Outline of development of the Daisy

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Editorial note: material omitted by, or at variance with, the versions proposed by Swinton[1] and/or Saunders[2] is indicated in the endnotes. The endnotes also indicate the beginnings of new manuscript pages. Text in brackets [...] indicates material editorial additions, for example figure captions. Minor typos are left uncorrected in order to show the unfinished state of the originals (both typescript and handwritten manuscript pages), but may be commented on in the notes. Very minor typos are corrected without comment.

[3] The theory developed in this paper is limited by a number of assumptions which are by no means always satisfied. Two are of special importance:

(i) That the pattern passes through a long developmental period without forming any visible structures, and indeed without the chemical patterns modifying in any way the geometry of the system. When the visible structures are finally formed, this is done without essential alteration of the chemical pattern.

(ii) That the pattern is always developed within a ring so narrow that it may reasonably be treated as a portion of a cylinder.

The first of these assumptions is one which it would be very difficult to avoid making[4]. It would be exceedingly difficult to know what to assume about the anatomical changes. For the majority of plants this assumption is probably false. In the development of the capitulum of a daisy it seems to be more or less correct, however. The capitulum is appreciably separated from the rest of the plant by a length of petiole before the development of the capitulum starts. Thus a new start is made in the development of the capitulum. It is not appreciably influenced by the proximal structures. That this is the case is confirmed by the following facts:

(a) The directions of the generating spirals of the rosette and of the capitulum are statistically independent. Thus of 15 capitula and corresponding rosettes examined by the author, 4 cases had both rosette and capitulum left handed. [5] In five cases the rosette was left handed but the capitulum right handed, and in four the rosette right handed and the capitulum left handed; in one case both were right handed. Thus in nine out of the fifteen cases, the rosette and the capitulum were in opposite[6] directions.

(b) Beneath the thirteen bracts enclosing the capitulum, there are no other distinguishable structures.

It is suggested that the development of the daisy proceeds essentially as follows. First, the petiole grows up from the rosette without any differentiation either of a visible anatomical form or of an invisible chemical form. Subsequently, the distal end of the petiole undergoes two kinds of change. Its diameter increases, and at the same time a chemical pattern begins to form[7]. The wavelength of this pattern[8] is determined by purely chemical considerations, and there is therefore little reason

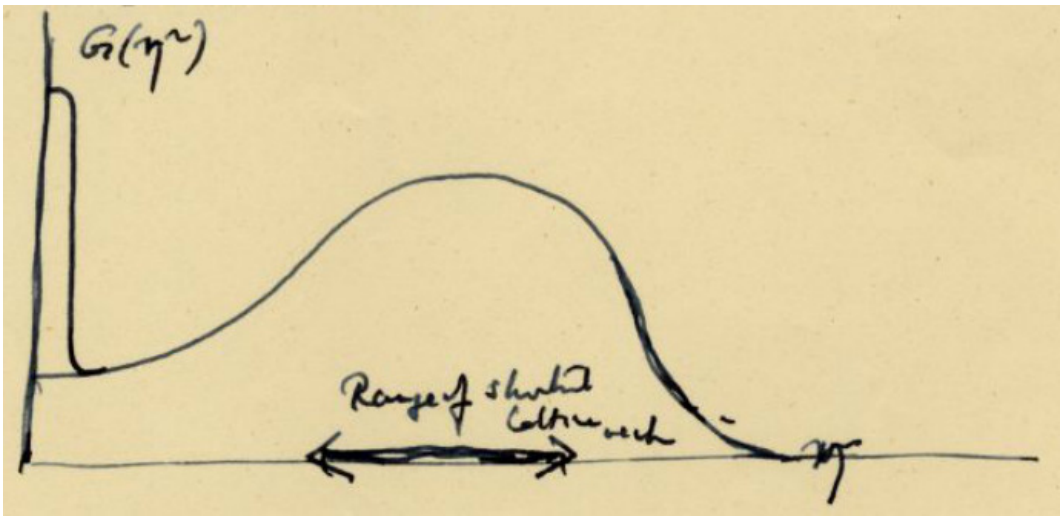


Figure 1: [Editorial note: Graph of $G(\boldsymbol{\eta}^2)$ against $\boldsymbol{\eta}^2$. The annotation reads 'Range of shortest lattice vector'. Note that the left-hand-side of the curve has been redrawn to produce a local maximum at $\boldsymbol{\eta} = 0$, to agree better with the forms of the equations discussed in the section headed 'The equation chosen for computation' below. Detail taken from page AMT/C/24/6. Copyright © W.R. Owens.]

to expect the wavelength to change much. As the diameter increases further, therefore, the pattern will have to change in order that it may continue to fit on the petiole with its new diameter. A very rough description of the concentration patterns during this process may be described as follows:

[9] The concentration U of one of the morphogen concentrations $\mathbf{x} = (\rho\theta, z)$ is to be given by the formula

$$U = \sum_{\boldsymbol{\eta}} \mathrm{e}^{\mathrm{i}(\boldsymbol{\eta},\mathbf{x})} G(\boldsymbol{\eta}^2) W(\mathbf{x}) \tag{1}$$

where the summation is to be over the lattice $\begin{pmatrix} A & B \\ C & D \end{pmatrix}$ reciprocal to $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$. The function $G(\boldsymbol{\eta}^2)$ is to have a maximum near the square of the shortest vector of the lattice $\begin{pmatrix} A & B \\ C & D \end{pmatrix}$. A suitable form for $G(\boldsymbol{\eta}^2)$ and the suitable range for the shortest vectors of the reciprocal lattice [10] $\begin{pmatrix} A & B \\ C & D \end{pmatrix}$ are given in Figure 1.

The function $W(\mathbf{x})$ should depend only on z and typically may be of the form $\exp(-z^2/2\sigma^2)$. The ratio of the standard deviation σ to the shortest vectors of the lattice $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ is probably between 2 and 5. The inclusion of this factor $W(\mathbf{x})$ of course results in the pattern not having the symmetry of the lattice $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$, or of any other lattice. But it is nevertheless possible to use the lattice $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ applying to the formula (1) to describe the pattern instead of the symmetry lattice. It remains only then to describe what in the lattice is to be used for each value of the diameter of the petiole. [11] A suitable form for the lattice is the limiting divergence angle lattice described in

Part I. Clearly this description cannot hold at all times. It breaks down for the period during which the pattern is beginning to form. There may also be a period during which there is a pattern with reflexion symmetry (e.g., a decussate pattern), and the formula above will be invalid for this period also. The sections which follow are concerned with considering the chemical conditions under which this sort of description of the pattern very broadly holds.

At a certain point in the development of the daisy, the anatomical changes begin. From this point, as has been mentioned, it becomes hopelessly impracticable to follow the process mathematically; nevertheless it will be as well to describe how the process does proceed (at least in the author's opinion). In the regions of high concentration of one of the morphogens, growth is accelerated, and subsequently florets appear. Also, the chemical pattern begins to spread inwards towards the apex, and the florets follow it. The wave length of course remains essentially unaltered during this inward movement, and therefore, as the apex is approached the parastichy numbers fall, producing the usual disc pattern, possibly with some slight irregularity at the very centre. There may still be some growth of the capitulum itself, but the pattern can no longer adjust itself to keep the wavelength constant. Either the chemical pattern has lost all its importance and gives way to[12] the relatively unchangeable anatomical pattern or else secretions from the new structures ensure that the wavelength of the chemical pattern increases with that of the anatomical pattern.

A special point arises in connection with the daisy, the formation of the ring of 13 bracts. This number is very constant. The author does not recall finding any specimen with a different number of bracts, excepting a very few deformed or damaged specimens. It is suggested that this ring of bracts is formed as follows. Within the band of lattice pattern there appears at some stage a ring of reduced activity, so that the band becomes divided into two separate bands. The more distal of these bands continues its development and eventually forms the floret pattern. The proximal band, however, is rather narrow and weak (it is fruitless[13] to enquire why). [14] This narrowness results in its degenerating from a lattice pattern into a ring pattern, i.e. into a ring of maxima uniformly placed round the cylinder. This process is described in ... .

The number of maxima in the ring under these circumstances will be one of the three principal parastichy numbers, usually the largest of the three. In view of the fact that the daisy develops according to the normal Fibonacci pattern, this number must be expected to be a Fibonacci number, as it is.

[15] In order to justify this account it is necessary to describe a chemical system for which the pattern develops accordingly. No actual system will actually be described, nor even imaginary chemical reactions as described in Turing (1951). However a partial differential equation will be obtained which is thought to give a good approximation to mark the behaviour of certain kinds of chemical system. The differential equation has a number of parameters and it is necessary to find values for these parameters which will make the differential equation behave appropriately. The choice of parameters is largely made on theoretical grounds, described in this paper, but in order to be sure that the differential equation does really describe a development such as that mentioned above, it is necessary to follow its behaviour by computation.

[16] Considerations governing the choice of parameters

The assumptions to be made concerning the development of the pattern are

(i) That the pattern is described by functions U, V of position on the cylinder and of time,

satisfying the partial differential equations

$$\begin{aligned} \frac{\partial U}{\partial t} &= \phi(\nabla^2)U + I(\mathbf{x},t)U + GU^2 - HUV \\ V &= \psi(\nabla^2)U^2 \end{aligned}$$

(ii) The operator $\phi(\nabla^2)$ is supposed to take the form

$$\phi(\nabla^2) = I_2\left(1 + \frac{\nabla^2}{k_0^2}\right)^2$$

(iii) The operator $\psi(\nabla^2)$ is supposed to take the form

$$\psi(\nabla^2) = \frac{1}{1 - \nabla^2/R^2}$$

though in the computations other forms may be used, taking the value zero outside a finite region.

(iv) A quasi-steady state is assumed to hold, i.e. the time derivative $\partial U/\partial t$ is supposed to be zero, or so near zero as is consistent with slow changes in the radius of the cylinder. This assumption of course implies that certain details as to the effect of the growth on the equation need not be considered.

(v) The function $I(\mathbf{x},t)$ is supposed given in advance. At each time it may be supposed to take the form $I_0 - I_2 z^2/\ell^2$. The quantity I_0 is initially supposed to be negative and to increase to an asymptotic value, reaching very near to it when the optimum wavelength is about one third of a circumference. The quantity ℓ can remain very nearly constant or increase slightly with increasing radius. [17] Clearly in view of (iv), it is only the variation of I_0 and ℓ with radius which is significant, not the variation with time.

If we concentrate our attention on the period of time in which the optimum wavelength is less than a third of a circumference, I_0 and ℓ may be taken as constants, i.e., on a par with G, H, I_2, k_0, R. We have to consider what are appropriate values for these seven quantities. Of the seven quantities there are really only four that are dimensionless. In other words, if we are quite uninterested in the units of time, length and concentration, new units may be introduced which will result in three of these parameters taking the value unity. Actually it is not advisable to do this reduction in every context. A certain amount of interest attaches to the relation of the time and space scales of the phenomena and the diffusion constants for the morphogens in the tissue. The enormous variety of possible reaction constants, and the fact that exceedingly weak concentrations of morphogens could be effective to influence growth, mean that our ignorance of the other two dimensionful quantities is too great for there to be any value in considering them in detail.

If three of the parameters are to be taken as unity, appropriate ones seem to be k_0, fixing the unit of length as the optimum radian wavelength, I_2, fixing the unit of time, and G, fixing the unit of concentration.

[18] The parameters required are thus reduced to four, viz R, H, I_0, ℓ. When actual computations are being carried out, the number of quantities to be specified is again increased to seven by the inclusion of the radius ρ, and two other quantities I_1 and h concerned with the method of calculation. Of these, only the role of h need be mentioned here. In the actual calculations the function $I_0 - z^2/\ell^2$ is replaced by $I_0 - \frac{h^2}{\pi^2\ell^2}\sin^2\frac{\pi z}{h}$, and the pattern is periodic in z with period h. But this is of course

only a mathematical device. The calculations are applied to the Fourier coefficients of U and the number of these that has to be considered is proportional to h. One therefore has to make h as small as possible without the function[19] $I_0 - \frac{h^2}{\pi^2\ell^2}\sin^2\frac{\pi z}{h}$ differing too much from $I_0 - z^2/\ell^2$ and, what is more important, without the bands of pattern becoming so close as to influence one another appreciably.

The main consideration governing the choice of the quantity R is that an excessively small value has the effect that large areas of more or less uniform pattern tend to be unstable and to break up into a number of separate patches. This phenomenon may be explained as follows. The amplitude of the waves is largely controlled by the concentration V of 'poison'. If the quantity R is small, it means that the poison diffuses very fast. This reduces its power of control, for if the U values are large in a patch and large quantities of poison are produced, the effect of the poison will mainly be to diffuse out of the patch and prevent the increase of U in the neighbourhood.

[20] Another way of expressing the effect is that the poison, acting through the HUV term, prevents the growth of waves whose wave vectors are near to that of a strong wave train. The quantity R expresses essentially the range of action in the wave-vector space. If it is too small, there will be liberty for 'side bands' to develop round the strong components. These side bands will represent the modulation of the patchiness. If R is allowed to become too large, it can happen that this 'side band suppression' effect even prevents the formation of a hexagonal lattice; neighbouring points around the hexagon of wave-vectors suppress one another. This however happens only with certain values of the other parameters. In the actual calculations (initially, at any rate) the function chosen for $\psi(\nabla^2)$ was given by[21]

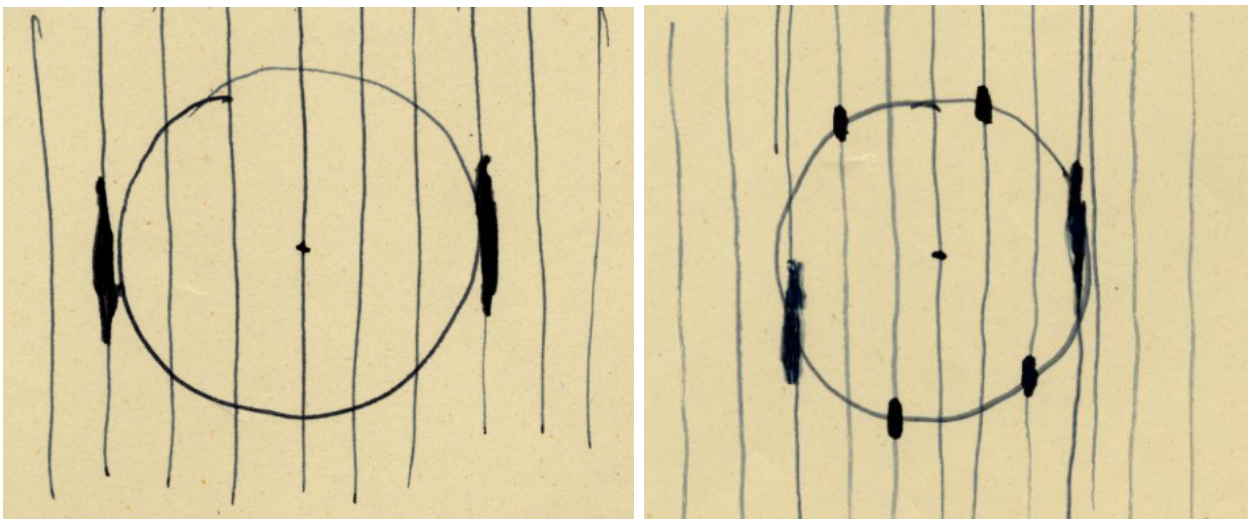
$$\psi(r^2) \quad = \quad \begin{cases} \left(1 - \left(\frac{r}{r_{\max}}\right)^2\right)^2, & r \le r_{\max}, \\ 0, & r \ge r_{\max} \end{cases} \tag{2}$$

with $\frac{r_{\max}}{k_0}$ usually about $\frac{1}{\sqrt{2}}$. [22] (This function calculated in 'Subgroup smooth'.)

[23] The choice of the parameters H, I_0, ℓ is assisted by obtaining an approximate form of solution valid for patterns covering a large area, i.e. in effect with ℓ very large. One may then, as a very crude approximation, suppose that when $I(\mathbf{x}, t)$ varies from place to place one may find near each point more or less the solution which would apply over the whole plane if the value of I appropriate for that point were applied to the whole plane. A nomogram for this purpose is given elsewhere. Another approach to the problem is provided by considering the effect of the terms $\phi(\nabla^2)U$ and $I(\mathbf{x}, t)U$ taken in conjunction in the absence of the terms $GU^2 - HUV$. The term $I(\mathbf{x}, t)U$ may then be regarded as modifying the effect of the $\psi(\nabla^2)U$ term, so that $\psi(\nabla^2)U$ has to be replaced by another function of the wave vector, no longer dependent on the length alone. Having expressed the effect of the $I(\mathbf{x}, t)$ term in this way, it may be assumed, as another (alternative) crude approximation, that the effect of this term is the same even in the presence of the terms $GU^2 - HUV$. Clearly this approximation will not be too unreasonable if the really important term is $\phi(\nabla^2)U$.

[24] Early stages in pattern formation

The most probable course of pattern formation in its early stages is something as follows. The value of I_0 remains sufficiently small to preclude the formation of any pattern until ρk_0 has a value somewhere between 2 and 3. At this stage, when I_0 reaches the appropriate value the homogeneous distribution (or at least θ-independent) breaks up and gives rise to a pattern which is symmetrical under rotation through 120°, i.e., which has three maxima and a reciprocal lattice pattern as below [i.e. in Figure 2(a)].



(a) (b)

Figure 2: [Editorial note: sketches of reciprocal lattices that are those referred to in the text. Both figures are details from AMT/C/24/15. Copyright © W.R. Owens.]

If I_0 increases further, this pattern itself becomes unstable and develops into a more or less hexagonal pattern without reflection symmetry, as below [i.e. in Figure 2(b)]. [25]

[26] The equation chosen for computation

The conclusion of the preceding section is that the chemical behaviour of the morphogens should be described by the equations

$$\begin{aligned} \frac{dU}{dt} &= \phi(\nabla^2)U + I(\mathbf{x})U + GU^2 - HUV \\ \frac{dV}{dt} &= \psi(\nabla^2)V + KU^2 \end{aligned}$$

It is necessary to choose some particular functions to replace the arbitrary functions ϕ, ψ, I, parameters being allowed, and to discuss the values of such parameters and of K, G, H which would be most appropriate.

In the second equation determining the distribution of concentration V, it will be appropriate for the term $\psi(\nabla^2)$ to represent a combination of diffusion and monomolecular decay, thus

$$\frac{dV}{dt} = C_1\nabla^2 V - C_2 V + C_3 U^2$$

If the diffusion and decay occur fast by comparison with the reactions which are responsible for the term KU^2, or if one is really only interested in equilibrium effects, one may put $V = \frac{C_3}{C_2}\frac{U^2}{1-\frac{C_1}{C_2}\nabla^2}$.

The essential property required of the function ϕ is that it should have a maximum for some real (negative) argument. The most natural form for it is therefore $-A(\nabla^2 + k_0^2)^2$. Then $2\pi/k_0$ is the optimum wavelength, i.e. the wavelength of the waves which are least quickly damped out. (This form of the function is not one of the forms which arose in section ... of Turing I but is a limiting case of such forms.)

[27] One should allow for a constant term either in the wavelength function $\phi(\nabla^2)$ or the position function $I(\mathbf{x})$ and since it has not been included in the former it will have to be included in the latter. If one is interested in development on a surface of revolution, whose points are described by coordinates (z, θ), whose metric is $ds^2 = \rho^2 d\theta^2 + dz^2$. If diffusion is limited to the surface then $\nabla^2 V$ means $\frac{1}{\rho^2}\frac{\partial^2 V}{\partial \theta^2} + \frac{1}{\rho}\frac{d}{dz}\left(\rho \frac{\partial V}{\partial z}\right)$. The function $I(\mathbf{x})$ must be axially symmetrical, and so must be a function of z only. The assumption made here is that the surface of revolution is a cylinder, so that ρ is constant, and that $I(\mathbf{x})$ takes the form $I - Lz^2$. Making use of all these assumptions the equation may be written

$$\frac{\partial U}{\partial t} = -A(\nabla^2 + k_0^2)^2 U + IU - Lz^2 U + GU^2 - H\frac{C_3}{C_2}\left(\frac{U^2}{1 - \frac{C_1}{C_2}\nabla^2}\right)U$$

Before computing one must remove some of the otiose constants by reducing the equation to a dimensionless form. Clearly one may suppose $C_3 = C_2$ and put $C_1/C_2 = \sigma^2/k_0^2$. Multiplying both sides of the equation by $\frac{G}{A^2 k_0^8}$ it may be written

$$\frac{d\left(\frac{GU}{Ak_0^4}\right)}{d(Ak_0^4 t)} = \left(-\left(1 + \frac{\nabla^2}{k_0^2}\right)^2 + \frac{I}{Ak_0^4} - \frac{L}{Ak_0^6}(k_0 z)^2\right)\left(\frac{GU}{Ak_0^4}\right) + \left(\frac{GU}{Ak_0^4}\right)^2 - \frac{HAk_0^4}{G^2}\frac{\left(\frac{GU}{Ak_0^4}\right)^2}{1 - \frac{\sigma^2\nabla^2}{k_0^2}} \cdot \frac{GU}{Ak_0^4}$$

[28] If one then takes $t' = Ak_0^4 t$, $U' = \frac{GU}{Ak_0^4}$, $I' = I/(Ak_0^4)$, $L' = L/(Ak_0^6)$, $H' = \frac{HAk_0^4}{G^2}$ and $z' = k_0 z$, $\nabla'^2 = \nabla^2/k_0^2$ the equation may be written

$$\frac{dU'}{dt'} = -(1 + \nabla^2)^2 U' + I'U' - L'z'^2 U' + U'^2 - H'\left(\frac{U'^2}{1 - \sigma^2\nabla'^2}\right)U, \quad [29]$$

$$\nabla'^2 = \frac{1}{\rho'^2}\left(\frac{d}{d\theta}\right)^2 + \frac{d^2}{dz'^2}$$

This form will be used, but with the dashes omitted.

It will be seen that there are now five parameters

The radius ρ in optimum radian wavelengths

The instability I.

The width parameter $L^{-1/2}$ (in optimum radian wavelengths).

The amplitude controlling factor H.

The amplitude control diffusion factor σ.

The optimum radian wavelength has been chosen to be the unit of length, and the unit of time has been chosen in such a way that there is a unit difference in exponential rate of growth between the waves of infinitely long wavelength and those of optimum wavelength.

[30] Lattice solutions and their stability

In the case where $L = 0$ the equations will usually have equilibrium solutions which have lattice symmetry. Such equilibrium solutions are in fact phyllotactic systems in the sense of part I [31].

The phyllotactic systems of botany do not arise in this way, as will appear in ... . Nevertheless a discussion of these equilibrium solutions will throw some light on the problem.

If one is given a particular lattice of congruences and the values of the parameters I, H, σ it is possible to calculate the equilbrium function U. This is usually a task with the range of hand computation. The function U may best be given as a sum over the inverse lattice

$$U = \sum A_{\mathbf{u}} \mathrm{e}^{\mathrm{i}(\mathbf{x},\mathbf{u})}$$

From a trial value of the coefficients $A_{\mathbf{u}}$ one may calculate the coefficients in U^2 and so in $\frac{U^2}{1-\sigma^2\nabla^2}$ and then in $H\left(\frac{U^2}{1-\sigma^2\nabla^2}\right)U$, and thus the whole of the right hand side of (...). The coefficients are then altered so that the error will be corrected by the change in $(I+(1+\nabla^2)^2)U$ and the process repeated.

In practice a good idea of the behaviour of the solutions can be obtained by considering only relatively few terms in (...). [32] The most satisfactory assumption is to consider the zero vector and the three principal (inverse) vectors, each with positive and with negative sign. If these non-zero vectors are numbered $\mathbf{k}_1, \mathbf{k}_2, \ldots, \mathbf{k}_6$ in the anticlockwise order of their directions, and if the suffixes are reckoned modulo six, then $\mathbf{k}_{r-1} + \mathbf{k}_{r+1} = \mathbf{k}_r$. The form assumed for U is now

$$U_0 = \xi + \sum_{r=1}^{6} \eta_r \mathrm{e}^{\mathrm{i}(\mathbf{x},\mathbf{k}_r)}$$

where ξ is real and $\eta_r = \bar{\eta}_{r+3}$. The assumption that there are no other terms would have been justified if $\phi(-r^2)$ had the value $-\infty$ for r greater than a certain r_1, which is itself greater than the first three principal inverse vectors, but shorter than any of the other non-zero vectors of the lattice. It will be convenient to make this assumption for definiteness. It will also be supposed that $\psi(-r^2) = 0$ if r exceeds a certain value r_0 which is itself less than the length of the principal inverse vector. Now

$$U_0^2 = \xi^2 + \sum_{r=1}^{6} |\eta_r|^2 + 2\sum_{r=1}^{6} \eta_{r-1}\eta_{r+1}\mathrm{e}^{\mathrm{i}(\mathbf{x},\mathbf{k}_r)} + 2\xi\sum_{r=1}^{6} \eta_r \mathrm{e}^{\mathrm{i}(\mathbf{x},\mathbf{k}_r)}$$

+ terms with wave vectors longer than r_1.

From this one may deduce that $\psi(\nabla^2)U^2$ is the constant $V = \xi^2 + 2\sum_{r=1}^{3}|\eta_r|^2$. The conditions for equilibrium are then

$$\begin{aligned} (\phi(0) - HV)\xi + V &= 0 \\ (\phi(-\mathbf{k}_r^2) - HV + 2\xi)\eta_r + 2\eta_{r-1}\eta_{r+1} &= 0 \end{aligned}$$

[33] By a change of origin one may ensure that the coefficients η_r are all real. They will therefore be supposed to be so. It will be shown later that the equilibrium is unstable unless also ξ and $\eta_1\eta_2\eta_3$ are positive, and in this case one may by a further change of origin ensure that each η_r is positive.

To investigate stability one may put $U = U_0 + \varepsilon \mathrm{e}^{\mathrm{i}(\boldsymbol{\chi},\mathbf{x})}W$ where W is a sum of the form ... , viz

$$W = x + \sum_{r=1}^{6} y_r \mathrm{e}^{\mathrm{i}(\mathbf{k}_r,\mathbf{x})}$$

Such terms, with a given $\boldsymbol{\chi}$, interact on one another in the variational equation, but do not act on terms with other values of $\boldsymbol{\chi}$. It will be supposed that $\boldsymbol{\chi}$ is sufficiently small that the assumptions

made about the functions ϕ, ψ and the various vectors of the lattice still remain true when those vectors are increased by $\boldsymbol{\chi}$. The variational equation satisfied by W is

$$\frac{dW}{dt} = \mathrm{e}^{-\mathrm{i}(\boldsymbol{\chi},\mathbf{x})}\phi(\nabla^2)\mathrm{e}^{\mathrm{i}(\boldsymbol{\chi},\mathbf{x})}W + 2WU_0 - 2HU_0\mathrm{e}^{-\mathrm{i}(\boldsymbol{\chi},\mathbf{x})}\psi(\nabla^2)\mathrm{e}^{\mathrm{i}(\boldsymbol{\chi},\mathbf{x})}(WU_0) - HWV$$

i.e.

$$\begin{aligned}
\frac{dx}{dt} &= \phi(-\boldsymbol{\chi}^2)x + x\xi + 2\sum_{r=1}^{6}\eta_r y_{r+3} - 2H\xi\psi(-\boldsymbol{\chi}^2)\left(x\xi + \sum \eta_r y_{r+3}\right) \\
\frac{dy_r}{dt} &= \left(\phi(-(\mathbf{k}_r+\boldsymbol{\chi})^2) + 2\xi - HV\right)y_r + 2\eta_{r-1}y_{r+1} + 2\eta_{r+1}y_{r-1} + 2x\eta_r \\
&\quad -2H\eta_r\psi(-\boldsymbol{\chi}^2)\left(x\xi + \sum \eta_r y_{r+3}\right)
\end{aligned}$$

[34] Now putting

$$\begin{aligned}
y_r^{(+)} &= \frac{1}{\sqrt{2}}(y_r + y_{r+3}) \\
y_r^{(-)} &= \frac{1}{\sqrt{2}}(y_r - y_{r+3})
\end{aligned}$$

so that

$$\eta_r = \eta_{r+3} \qquad y_r^{(+)} = y_{r+3}^{(+)} \qquad y_{r+3}^{(-)} = -y_r^{(-)}$$

$$\begin{aligned}
\frac{dx}{dt} &= \left(\phi(-\boldsymbol{\chi}^2) + 2\xi - HV - 2H\xi^2\psi(-\boldsymbol{\chi}^2)\right)x + 2\sqrt{2}\sum_{r=1}^{3}\eta_r y_r^{(+)}\left(1 - H\xi\psi(-\boldsymbol{\chi}^2)\right) \\
\frac{dy_r^{(+)}}{dt} &= \left(\frac{\phi(-(\mathbf{k}_r+\boldsymbol{\chi})^2)) + \phi(-(\mathbf{k}_r-\boldsymbol{\chi})^2)}{2} + 2\xi - Hx\right)y_r^{(+)} \\
&\quad + \frac{\phi(-(\mathbf{k}_r+\boldsymbol{\chi})^2) - \phi(-(\mathbf{k}_r-\boldsymbol{\chi})^2)}{2}y_r^{(-)} + 2\eta_{r-1}y_{r+1}^{(+)} + 2\eta_{r+1}y_{r-1}^{(+)} \\
&\quad + 2\sqrt{2}(1 - H\xi\psi(-\boldsymbol{\chi}^2))\eta_r x - 4H\eta_r\psi(-\boldsymbol{\chi}^2)\sum_{s=1}^{3}\eta_s y_s^{(+)} \\
\frac{dy_r^{(-)}}{dt} &= \frac{\phi(-(\mathbf{k}_r+\boldsymbol{\chi})^2) - \phi(-(\mathbf{k}_r-\boldsymbol{\chi})^2)}{2}y_r^{(+)} + 2\eta_{r-1}y_{r+1}^{(-)} + 2\eta_{r+1}y_{r-1}^{(-)} \\
&\quad + \left(\frac{\phi(-(\mathbf{k}_r+\boldsymbol{\chi})^2) + \phi(-(\mathbf{k}_r-\boldsymbol{\chi})^2)}{2} + 2\xi - HV\right)y_r^{(-)}
\end{aligned}$$

The case $\boldsymbol{\chi} = 0$ is of great importance. One may first investigate the behaviour of $y_1^{(-)}$, $y_2^{(-)}$, $y_3^{(-)}$.

$$\begin{aligned}
\frac{1}{2}\frac{dy_r^{(-)}}{dt} &= \eta_{r-1}y_{r+1}^{(-)} + \eta_{r+1}y_{r-1}^{(-)} + \frac{1}{2}(\phi(-\mathbf{k}_r^2) + 2\xi - HV)y_r^{(-)} \\
&= \eta_{r-1}y_{r+1}^{(-)} + \eta_{r+1}y_{r-1}^{(-)} - \frac{\eta_{r-1}\eta_{r+1}}{\eta_r}y_r^{(-)}
\end{aligned}$$

i.e.

$$\frac{1}{2}\frac{dy_r^{(-)}}{dt} = \sum A_{rs}y_s^{(-)}$$

$$A_{rs} = \begin{pmatrix} -\frac{\eta_2\eta_3}{\eta_1} & \eta_3 & -\eta_2 \\ \eta_3 & -\frac{\eta_1\eta_3}{\eta_2} & \eta_1 \\ -\eta_2 & \eta_1 & -\frac{\eta_1\eta_2}{\eta_3} \end{pmatrix}$$

[35] [36] The eigenvectors are $(\eta_1, 0, -\eta_3)$ and $(0, \eta_2, \eta_3)$ both with eigenvalue 0 and $(\eta_1^{-1}, -\eta_2^{-1}, \eta_3^{-1})$ with eigenvalue $-\eta_1\eta_2\eta_3(\eta_1^{-2} + \eta_2^{-2} + \eta_3^{-2})$.

There is thus instability if $\eta_1\eta_2\eta_3 < 0$ and so we may suppose $\eta_1\eta_2\eta_3 > 0$, and, if necessary by a change of origin, one may arrange that η_1, η_2, η_3 are all positive. The eigenvectors with eigenvalue 0 correspond to small shifts of origin.

The matrix corresponding to x, $y_1^{(+)}$, $y_2^{(+)}$, $y_3^{(+)}$ [37] is

$$2\begin{pmatrix} \mu_0 & \sqrt{2}\eta_1(1-H\xi) & \sqrt{2}\eta_2(1-H\xi) & \sqrt{2}\eta_3(1-H\xi) \\ \sqrt{2}\eta_1(1-H\xi) & -\frac{\eta_2\eta_3}{\eta_1} - 2H\eta_1^2 & \eta_3 - 2H\eta_1\eta_2 & \eta_2 - 2H\eta_1\eta_3 \\ \sqrt{2}\eta_2(1-H\xi) & \eta_3 - 2H\eta_1\eta_2 & -\frac{\eta_1\eta_3}{\eta_2} - 2H\eta_2^2 & \eta_1 - 2H\eta_2\eta_3 \\ \sqrt{2}\eta_3(1-H\xi) & \eta_2 - 2H\eta_1\eta_3 & \eta_1 - 2H\eta_2\eta_3 & -\frac{\eta_1\eta_2}{\eta_3} - 2H\eta_3^2 \end{pmatrix}$$

$$\begin{aligned} 2\mu_0 &= \phi(0) - HV + 2\xi(1-H\xi) \\ &= -\frac{V}{\xi} + 2\xi(1-H\xi) \end{aligned}$$

[38] It is not proposed to investigate the eigenvectors of this matrix in the gneral case, but only in the case that $\mathbf{k}_1^2 = \mathbf{k}_2^2 = \mathbf{k}_3^2 = k^2$, $\eta_1 = \eta_2 = \eta_3 = \eta$. There are two eigenvectors of the form (x, y, y, y), with eigenvalues satisfying the equations

$$\begin{aligned} \mu_0 x + 3\gamma y &= \frac{1}{2}\lambda x \\ \gamma x + (\eta - 6H\eta^2)y &= \frac{1}{2}\lambda y \end{aligned}$$

where $\gamma = \sqrt{2}\gamma(1 - H\xi)$, i.e.

$$\frac{1}{4}\lambda^2 - \frac{1}{2}\lambda(\eta - 6H\eta^2 + \mu_0) + \mu_0(\eta - 6H\eta^2) - 3\gamma^2 = 0$$

There are also eigenvectors $(0, 1, \omega, \omega^2)$, $(0, 1, \omega^2, \omega)$ where $1 + \omega + \omega^2 = 0$, each with the eigenvalue -4η which is negative. The equilibrium is stable therefore provided both roots of (...) are negative, i.e. provided $6H\eta^2 - \eta - \mu_0$ and $\mu_0(\eta - 6H\eta^2) - 3\gamma^2$ are both positive. Now $6H\eta^2 - \eta - \mu_0 = 6H\eta^2 + \frac{1}{2}\phi(-\mathbf{k}^2) - \frac{1}{2}\phi(0) + \xi^2 H$ and is positive provided $\phi(-\mathbf{k}^2) \geq \phi(0)$ which certainly applies for all practical cases.

[39] The roots of (...) may perhaps be most satisfactorily investigated by considering that this is also the equation for the stability of the equation

$$\begin{aligned} \frac{d\xi}{dt} &= (\phi(0) - HV)\xi + V \\ \frac{d\eta}{dt} &= (\phi(-k^2) - HV + 2\xi)\eta + 2\eta^2 \end{aligned}$$

arising by putting $\eta_1 = \eta_2 = \eta_3 = \eta_4 = \eta_5 = \eta_6 = \eta$ in (...). Put $\phi(0) = X$, $\phi(-k^2) = Y$

$$\begin{aligned} \frac{d\xi}{dt} &= X\xi - F(\xi, \eta, H)\xi \qquad F(\xi, \eta) = (\xi^2 + 6\eta^2)\left(H - \frac{1}{\xi}\right) \\ \frac{d\eta}{dt} &= Y\eta - G(\xi, \eta, H)\eta \qquad G(\xi, \eta) = -2\xi - 2\eta + H(\xi^2 + 6\eta^2) \end{aligned}$$

The equilibrium conditions are then $X = F$, $Y = G$. The condition for stability is that the matrix

$$\begin{pmatrix} X - F - \xi\frac{\partial F}{\partial \xi} & -\xi\frac{\partial F}{\partial \eta} \\ -\eta\frac{\partial G}{\partial \xi} & Y - G - \eta\frac{\partial G}{\partial \eta} \end{pmatrix}$$

[40] has no characteristic root with positive real part, i.e. that the trace be non-positive and the determinant non negative. The trace is

$$\begin{aligned} -\xi\frac{\partial F}{\partial \xi} - \eta\frac{\partial G}{\partial \eta} &= -2\xi^2\left(H - \frac{1}{\xi}\right) - \frac{1}{\xi}(\xi^2 + 6\eta^2) + 2\eta - 12\eta^2 \\ &= F - G - 2\xi^2 H - 2\eta^2 \end{aligned}$$

and is negative since $F - G = X - Y < 0$.

[41] The determinant is $\xi\eta\left(\frac{\partial F}{\partial \xi}\frac{\partial G}{\partial \eta} - \frac{\partial F}{\partial \eta}\frac{\partial G}{\partial \xi}\right)$ i.e. $\xi\eta\frac{\partial(F,G)}{\partial(\xi,\eta)}$ or one might write it as $\xi\eta\frac{\partial(X,Y)}{\partial(\xi,\eta)}$ if F is identified with X and G with Y. The question as to the stability is therefore very closely related to the question as to how the values of ξ, η are to be obtained from the values of X, Y, H. The regions of stability are divided from the regions of instability by curves on which either $\xi = 0$ or on which the Jacobian $\frac{\partial(F,G)}{\partial(\xi,\eta)}$ vanishes. P.T.O.[42]

A convenient method of obtaining the values of ξ, η from X, Y, H is first to make a change of scale which will result in $Y - X$ having the value 1, thus

$$\begin{aligned} \frac{d(\xi/(Y-X)}{t(Y-X)} &= \frac{X}{Y-X}\frac{\xi}{Y-X} - F\left(\frac{\xi}{Y-X}, \frac{\eta}{Y-X}, H(Y-X)\right)\frac{\xi}{Y-X} \\ \frac{d(\eta/(Y-X))}{d(t(Y-X))} &= \frac{Y}{Y-X}\frac{\eta}{Y-X} - G\left(\frac{\xi}{Y-X}, \frac{\eta}{Y-X}, H(Y-X)\right)\frac{\xi}{Y-X} \end{aligned}$$

However the condition $Y - X = 1$ automatically applies with the form of equation adopted in section ... . When this condition applies the equilibrium condition can be written

$$-2\eta - 2\xi = x - HV = 1 - \frac{V}{\xi} \qquad (\ldots)$$

The relation

$$\xi^2 + 2\eta\xi - 6\eta^2 + \xi = 0 \qquad (\ldots)$$

therefore connects ξ and η independently of the values of X and H.

[43] A convenient parametric form of this relation is obtained by expressing both ξ andη in terms of the ratio $\sigma = \eta/\xi$. For each value of σ one also obtains a value of V and a linear relation between X and H. These lines in the (X, H) plane envelope a curve. The curve and the relations of ξ, η, V, σ are given by

$$\begin{aligned} \xi^{-1} &= 6\sigma^2 - 2\sigma - 1, \qquad \eta^{-1} = \xi^{-1}\sigma^{-1} \\ H_1^{-1} &= 2\xi + \frac{6}{14 + \eta^{-1}}, \qquad V = \xi^2 + 6\eta^2 \\ X_1 &= VH_1 - 2\xi - 2\eta \end{aligned}$$

The curve provides a convenient method for obtaining the values of ξ, η corresponding to given (X_0, H_0). From (X_0, H_0) one may draw a tangent to the envelope. The slope of this tangent determines the value of V, and therefore of σ, ξ, η. The curve is shown in Fig X [i.e. Figure 3

below.] which also includes nomographic arrangements for determining ξ and η. This method of determining ξ and η also settles the stability question. Double roots for ξ, η are obtained when two tangents from (X_0, H_0) coincide, i.e. when (X_0, H_0) lies on the envelope itself. Such points separate the regions of stability from the regions of instability in the plane of (σ, H_0). Stable solutions are obtained from tangents such that the value H_1 at the point of contact is less than H_0 at the point from which the tangent is drawn.

[Summary]

[44] The solutions which are to be considered in this paper are ones which resemble in some way or other these lattice solutions with $\eta_1 = \eta_2 = \eta_3$. They are very stable under changes which are centrally symmetrically, or if they are unstable for such changes the effect of such a change is for the function to drop to zero. There is no need therefore to give much further consideration to stability under symmetrical disturbances, provided that the existence of equilibrium has been investigated. The disturbances which are centrally antisymmetrical (about a centre of symmetry of the solution itself) must however be considered in further detail. This is partly because in the computations it is proposed to consider only solutions which have a centre of symmetry. If a solution has a centre of symmetry at one moment it will of course continue to have such symmetry thereafter, but only provided it is not disturbed. It is essential that the solutions be stable with respect to antisymmetrical disturbances in order that the computations should describe the facts reasonably. As has been seen there is every reason to expect that there is stability with respect to symmetrical disturbances, but even if there were not, this fact would appear in the computation. It is fortunate therefore that it was possible to investigate the stability with respect to the antisymmetrical disturbances without making the assumption $\eta_1 = \eta_2 = \eta_3$. For one of the characteristic disturbances (with $\boldsymbol{\chi} = 0$) there is very high stability, [45] (characteristic value $-\eta_1\eta_2\eta_3 \sum \frac{1}{\eta_i^2}$). The other two characteristic disturbances (at ...) are equivalent to small displacements of the lattice. The characteristic value is zero for both, and it is necessary therefore to consider the problem with more accurate assumptions before it is possible to tell whether there is stability or not.

Notes

[1] A.M. Turing, Outline of the Development of the Daisy. Updated by J. Swinton. Pages 860–865 in *Alan Turing: His Life and Impact* Eds S.B. Cooper and J. Van Leeuwen. Elsevier (2013)

[2] A.M. Turing, *Collected Works of A.M. Turing: Morphogenesis*. Edited by P.T. Saunders. Elsevier, Amsterdam (1992)

[3] Start of page AMT/C/24/4.

[4] The word 'making' is omitted by Saunders and by Swinton.

[5] Start of page AMT/C/24/5.

[6] Saunders and Swinton both give 'different' instead of 'opposite' here.

[7] The three words 'begins to form' are omitted by Saunders and Swinton.

[8] The text 'The wavelength of this pattern' is also omitted by Saunders and Swinton.

[9] Start of page AMT/C/24/6.

[10] Saunders and Swinton have $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ here instead of $\begin{pmatrix} A & B \\ C & D \end{pmatrix}$. The latter is correct.

[11] Start of page AMT/C/24/7.

[12] Start of page AMT/C/24/8.

[13] Corrected from Saunders and Swinton who have 'pointless' instead of 'fruitless'.

[14] The entire sentence 'This narrowness ... round the cylinder' was omitted by Saunders and Swinton.

[15] Start of page AMT/C/24/9.

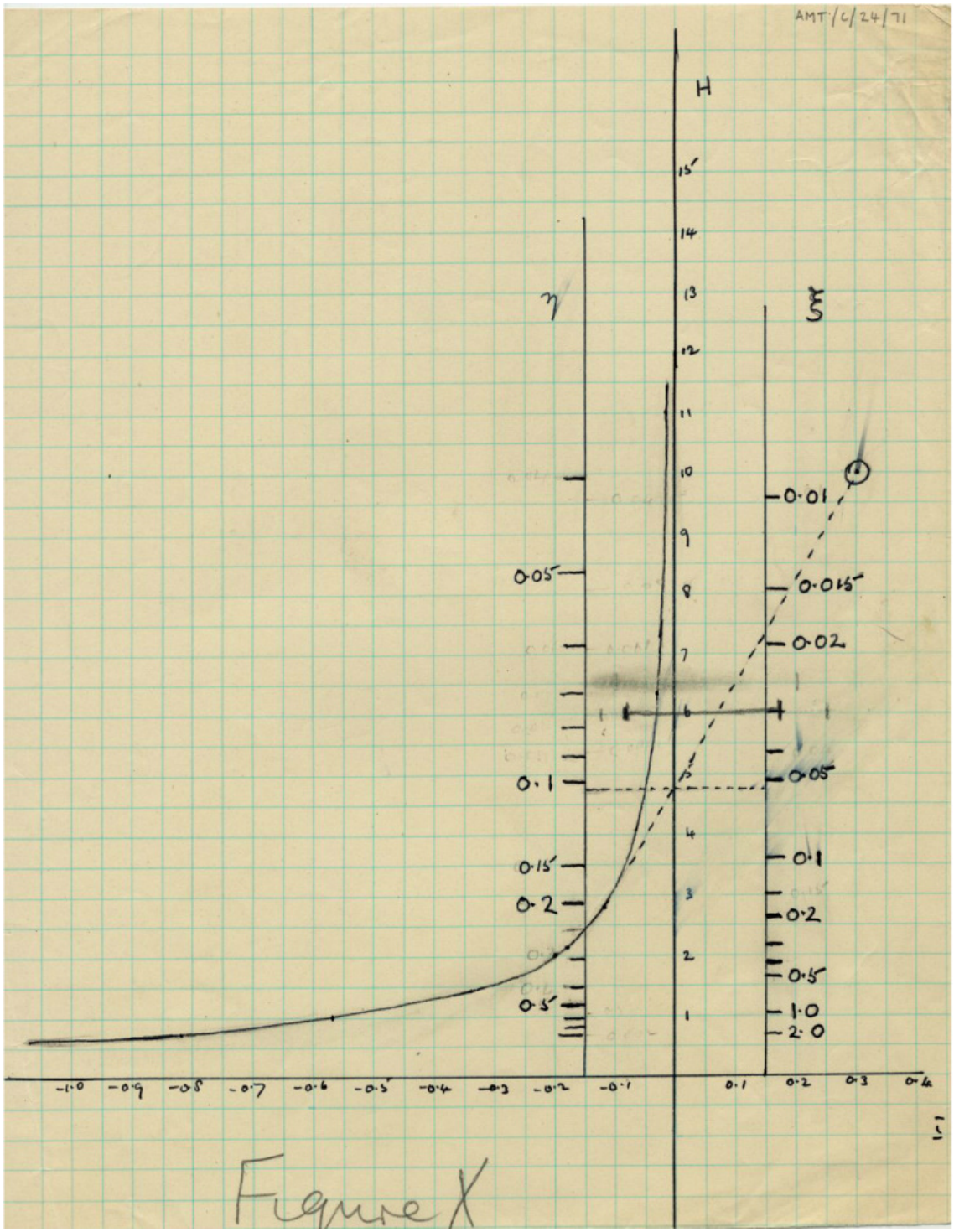


Figure 3: [Editorial note: This figure is a detail taken from AMT/C/24/71. It is plotted in ink with the pencil addition 'Figure X' below the figure. It is therefore almost certainly the 'Fig X' referred to on page AMT/C/24/73. Copyright © W.R. Owens.]

[16]Start of page AMT/C/24/10. Note that no section number is given for this or any subsequent section of the manuscript.

[17]Start of page AMT/C/24/11.

[18]Start of page AMT/C/24/12.

[19]Saunders and Swinton have 'pattern' here instead of the word 'function'. I have corrected the formula that follows as it appears incorrectly in Swinton's edition (as also a few lines earlier).

[20]Start of page AMT/C/24/13.

[21]The words 'given by' were omitted by Saunders and Swinton.

[22]Saunders' text finishes at this point.

[23]Start of page AMT/C/24/14.

[24]Start of page AMT/C/24/15.

[25]Swinton's text finishes at this point.

[26]Start of page AMT/C/24/27.

[27]Start of page AMT/C/24/28.

[28]Start of page AMT/C/24/29.

[29]This last factor of U is written as U^2 in the manuscript but U follows from the previous line and is mathematically correct.

[30]Start of page AMT/C/24/68.

[31]Presumably referring to Part I of the manuscript *Morphogen Theory of Phyllotaxis*, referred to in the main paper as *MTP I*

[32]Start of page AMT/C/24/69.

[33]Start of page AMT/C/24/70.

[34]Start of page AMT/C/27/47.

[35]The left hand side entry of the centre row reads $-\eta_3$ in the original manuscript and the lower right hand corner entry of this matrix reads $-\frac{\eta_2\eta_3}{\eta_1}$ in the original manuscript: these typos are clearly mathematically incorrect and so have been corrected here.

[36]Start of page AMT/C/27/48.

[37]In the original manuscript this list is given as x, $y_1^{(-)}$, $y_2^{(-)}$, $y_3^{(-)}$ but this seems to be clearly wrong given what follows.

[38]Start of page AMT/C/27/49.

[39]Start of page AMT/C/27/50.

[40]The lower left entry of this matrix reads $-\eta\frac{\partial G}{\partial \eta}$ in the original manuscript: this typo has been corrected.

[41]Start of page AMT/C/24/30.

[42]The text on the other side of this page, which is archived as page AMT/C/24/31, reads as follows: 'The points where the Jacobian vanishes are those where there are double roots for ξ, η for given X, Y, H.'

[43]Start of page AMT/C/24/73.

[44]Start of page AMT/C/24/72.

[45]Start of page AMT/C/24/74.