \sqrt{v_k}\,(w_k - w_k^*)\,\beta_{kr} W_{22}^{-1}\,(\alpha_r) \Bigg),$$

or, using the summation convention, we write for each l and each r

$$X_{lr} = q_r \sqrt{v_k} \beta_{kr} W_{1l}^{-1}\,(\alpha_r)\,(u_k - u_k^*)$$
$$+ q_r \sqrt{v_k} \beta_{kr} W_{2l}^{-1}\,(\alpha_r)\,(w_k - w_k^*). \qquad (39)$$

Now, by calculating the time derivatives of the last equality, we obtain Equation (II.2.8) in MPT, page 96:

$$\frac{dX_{lr}}{dt} = q_r \sqrt{v_k} \beta_{kr}$$
$$\times \left[W_{1l}^{-1}\,(\alpha_r)\,\frac{du_k}{dt} + W_{2l}^{-1}\,(\alpha_r)\,\frac{dw_k}{dt} \right]. \qquad (40)$$

This last equation is written for each r, so there is a double summation, over k and over l. We now substitute du_k/dt, and dw_k/dt in (40), in terms of the quadratic approach introduced above and using (33) we get

$$u_k - u_k^* = W_{11}^{(0)} V_k + W_{11}^{(1)} U_k,$$
$$w_k - w_k^* = W_{12}^{(0)} V_k + W_{12}^{(1)} U_k.$$

Thus, du_k/dt, dw_k/dt can be written as

$$\frac{du_r}{dt} = -\frac{\mu_u}{v_r} \sum g_{rs} u_s + a_u\,(u_r - u_r^*) + a_w\,(w_r - w_r^*)$$
$$+ K_{11} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r \right)^2$$
$$+ K_{12} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r \right) \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r \right)$$
$$+ K_{22} \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r \right)^2,$$

$$\frac{dw_r}{dt} = -\frac{\mu_w}{v_r} \sum g_{rs} w_s + b_u\,(u_r - u_r^*) + b_w\,(w_r - w_r^*)$$
$$+ L_{11} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r \right)^2$$
$$+ L_{12} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r \right) \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r \right)$$
$$+ L_{22} \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r \right)^2.$$

We now will write the last equations in a more manageable way, by first writing down the diffusion and linear parts in terms of X_{lr} and W_{ml}. The diffusion terms for du_k/dt are $-\frac{\mu_u}{v_k} \sum g_{ks} u_s$, which can be written, using the summation convention, as $-\frac{\mu_u}{v_k} g_{ks} u_s$, for each k. Now, from (30), we see that for each s

$$u_s = \frac{1}{\sqrt{v_s}} \left(\frac{1}{q_r} X_{lr} W_{1l}\,(\alpha_r)\,\beta_{sr} \right) + u_s^*,$$
$$w_s = \frac{1}{\sqrt{v_s}} \left(\frac{1}{q_r} X_{lr} W_{12}\,(\alpha_r)\,\beta_{sr} \right) + w_s^*. \qquad (41)$$

Also, from (6), we have

$$g_{ks} = \sqrt{v_k v_s} \alpha_r \beta_{kr} \beta_{sr}.$$

Thus, the diffusion part for du_k/dt is

$$-\frac{\mu_u}{v_k} g_{ks} u_s = -\frac{\mu_u}{v_k} \Bigg[\sqrt{v_k v_s} \alpha_r \beta_{kr} \beta_{sr}$$
$$\times \left(\frac{1}{\sqrt{v_s}} \frac{1}{q_r} X_{lr} W_{1l}\,(\alpha_r)\,\beta_{sr} + u_s^* \right) \Bigg]$$
$$= -\frac{\mu_u}{\sqrt{v_k}} \left[\alpha_r \beta_{kr} \beta_{sr} \beta_{sr} \left(\frac{1}{q_r} X_{lr} W_{1l}\,(\alpha_r) + \sqrt{v_s} \beta_{sr}^{-1} u_s^* \right) \right]$$
$$= -\frac{\mu_u}{\sqrt{v_k}} \left[\alpha_r \beta_{kr} \left(\frac{1}{q_r} X_{lr} W_{1l}\,(\alpha_r) + \sqrt{v_s} \beta_{kr} \beta_{sr} u_s^* \right) \right].$$

By evaluating dw_k/dt and noticing that $\beta_{kr}\beta_{sr} = 0$ we get

$$-\frac{\mu_u}{v_k} g_{ks} u_s = -\frac{\mu_u}{\sqrt{v_k}} \left[\alpha_r \beta_{kr} \frac{1}{q_r} X_{lr} W_{1l}\left(\alpha_r\right)\right], \tag{42}$$

$$-\frac{\mu_w}{v_k} g_{ks} w_s = -\frac{\mu_w}{v_k} \left[\alpha_r \beta_{kr} \frac{1}{q_r} X_{lr} W_{l2}\left(\alpha_r\right)\right]. \tag{43}$$

Analogously, by virtue of (41), we write the linear terms for du_k/dt and dw_k/dt as follows

$$\begin{aligned} &a_u\left(u_k - u_k^*\right) + a_w\left(w_k - w_k^*\right) \\ &\quad = \frac{1}{\sqrt{v_k}} \frac{1}{q_r} X_{lr} \beta_{kr} \left[a_u W_{l1}\left(\alpha_r\right) + a_w W_{l2}\left(\alpha_r\right)\right], \end{aligned} \tag{44}$$

$$\begin{aligned} &b_u\left(u_k - u_k^*\right) + b_w\left(w_k - w_k^*\right) \\ &\quad = \frac{1}{\sqrt{v_k}} \frac{1}{q_r} X_{lr} \beta_{kr} \left[b_u W_{l1}\left(\alpha_r\right) + b_w W_{l2}\left(\alpha_r\right)\right]. \end{aligned} \tag{45}$$

Then, the substitution of the diffusion and linear terms in (40) yields

$$\begin{aligned} \frac{dX_{lr}}{dt} &= q_r \sqrt{v_k} \beta_{kr} \\ &\times \left[-\frac{\mu_u}{\sqrt{v_k}} W_{1l}^{-1}\left(\alpha_r\right) \left(\alpha_r \beta_{kr} \frac{1}{q_r} X_{lr} W_{1l}\left(\alpha_r\right)\right)\right] \\ &+ q_r \sqrt{v_k} \beta_{kr} \left[W_{1l}^{-1}\left(\alpha_r\right) \frac{1}{\sqrt{v_k}} \frac{1}{q_r} X_{lr} \beta_{kr} (a_u W_{l1}(\alpha_r) \right. \\ &\left. + a_w W_{l2}\left(\alpha_r\right))\right] + q_r \sqrt{v_k} \beta_{kr} \left[-\frac{\mu_w}{\sqrt{v_k}} W_{2l}^{-1}(\alpha_r) \right. \\ &\left. \left(\alpha_r \beta_{kr} \frac{1}{q_r} X_{lr} W_{l2}\left(\alpha_r\right)\right)\right] + q_r \sqrt{v_k} \beta_{kr} \left[W_{2l}^{-1}(\alpha_r) \right. \\ &\left. \times \frac{1}{\sqrt{v_k}} \frac{1}{q_r} X_{lr} \beta_{kr} \left(b_u W_{l1}\left(\alpha_r\right) + b_w W_{l2}\left(\alpha_r\right)\right)\right]. \end{aligned}$$

By simplification and rearrangement of terms we have

$$\begin{aligned} \frac{dX_{lr}}{dt} &= X_{lr}\big(-\mu_u \alpha_r + a_u W_{1l}^{-1}\left(\alpha_r\right) W_{l1}\left(\alpha_r\right) \\ &+ a_w W_{1l}^{-1}\left(\alpha_r\right) W_{l2}\left(\alpha_r\right)\big) + X_{lr}\big(-\mu_w \alpha_r \\ &+ b_u W_{l2}^{-1}\left(\alpha_r\right) W_{l1}\left(\alpha_r\right) + b_w W_{l2}^{-1}\left(\alpha_r\right) W_{l2}\left(\alpha_r\right)\big). \end{aligned} \tag{46}$$

From (25) we have

$$\begin{aligned} p_r &= -\mu_u \alpha_r + a_u W_{11}\left(\alpha_r\right) W_{11}^{-1}\left(\alpha_r\right) \\ &\quad + a_w W_{21}\left(\alpha_r\right) W_{1l}^{-1}\left(\alpha_r\right), \end{aligned}$$

and from (26)

$$\begin{aligned} p_r' &= -\mu_w \alpha_r + b_u W_{12}\left(\alpha_r\right) W_{22}^{-1}\left(\alpha_r\right) \\ &\quad + b_w W_{22}\left(\alpha_r\right) W_{22}^{-1}\left(\alpha_r\right). \end{aligned}$$

Then, by substituting these expressions in (46) and including the quadratic terms one gets

$$\begin{aligned} \frac{dX_{lr}}{dt} &= p_r X_{lr} + p_r' X_{lr} + q_r \sum_k \sqrt{v_k} \beta_{kr} \\ &\times \left[W_{1l}^{-1}\left(\alpha_r\right) K_{11} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r\right)^2 \right. \\ &+ W_{1l}^{-1}\left(\alpha_r\right) K_{12} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r\right) \\ &\times \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r\right) \\ &+ W_{1l}^{-1}\left(\alpha_r\right) K_{22} \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r\right)^2 \\ &+ W_{2l}^{-1}\left(\alpha_r\right) L_{11} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r\right)^2 \\ &+ W_{2l}^{-1}\left(\alpha_r\right) L_{12} \left(W_{11}^{(0)} V_r + W_{11}^{(1)} U_r\right) \\ &\times \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r\right) \\ &\left. + W_{2l}^{-1}\left(\alpha_r\right) L_{22} \left(W_{12}^{(0)} V_r + W_{12}^{(1)} U_r\right)^2\right]. \end{aligned}$$

By writing down this last equation in terms of $X_{lr}^{(0)}$ and $X_{lr}^{(1)}$, one gets Eq. (II.2.9) in MPT, page 96. Finally, by expanding the quadratic expressions and grouping similar terms, we can write this equations in a more abbreviated way:

$$\begin{aligned} \frac{dX_{lr}}{dt} &= p_r X_{lr} + p_r' X_{lr} + q_r \sum_k \sqrt{v_k} \beta_{kr} \\ &\times \left[W_{1l}^{-1}\left(\alpha_r\right) \left(F_1^{(1)} V_r^2 + F_1^{(2)} V_r U_r + F_1^{(3)} U_r^2\right)\right] \\ &+ q_r \sum_k \sqrt{v_k} \beta_{kr} \left[W_{2l}^{-1}\left(\alpha_r\right) \right. \\ &\left. \times \left(F_2^{(1)} V_r^2 + F_2^{(2)} V_r U_r + F_2^{(3)} U_r^2\right)\right], \end{aligned}$$

which corresponds to (II.2.10) in MPT, page 96. Here, the values for $F_1^{(j)}$ are

$$\begin{aligned} F_1^{(1)} &= K_{11} \left(W_{11}^{(0)}\right)^2 + K_{12} W_{11}^{(0)} W_{12}^{(0)} + K_{22} \left(W_{12}^{(0)}\right)^2, \\ F_1^{(2)} &= K_{11} W_{11}^{(0)} W_{11}^{(1)} + K_{12} \left(W_{11}^{(0)} W_{12}^{(1)} + W_{11}^{(1)} W_{12}^{(0)}\right) \\ &\quad + 2K_{22} W_{12}^{(0)} W_{12}^{(1)}, \\ F_1^{(3)} &= K_{11} \left(W_{11}^{(1)}\right)^2 + K_{12} W_{11}^{(1)} W_{12}^{(1)} + K_{22} \left(W_{12}^{(1)}\right)^2. \end{aligned}$$

$F_2^{(j)}$ can be similarly defined by replacing K_{ml} by L_{ml}.

3. Conclusions

In this work we presented Alan Turing's mathematical theory for plant pattern formation in a detailed and didactic way. The importance of this analysis is evident given the fundamental role that Turing's published work for (animal) morphogenesis has played for understanding a number of morphogenetic phenomena [3], since it constitutes a simple mechanisms that can lead to pattern formation in living organisms [24]. The results detailed here, unpublished in Turing's time, constitute a discrete formulation for plant morphogenesis and can as well give insights and a deeper understanding of biological phenomena, in which the cell-cell interactions are of main importance. We believe that the discrete theory has not deserved enough attention and it is the purpose of this paper to alleviate this situation.

Thus, we worked out Turing's theory of phyllotaxis for a simple case in which there are only three cells and two morphogens, u and w. This procedure allowed to clarify and follow the whole calculations and mathematical manipulations needed to establish the RD system in a solvable way, and thus find its solutions. This simple approach is not, however, limiting, because the analysis can be easily extended for an arbitrary number of cells and morphogens. This is clear from equation (20), whose derivation shows how to separate the whole $n\times m$ system of equations into n sets of m linear equations, for the case of n cells and m distinct morphogens. Turing's model for phyllotaxis also allows to establish the equations for any geometrical configuration of cells, by means of the diffusion matrix, which turns out to be a very simple and ingenious idea. The diffusion matrix makes up a very useful tool to explore how the solutions are affected by the geometry of the domain.

A summary of the procedure needed to apply the discrete model proposed by Turing is as follows. After linearising and introducing the appropriate variables, the solution for the morphogen equations are given in Sec. 2.2. (Eq. (21)). The behaviour of these solutions depends on the roots p_r, which are the eigenvalues of the full linearised RD system (20). These eigenvalues depend on the values for the wavelengths α_r. By means of the dispersion relation (Eq. (52) in the Appendix) one can choose only those wavelengths that will drive the solutions to the fastest exponential growth. Derivation of this optimum wavelengths gives a number of restrictions on the diffusion coefficients μ_u and μ_w (Eqs. (54) and (58)) and the components of the stability matrix a_u, b_u, a_w, b_w (50). Thus, the analysis we present in the Appendix gives all the conditions for Turing instability for a discrete system that was not worked out by Turing in MTP nor, as far as we know, by anyone else. On the basis of the results obtained by the linear approach, we finally give the morphogen equations for the case in which the reaction rates are quadratic functions of u and w (Sec. 2.4.). Through the linear case it was possible to set the quadratic system in an easy to solve way, which depends entirely on the roots p_r.

The Turing's results presented here might be very useful for those interested in modelling pattern formation phenomena from a discrete point of view.

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Appendix

In this section we derive the necessary and sufficient conditions for Turing instability of the RD system. That is, we obtain conditions for the system to be stable in absence of spatial perturbations, but unstable when diffusion is present. The optimum wavelengths α_r, for exponential drift, will be determined.

In absence of spatial variation the system is

$$\frac{du_r^{(2)}}{dt} = f(u,w), \qquad \frac{dw_r^{(2)}}{dt} = g(u,w). \tag{47}$$

By linearisation about the equilibrium (u^*, w^*), (47) becomes

$$\begin{pmatrix} \frac{du_r^{(3)}}{dt} \\ \frac{dw_r^{(3)}}{dt} \end{pmatrix} = \begin{pmatrix} a_u & a_w \\ b_u & b_w \end{pmatrix} \begin{pmatrix} u_r^{(3)} \\ w_r^{(3)} \end{pmatrix} = A \begin{pmatrix} u_r^{(3)} \\ w_r^{(3)} \end{pmatrix},$$

where

$$u_r^{(3)} = \left(u_r^{(2)} - u_r^*\right),\ w_r^{(3)} = \left(w_r^{(2)} - w_r^*\right),$$

and A is the stability matrix. The equilibrium point $u_r^{(3)} = w_r^{(3)} = 0$ should be stable, so the solutions λ of $\det(A-\lambda I)=0$ should have negative real part. By computing the determinant we have

$$\det(A-\lambda I) = \lambda^2 - \lambda \mathrm{tr}\,(A) + \det\,(A)\,, \tag{48}$$

so

$$\lambda = \frac{1}{2}\left(\mathrm{tr}\,(A) \pm \sqrt{\mathrm{tr}\,(A)^2 - 4\det\,(A)}\right). \tag{49}$$

Thus, $\mathrm{Re}\,(\lambda) < 0$ requires

$$\mathrm{tr}\,(A) = a_u + b_w < 0 \quad \text{and}$$
$$\det\,(A) = a_u b_w - a_w b_u > 0. \tag{50}$$

Now considering the full linearised RD system

$$\begin{pmatrix} \frac{du_r^{(3)}}{dt} \\ \frac{dw_r^{(3)}}{dt} \end{pmatrix} = \begin{pmatrix} -\alpha_r\mu_u + a_u & a_w \\ b_u & -\alpha_r\mu_w + b_w \end{pmatrix} \begin{pmatrix} u_r^{(3)} \\ w_r^{(3)} \end{pmatrix},$$

which can be written as

$$\dot{U}_r^{(3)} = B_r U_r^{(3)}. \tag{51}$$

By taking into account the spatial terms, we now look for the conditions neccesary to drive the system to instability. From the determinant

$$\det\left(pI - B_r\right) = 0,$$

we obtain the eigenvalues $p\left(\alpha_r\right) = p_r$ as functions of the wavelengths α_r, as the roots of

$$p^2 - p\left[\alpha_r\left(\mu_u + \mu_w\right) - \left(a_u + b_w\right)\right] + h\left(\alpha_r\right) = 0, \quad (52)$$

where

$$h\left(\alpha_r\right) = \alpha_r^2 \mu_u \mu_w - \alpha_r\left(\mu_u b_w + \mu_w a_u\right) + \det\left(A\right).$$

The solutions, p, of (52) must satisfy Re $\left(p\left(\alpha_r\right)\right) > 0$ for some $\alpha_r \neq 0$. These are

$$\begin{aligned} 2p_r = &- \left[\alpha_r\left(\mu_u + \mu_w\right) - \left(a_u + b_w\right)\right] \\ &\pm \sqrt{\left[\alpha_r\left(\mu_u + \mu_w\right) - \left(a_u + b_w\right)\right]^2 - 4h\left(\alpha_r\right)}. \end{aligned} \quad (53)$$

Since tr$(A) < 0$, we have from (53) that Re $\left(p\left(\alpha_r\right)\right) > 0$ can be achieved only if $h\left(\alpha_r\right) < 0$, for some $\alpha_r \neq 0$. Since $\det\left(A\right)$ should be positive, the only possibility for $h\left(\alpha_r\right)$ to be negative is that

$$\left(\mu_u b_w + \mu_w a_u\right) > 0. \quad (54)$$

Taking into account (50), we conclude that $\mu_u \neq \mu_w$. These are the necessary conditions for instability, but they are not sufficient; for $h\left(\alpha_r\right)$ to be negative, its minimum must be negative too, so by differentiation of h with respect to α_r, we have

$$h'(\alpha_r) = 2\alpha_r \mu_u \mu_w - \left(\mu_u b_w + \mu_w a_u\right),$$

so the minimum of h is attained at

$$\alpha_{r_m} = \frac{\left(\mu_u b_w + \mu_w a_u\right)}{2\mu_u \mu_w}, \quad (55)$$

and it is equal to

$$h_{\text{min}} = -\frac{\left(\mu_u b_w + \mu_w a_u\right)^2}{4\mu_u \mu_w} + \det\left(A\right). \quad (56)$$

Since h_{min} must be negative, the condition for $h(\alpha_r) < 0$ is

$$\det(A) < \frac{\left(\mu_u b_w + \mu_w a_u\right)^2}{4\mu_u \mu_w}. \quad (57)$$

At the onset of instability (bifurcation) $h_{\text{min}} = 0$, so $\det\left(A\right) = \left(\mu_u b_w + \mu_w a_u\right)^2 / 4\mu_u \mu_w$. Thus, by defining $\mu = \mu_w / \mu_u$, we can obtain the critical diffusion coefficients μ_{u_c}, μ_{w_c} and $\mu_c = \mu_{w_c} / \mu_{u_c}$ as the appropriate roots of

$$\begin{aligned} &\left(\mu a_u + b_w\right)^2 - 4\mu \det(A) \\ &\quad = \mu^2 a_u^2 + 2\mu\left(a_u b_w - 2\det(A)\right) + b_w^2. \end{aligned} \quad (58)$$

The critical wavelength α_{r_c} is then

$$\alpha_{r_c} = \frac{\left(\mu_{u_c} b_w + \mu_{w_c} a_u\right)}{2\mu_{u_c} \mu_{w_c}}. \quad (59)$$

Then, for $\mu > \mu_c$ there exists a range $\alpha_{r_1} < \alpha_{r_c} < \alpha_{r_2}$ for which $h\left(\alpha_r\right) < 0$. Here, α_{r_1} and α_{r_2} are the two different roots of $h(\alpha_r)$, provided that $\mu > \mu_c$:

$$\alpha_{r_{1,2}} = \frac{\mu_u b_w + \mu_w a_u \pm \sqrt{\left(\mu_u b_w + \mu_w a_u\right)^2 - 4\mu_u \mu_w \det(A)}}{2\mu_u \mu_w}. \quad (60)$$

Thus Re $\left(p\left(\alpha_r\right)\right) > 0$ for all $\alpha_r \in \left(\alpha_{r_1}, \alpha_{r_2}\right)$, and there exists α_{r_0} in this same range for which the polynomial $p^2 - p\left[\alpha_r\left(\mu_u + \mu_w\right) - \left(a_u + b_w\right)\right] + h\left(\alpha_r\right)$ has a maximum, that is, Re $\left(p\left(\alpha_{r_0}\right)\right)$ is maximum. We call α_{r_0} to the *optimum wavelength*. Solutions (33) are then expressed only in terms of the optimum wavelength and the wavelengths near zero.

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i. The summation convention states that the repetition of an index in a term denotes summation with respect to that index over its range. For example, the expression $a_i x_i = p$ means $a_1 x_1 + a_2 x_2 + ... + a_n x_n = p$.

ii. It could be that one of these eigenvalues is zero. If this is the case, it is however possible to follow a quadratic approach, which is presented in Sec. 2.4..

iii. For the patterns to arise, the system cannot stay in a state of equilibrium, but it rather needs to come upon Turing instability.

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