PERIODIC SOLUTIONS OF THE SUNFLOWER EQUATION: $\ddot{x} + (a/r)\dot{x} + (b/r) \sin x(t - r) = 0$*

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Abstract. In 1967 Israelsson and Johnsson proposed a model for the geotropic circumnutations of Helianthus annus. The existence of a geotropic reaction time is reflected in the delay r of the equation. Numerical computations suggested the existence of periodic solutions. In this paper, we prove the existence of periodic solutions for a range of the values of the parameters a,b,r. We use Razumikhin-type functions to prove the boundedness of all solutions. We then prove the existence of periodic solutions of small amplitude using the Hopf bifurcation theorem. Finally, we use a fixed-point theorem on a cone to prove the existence of periodic solutions of large amplitude.

1. A model for the geotropic circumnutations of the helianthus annus. In this section we present a model proposed by Israelsson and Johnsson [11] to explain the helical movements of the tip of growing plants.

The study of these movements goes back to Mohl [15] and Palm [18] in 1827. In 1865 Darwin [5] explained the oscillations as the bending of the plant due to differential growth on the sides of the stem. Baranetzki [2] used a clinostat to prove that the oscillations were due to the influence of the gravity. Gradmann [6] proposed an explanation based in the lateral auxin transport due to the influence of the gravity. He also suggested a connection between the reaction time and the period of the oscillations. (See Israelsson and Johnsson [11] for further details and literature.)

In order to investigate the influence of the gravity on the oscillations, the clinostat was used. In the clinostat, the plant is rotated along the longitudinal axis, while held in a horizontal position so that the stem is parallel to the ground. This makes the influence of gravity uniform all around the stem. It was observed that after some time the regular oscillations of the tip of the plant ceased, as expected.

The next experiment consisted in leaving the plant lying on its side for ten minutes and then returning it to the vertical position. For about twenty minutes nothing happened, and then the tip of the plant bent to one side. It kept bending until it reached a certain point and then it turned back, bending to the other side. It would then oscillate with a certain period T.

The interpretation of the experiment is as follows: during the time the plant was laying on its side (exposure time), growth hormone (auxin) accumulated on this side, say the left. Then the plant was set back in the vertical position and nothing happened for twenty more minutes. This means that the effect of the auxin accumulation is not felt immediately—

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there is a geotropic reaction time. After this time, the plant reacts to what happened thirty minutes before and bends to the right. After a while the auxin starts accumulating, now on the right side. Some time later there is more hormone on the right side, it grows faster and the plant bends to the left, and so on.

Increasing the exposure time increases the amplitude of the initial oscillations. For some plants these oscillations die out, while for others they are self-exciting, i.e. the plant starts oscillating by itself with a small amplitude which increases until it reaches a steady state, oscillating with constant amplitude.

The period of the oscillations and the geotropic reaction time of the Helianthus annus depend strongly on the temperature. The period changes from 100 minutes at 35°C to 270 minutes at 15°C, while in the same temperature interval the geotropic reaction time goes from 55 to 18 minutes.

We shall need the following equations. Let L_i, $i = 1, 2$ be the lengths of the sides of the stem and C_i the auxin concentration on these sides. It has been found that the increase of length per unit time is proportional to the concentration of auxin on that side:

$$dL_i/dt = K_1 C_i, \qquad i = 1, 2. \tag{1.1}$$

When the stem was tilted to one side it was found that more auxin accumulated on this side than on the other. The difference in concentration is proportional to the angle α which the stem makes with a plumb line. Let C_1, C_2 be the concentrations on sides 1 and 2:

$$\Delta C = C_1 - C_2 = K_2 \sin \alpha. \tag{1.2}$$

Refer to Fig. 1, and assume for simplicity that the stem is passing through the vertical position (i.e., $\alpha = 0$). In an increment of time Δt, the side L_1 has grown ΔL_1 farther than

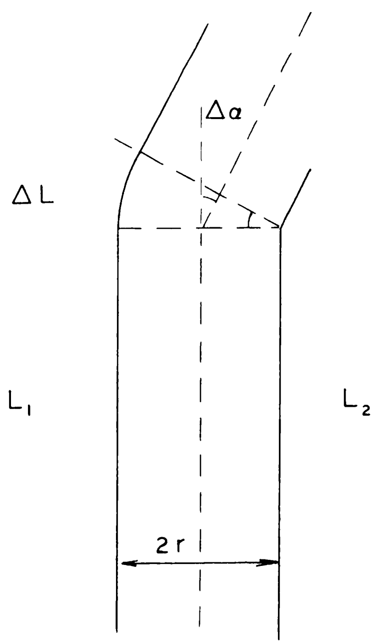

FIG. 1.

the side L_2, which has grown only ΔL_2, and so the stem is tilted by an angle $\Delta\alpha$. If d is the diameter of the stem we have $d\cdot\Delta\alpha = \Delta L = \Delta L_1 - \Delta L_2$, from which we obtain

$$\frac{d\alpha}{dt} = \frac{1}{d}\left(\frac{dL_1}{dt} - \frac{dL_2}{dt}\right)$$

and, from (1.1),

$$d\alpha/dt = \frac{1}{d} K_1 (C_1 - C_2) = (-K_1/d)(C_2 - C_1). \tag{1.3}$$

If we were to substitute (1.2) into (1.3) we would be assuming that the influence of the position on the auxin concentration is instantaneous.

To take into account the geotropic reaction time r, we assume that only positions of the plant before the time $(t - r)$ influence the auxin gradient bending the plant at time t. We can also assume that the auxin gradient is less dependent upon the position of the plant a long time ago and more dependent on the position at time $t - r$. Thus, we introduce an exponential discount function. We can write

$$C_2(t) - C_1(t) = K_2 \int_1^\infty \exp(-a(s - 1) \sin \alpha(t - \mathrm{sr})\, ds, \tag{1.4}$$

and combining (1.3) and (1.4) we obtain

$$\dot\alpha = -b \int_1^\infty \exp(-a(s - 1) \sin \alpha(t - \mathrm{sr})\, ds, \tag{1.5}$$

where $b = K_1K_2/d$.

We can make the change of variables $\omega = \mathrm{sr} - t$ and obtain

$$\dot\alpha = -\frac{b}{r}\int_{r-t}^\infty \exp\left[-a\left(\frac{\omega + t - r}{r}\right)\right] \sin \alpha(-\omega)\, d\omega.$$

Taking the derivative, we obtain

$$\ddot\alpha + (a/r)\dot\alpha + (b/r) \sin \alpha(t - r) = 0 \tag{1.6}$$

which is the "sunflower equation".

Using numerical calculations Johnsson [12] determined the values of a, and b for which Eq. (1.5) has a numerical periodic solution with period 157 minutes, assuming a delay r of 30 minutes.

We will prove in the following sections that for all parameters in a certain range there exist periodic solutions of Eq. (1.6). Thus, the model reflects the experimental fact that we have periodic solutions at different temperatures, and for different plants.

2. Boundedness of the solutions. We shall show that for the parameters in a certain range all solutions of the system (1.6) are bounded.

We rewrite Eq. (1.6) as

$$\dot x = y$$

$$\dot y = -(a/r)y - (b/r) \sin x(t - r). \tag{2.1}$$

We will assume $a \geq b > 0$, and $a \geq 1$.

The initial values we need to define a solution of (2.1) are: an initial function $\phi \in$

$C[-r, 0] \to \mathbf{R}$ for the x component and an initial point $p \in \mathbf{R}$ for the y component. Thus, it is natural to pick as state space $C_0 \overset{\text{def}}{=} C[-r, 0] \times \mathbf{R}$. We will denote by $z(t, \psi) = (x(t, \psi), y(t, \psi))$ a solution of (2.1) with initial value $\psi = (\phi, p) \in C_0$. We write $z_t = (x_t, y(t))$ and by x_t we mean $x_t = x(t + \theta)$, $-r \le \theta \le 0$. (See Hale [9, 10] for notation and basic theorems.)

We shall use repeatedly the following obvious fact.

LEMMA 2.1. Let S be a set in $\mathbf{R}^2$ and V a continuously differentiable function $V: S \to \mathbf{R}$ such that for some $c \in \mathbf{R}$, $\Gamma = \{(x, y) \mid V(x, y) = c\}$ is a Jordan curve separating S into two disjoint parts $\{V \le c\}$ and $\{V > c\}$. If the derivative of V along the solutions of (2.1) is negative semidefinite, $\dot{V} \le 0$ on the curve Γ, then a solution of (2.1) cannot pass from $\{V \le c\}$ to $\{V > c\}$ across the curve Γ.

We can now prove the following lemma.

LEMMA 2.2. (*i*) The y component of $z(t)$ is ultimately bounded; in particular, for each solution $z(t)$ there exists a $t_1 < \infty$ such that for $t \ge t_1$ we have $|y_t| \le b/a$.

(*ii*) If a solution $z(t)$ is such that $|y_t| \le b/a$ for $t = t_1$ then $|x(t) - x(t - r)| \le (b/a)r$ for $t \ge t_1$.

(*iii*) Let $r < a/(a + 1)\, \pi(a/b)$ and $G = \{(x, y) \mid |y| \le (b/a), |x| \le \pi, |x + Ky| \le \pi\}$, where $K = a\pi/(a + 1)b$. If for some t^*, $z_{t^*} \in G$ and $|y_{t^*}| < b/a$ then $z_t \in G$ for all $t \ge t^*$.

Proof: (*i*) Define $V_1 = y^2/2$. The derivative of V_1 along the solutions of (2.1) satisfies

$$\dot{V}_1 = y(-(a/r)y - (b/r) \sin x(t - r)) \le -r^{-1} |y| \, (a\,|y| - b)$$

and for all $\epsilon > 0$ there exists a $\delta = \delta(\epsilon)$ such that $|y| \ge (b/a) + \epsilon$ implies $\dot{V}_1 < -\delta < 0$.

Let $0 < \epsilon < 1$ and, by restricting it further if necessary, $\epsilon < ab\pi/(a + b)r$.

Claim 1: For each solution $z(t) = (x(t), y(t))$ there exists a $t_0 > 0$ such that $|y(t_0)| < (b/a) + \epsilon$. Assume not. Then $|y(t)| \ge (b/a) + \epsilon$ for all $t > 0$ and $\dot{V}_1 \le -\delta < 0$. Integrating along the solution $z(t)$, we obtain

$$V_1(z(t)) - V_1(z(0)) = \int_0^t \dot{V}_1(z(s))\, ds \le -\delta t,$$

and for some t, $V_1(z(t)) < 0$, which is a contradiction. That proves the claim.

By Lemma 2.1 we also have $|y_t| \le (b/a) + \epsilon$ for all $t \ge t_0 + r$.

Claim 2: For each solution $z(t)$ there exists a finite $t_1 > t_0$ such that $|y(t_1)| < (b/a)$. Assume not; then $(b/a) \le |y(t)| \le (b/a) + \epsilon$ for $t > t_0$ and so

$$(b/a)(t - t_0) \le |x(t) - x(t_0)| \le ((b/a) + \epsilon)(t - t_0).$$

Since $\dot{x} = y$ and $|y| > (b/a)$, there exists $t_0 < t^* < t^{**}$ and $N > 0$ such that $|x(t^* - r)| = 2N\pi$ and $|x(t^{**} - r)| = (2N + 1)\pi$.

Consider first the case when $x(t^* - r) > 0$. For $t \in [t^*, t^{**}]$ we have $\sin x(t - r) \ge 0$ and since $\dot{y}(t) = -(a/r)y(t) - (b/r) \sin x(t - r)$, we have $\dot{y} \le -(a/r)y(t) \le -(a/r)(b/a) = -b/r$. Thus,

$$y(t) \le y(t^*) - (b/r)(t - t^*) \quad \text{for} \quad t \in [t^*, t^{**}].$$

We claim that $(b/r)(t^{**} - t^*) > \epsilon$. Indeed,

$$\pi = x(t^{**} - r) - x(t^* - r) \le ((b/a) + \epsilon)(t^{**} - t^*) \le \frac{b + a}{a}\,(t^{**} - t^*).$$

Thus, $(t^{**} - t^*) \ge a\pi/(a + b) > (r/b)\,\epsilon$, by the condition on ϵ, and so $(b/r)(t^{**} - t^*) > \epsilon$, as we wanted.

Now, $y(t^{**}) \leq y(t^*) - (b/r)(t^{**} - t^*) < y(t^*) - \epsilon \leq (b/a) + \epsilon - \epsilon = b/a$, which contradicts $(b/a) \leq |y(t)|$.

For the case $x(t^* - r) < 0$ one uses the same kind of argument.

By Lemma 2.1 we have $|y(t)| \leq (b/a)$ for $t \geq t_1$. This proves part (i).

(ii) We have $|\dot{x}| = |y| \leq b/a$ and $|x(t) - x(t-r)| \leq |\dot{x}|\ r \leq (b/a)r$.

(iii) Refer to Fig. 2, and consider the box—call it G—indicated. The line $x + Ky = \pi$ will cross the line $y = (b/a)$ at the point $x_0 = a\pi/(a+1)$.

From (ii) we also have

$$|x(t) - x(t-r)| \leq r\frac{b}{a} < a/(a+1)\pi(a/b)(b/a) = a/(a+1)\pi.$$

Thus, if $x(t-r) = 0$ we have $|x(t)| < x_0$, and if $x(t) \geq x_0$, $x(t-r) > 0$ (or, if $x(t) = -x_0$, $x(t-r) < 0$).

Consider the functions $V_1 = y^2/2$, $V_2 = x^2/2$, $V_3 = x + Ky$. *The derivatives along the solutions of (2.1) satisfy*

$$\dot{V}_1 \leq -r^{-1}|y|(a|y| - b), \qquad \dot{V}_2 = xy,$$

$$\dot{V}_3 = y + K(-(a/r)y - (b/r)\sin x(t-r)) = (1 - K(a/r))y - K(b/r)\sin x(t-r).$$

We have $1 - K(a/r) < 0$ since $r < aK = a/(a+1)\pi(a/b)$.

Assume that a solution $z(t)$ of (2.1) is such that for some $t_* > 0$, $z_{t^*} \in G$, $|y_{t^*}| < b/a$. Let us consider several cases.

If $z(t^*)$ is in the first quadrant, then $z(t)$ cannot get out of G across the line $y = (b/a)$ because $\dot{V}_1 \leq 0$ on this line and Lemma 2.1 applies. If $x(t) \geq x_0$ then $x(t-r) > 0$ and so $\dot{V}_3$

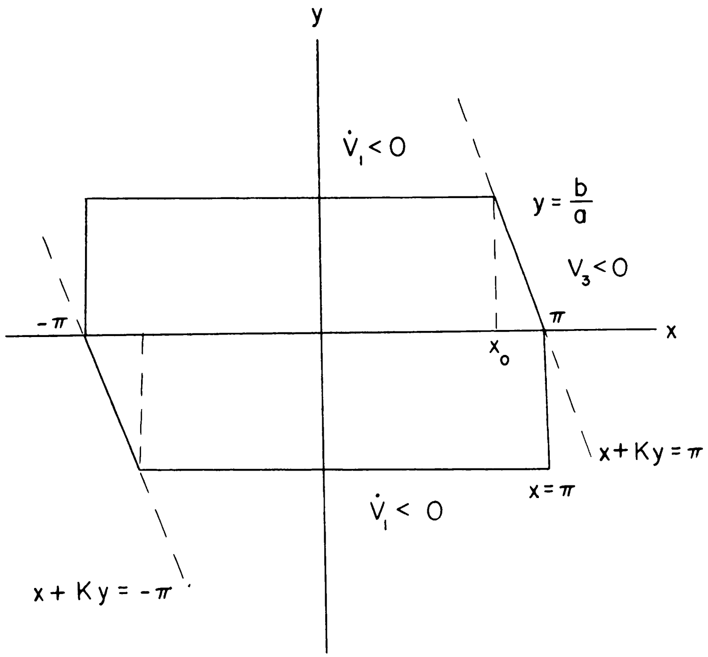

FIG. 2.

$\leq (1 - K(a/r))y - (b/r)\sin x(t - r) < 0$ and the solution cannot cross the line $x + Ky = \pi$. Thus, it remains in the first quadrant part of G or goes to the second quadrant.

If $z(t^*)$ is in the second quadrant, the solution $z(t)$ cannot cross the line $x = \pi$ because there $\dot{V}_2 \leq 0$ and Lemma 2.1 applies. It cannot cross $y = -(b/a)$ because $\dot{V}_1 \leq 0$.

In the third and fourth quadrants similar arguments prove that a solution cannot leave G.

That proves the third part of the Lemma 2.2.

Remark: Let

$$G_\epsilon = \{(x, y) \mid |y| \leq b/a, |x| \leq \pi - \epsilon, |x + Ky| \leq \pi - \epsilon\}.$$

It is clear from the proof of the lemma that for $\epsilon > 0$ sufficiently small, if $z_{t_1} \in G_\epsilon$, and $|y_{t_1}| < b/a$, then $z_t \in G_\epsilon$ for $t \geq t_1$.

THEOREM 2.1: If $r < (a/(a + 1))\pi a/b$ all solutions of (2.1) are bounded.

Proof: By Lemma 2.2 (i), for each solution $z(t)$ there exists a $t_1 > 0$ such that $|y_t| \leq (b/a)$ for $t \geq t_1$. There also exists an integer N, such that $|x(t_1)| \leq 2\pi N$.

We construct a box G as before but with $|x + Ky| = (2N + 1)\pi$ and use the same arguments as in Lemma 2.2 (iii) to prove that $z_t \in G$ for $t \geq t_1$.

3. Oscillations of small amplitude: Hopf bifurcation. In this section, we look for periodic solutions of small amplitude. It seems plausible that in a small neighborhood of the origin the system (2.1) would behave more or less like its linearized version. This statement is made precise in the Hopf bifurcation theorem.

Thus, we are interested in the solutions of the linear system

$$\begin{aligned} \dot{x} &= y \\ \dot{y} &= -(a/r)y - (b/r)x(t - r) \end{aligned} \tag{3.1}$$

which we will sometimes denote by $\dot{z} = L(a)z_t$, where $L(a)$ is a linear operator on C_0, depending on a.

The characteristic equation of (3.1) is

$$\Delta(\lambda) = \lambda^2 + (a/r)\lambda + (b/r)\exp(-\lambda r) = 0. \tag{3.2}$$

LEMMA 3.1: All solutions of (3.2) have negative real parts if and only if $(a/br)\zeta > \sin\zeta$, where ζ is the only root of $(1/br)\sigma^2 = \cos\sigma$ in $[0, \pi/2]$.

Proof: By Pontryagin's method (see Hale [10., Appendix]).

This lemma gives us a range of the parameters for which the origin of (3.1) is asymptotically stable.

LEMMA 3.2: There exists a r_0, $a/b < r_0 < a\pi/2b$, such that

(i) For $r < r_0$ all solutions of (3.2) have negative real parts,

(ii) For $r = r_0$ there is a conjugate pair of pure imaginary solutions.

(iii) For each $r > r_0$ there are precisely two roots of (3.2) with $\operatorname{Re}\lambda > 0$ and $-\pi/r < \operatorname{Im}\lambda < \pi/r$.

Proof: (i) By Lemma 3.1 we know that all solutions of (3.2) have negative real parts if and only if $(a/br)\zeta > \sin\zeta$ where ζ is the only root of $(1/br)\sigma^2 = \cos\sigma$ in $[0, \pi/2]$.

Refer to Fig. 3. We have $(a/br)\zeta > \sin\zeta$ if and only if the root t_1 of $g(\sigma) \overset{\text{def}}{=} (a/br)\sigma - \sin\sigma$ is smaller than ζ. For $r = a/b$ the line $u = (a/br)\sigma$ is tangent to $\sin\sigma$ at the origin and thus for $r \leq (a/b)$, $t_1 = 0$ and $t_1 < \zeta$. Also, for $r = a\pi/2b$ the root of $g(\sigma)$ is at $t_1 = \pi/2$. But $\zeta < \pi/2$, so in this case $t_1 > \zeta$. Thus, there must be a r_0, $a/b < r_0 < a\pi/2b$ for which the

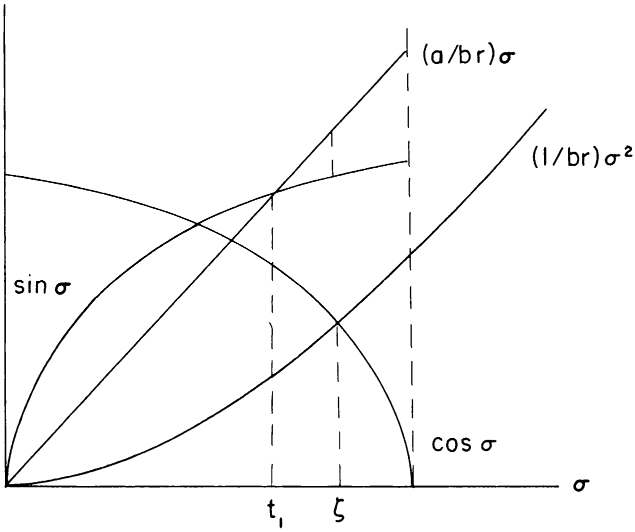

FIG. 3.

roots t_1 and ζ coincide, i.e. $g(\zeta) = 0$. For this value of r_0 we have

$$\begin{aligned}(a/br_0)\zeta &= \sin\zeta \\ (1/br_0)\zeta^2 &= \cos\zeta.\end{aligned} \tag{3.3}$$

It is also clear that for $r < r_0$, $t_1 < \zeta$, and so $(a/br)\zeta > \sin\zeta$ and all solutions have negative real parts.

(ii) Let $\lambda = \mu + i\sigma$ be a solution of (3.2). Then μ and σ satisfy

$$\begin{aligned}\mu^2 - \sigma^2 + (a/r)\mu + (b/r)\exp(-\mu r)\cos r\sigma &= 0 \\ 2\sigma\mu + (a/r)\sigma - (b/r)\exp(-\mu r)\sin r\sigma &= 0.\end{aligned} \tag{3.4}$$

For $r = r_0$ a solution of (3.4) is $\mu = 0$, $\sigma_0 = \pm(\zeta/r_0)$. Indeed, substituting for these values in (3.4), we obtain

$$-(\zeta/r_0)^2 + (b/r_0)\cos\zeta = 0$$
$$(a/r_0)(\zeta/r_0) - (b/r_0)\sin\zeta = 0$$

which are satisfied by (3.3).

(iii) There are two different proofs of this fact. One is due to Grafton [7] and can be found in Hale [9, Lemma 31.4] and the other is due to Nussbaum [16, Lemma 3.2].

In order to apply the Hopf bifurcation theorem, we have to study the variation of the spectrum of L, i.e. the roots of (3.2), when we change one parameter of the equation.

We can rewrite Eq. (2.1) as

$$\dot{z} = F(a, b, r, z_t).$$

If we choose r as a parameter, the dependence of F on r is complicated because r enters in the definition of z_t. Thus, we choose a as parameter.

The following lemma gives information on the behavior of the spectrum of $L(a)$ when the parameter a changes.

LEMMA 3.3: Let ζ be the root of $(1/br)\sigma^2 = \cos\sigma$ in $(0, \pi/2)$. For fixed r, and b there exists an a_0, $2br/\pi < a_0 < br$ such that $a_0 = (br/\zeta)\sin\zeta$ and

(i) If $a > a_0$ all solutions of (3.2) have negative real parts.

(ii) If $a = a_0$ there is a conjugate pair of pure imaginary roots, $\lambda_0 = \pm i\sigma_0$, and all characteristic roots $\lambda_j \neq \lambda_0$, satisfy $\lambda_j \neq m\lambda_0$ for any integer m.

(iii) There exists a $\epsilon > 0$ and a complex function $\lambda(a)$ with continuous derivative $\lambda'(a)$ defined in $[a_0 - \epsilon, a_0 + \epsilon]$. The function $\lambda(a)$ satisfies $\Delta(\lambda(a)) = 0$, $\lambda(a_0) = \pm i\sigma_0$, and Re $\lambda'(a_0) \neq 0$.

(iv) If $a < a_0$ there are precisely two roots of (3.2) with Re $\lambda > 0$ and $-\pi/r <$ Im $\lambda < \pi/r$.

Proof: (i) Refer to Fig. 3. As in the proof of Lemma 3.2, we have $(a/br)\zeta > \sin\zeta$ iff the root t_1 of $g(t) = (a/br)t - \sin t$ is smaller than ζ. For $a = rb$ the line $u = (a/br)t$ is tangent to $\sin t$ at the origin and thus for $a > rb$, $t_1 = 0$ and $t_1 < \zeta$. Also, for $a = 2br/\pi$, $t_1 = \pi/2$. But $\zeta < \pi/2$ and so $t_1 > \zeta$. Thus there must be a a_0, $2br/\pi < a_0\, br$ for which $t_1 = \zeta$.

From the equations

$$\begin{aligned}(a_0/br)\zeta &= \sin\zeta \\ (1/br)\zeta^2 &= \cos\zeta\end{aligned} \tag{3.5}$$

it is clear that $a_0 = (br/\zeta)\sin\zeta$. It is also clear that for $a > a_0$, $t_1 < \zeta$, and so $(a/br)\zeta > \sin\zeta$ and all solutions of (3.2) have negative real parts.

(ii) Let $\lambda = \mu + i\sigma$ be a solution of (3.2). Then μ and σ satisfy Eqs. (3.4) above.

For $a = a_0$, a solution λ_0 of this equation is $\mu = 0$ and $\sigma_0 = \pm(\zeta/r)$. Indeed, substituting in (3.4), we obtain

$$-(\zeta/r)^2 + (b/r)\cos\zeta = 0$$

$$(a/r)(\pm\zeta/r) - (b/r)\sin(\pm\zeta) = 0$$

which are satisfied by (3.5). It is clear that no multiple of this solution can satisfy Eqs. (3.5). Thus, no multiple of λ_0 is a solution and $\lambda_j \neq m\lambda_0$ for all solutions λ_j.

(iii) Let us write $\Delta(\lambda) = \Delta(\mu + i\sigma)$ as $G(\mu, \sigma, a)$ and Eqs. (3.4) as $G(\mu, \sigma, a) = 0$. By part (ii) we know that $G(0, \sigma_0, a_0) = 0$, where $\sigma_0 = \pm\zeta/r$, $a_0 < br$.

If the Jacobian of G with respect to μ and σ is different from zero at $(0, \sigma_0, a_0)$, by the implicit function theorem there exists a $\epsilon > 0$ and two continuously differentiable functions $\mu(a)$, $\sigma(a)$ defined in $[a_0 - \epsilon, a_0 + \epsilon]$ such that

$$J(\mu, \sigma, a) = \begin{pmatrix} 2\mu + (a/r) - b\exp(-\mu r)\cos r\sigma & -2\sigma - b\exp(-\mu r)\sin r\sigma \\ 2\sigma + b\exp(-\mu r)\sin r\sigma & 2\mu + (a/r) - b\exp(-\mu r)\cos r\sigma \end{pmatrix} \tag{3.6}$$

and

$$J(0, \sigma_0, a_0) = \begin{pmatrix} A & -B \\ B & A \end{pmatrix} \tag{3.7}$$

where $A = (a_0/r) - b\cos\sigma_0 r$, $B = 2\sigma_0 + b\sin\sigma_0 r$.

Thus, $|J| = A^2 + B^2 \neq 0$ since $B \neq 0$. Indeed, $r\sigma_0 = \pm\zeta$ and $2(\pm\zeta/r) + b\sin(\pm\zeta) \neq 0$ for $0 < \zeta < \pi/2$.

To show that Re $\lambda'(a_0) = \mu'(a_0) \neq 0$ we observe that in $[a_0 - \epsilon, a_0 + \epsilon]$, $G(\mu(a), \sigma(a), a) \equiv 0$; thus $dG/da = 0$ or

$$\frac{\partial G}{\partial \mu}\cdot\frac{d\mu}{da} + \frac{\partial G}{\partial \sigma}\cdot\frac{d\sigma}{da} + \frac{\partial G}{\partial a} = 0. \tag{3.8}$$

At the point $(0, \sigma_0, a_0)$, Eq. (3.8) has the form

$$\begin{aligned} A\mu' - B\sigma' &= 0 \\ B\mu' + A\sigma' &= -\sigma_0/r \end{aligned} \tag{3.9}$$

since $\partial G/\partial a = (\mu/r, \sigma/r)$. From (3.9), we obtain $(A^2 + B^2)\mu' = -B\sigma_0/r \neq 0$.

(iv) Same as in Lemma 3.2.

This proves the Lemma 3.3.

Let us now write Eq. (2.1) as

$$\dot{z} = F(a, z_t) = L(a)z_t + f(a, z_t) \tag{3.10}$$

where $L(a)$ is the linear part. We have the following

THEOREM 3.1: Eq. (2.1) has a Hopf bifurcation at $a = a_0$, where a_0 is defined in Lemma 3.3.

Proof: $F(a, \phi)$ has continuous first- and second-order derivatives in a and ϕ for $a \in \mathbf{R}$ and $\phi \in C$, and $F(a, 0) = 0$ for all a.

By (ii) and (iii) of Lemma 3.3, the hypotheses H1 and H2 of Theorem XI, 1.1 in Hale [10] are satisfied. Therefore there is a Hopf bifurcation at $a = a_0$. Thus, for $a > a_0$ the only periodic solution is the trivial one. For $a \leq a_0$, two non-trivial periodic solutions of small amplitude appear. The period of these solutions is close to the period of the linear part, $2\pi/\sigma_0$.

The value a_0 of the parameter a is dependent on the values of the other two parameters, $a_0 = a_0(b, r)$, which we considered fixed.

In this section we have found a small range for the parameter $[a_0 - \epsilon, a_0]$ for which there are periodic solutions of small amplitude. Here the parameter a_0 satisfies $2br/\pi < a_0 < br$, which can be written as $a_0/b < r < a_0\pi/2b$. This can be interpreted as follows. For these values of a_0 and b there is a value r of the delay such that for this value there is a periodic solution of small amplitude.

More generally, for any values of a and b satisfying the conditions in (2.1) there is an r such that the characteristic equation (3.2) has a root on the imaginary axis and there are no roots in the right-hand plane (Lemma 3.2). Consider now b and this r as fixed. The a_0 given by Lemma 3.3 will coincide with the given a, $a_0 = a$, and applying the Theorem we prove the existence of a periodic solution. Thus, given a and b, there is an r, $a/b < r < a\pi/2b$ for which there is a periodic solution of small amplitude.

In the next section we shall prove the existence of oscillations of large amplitude for all delay in the range $a/b < r_0 \leq r < (a/a + 1)a\pi/b$.

4. Periodic solutions of large amplitude. We are going to use the following approach (see Grafton [7], Nussbaum [16], Hale [9]). Assume we can find a set K in C_0 such that for all $\psi \in K$, there is a time $\tau(\psi)$ such that the solution $z(t; \psi)$ with initial value ψ satisfies $z_{\tau(\psi)}(\psi) \in K$. We could then define an operator A: $K \to K$ by $A\psi = z_{\tau(\psi)}(\psi)$.

If K is closed, bounded and convex and A is completely continuous, A would have a fixed point ϕ in K, $A\phi = \phi$. In this case $z(t, \phi)$ will be a periodic solution of period $\tau(\phi)$.

Since what we want are non-trivial periodic solutions, it is necessary to exclude from K

the equilibrium points (constant solutions). In applications it is difficult to construct a closed convex set K not including the zero function. But if, roughly speaking, the zero solution is unstable, then it is possible to prove that there is a non-trivial periodic solution.

Let us make precise these ideas. Let K be a subset of a Banach space X, and A a map A: $K\backslash\{x_0\} \to K$. We say that x_0 is an *ejective point* if there exists an open neighborhood G of x_0 such that for all $y \in G \cap K$ there exists an integer m such that $A^m y \notin G \cap K$.

We shall need the following theorem.

THEOREM 4.1 (Nussbaum). If K is a closed, bounded, convex, infinite-dimensional set in X, A: $K\backslash\{x_0\} \to K$ is completely continuous and x_0 is an ejective point of A, then there is a fixed point of A in $K\backslash\{x_0\}$.

We shall also need a criterion for knowing when a point is ejective. Let C be the space of continuous functions in $[-r, 0]$ with the sup norm. Consider the equation

$$\dot{x}(t) = L(x_t) + f(x_t) \tag{4.1}$$

where $L(x_t)$: $C \to \mathbf{R}^n$ is linear and continuous, f: $C \to \mathbf{R}^n$ is completely continuous, $f \in C^1$ and $f(0) = 0$.

Let

$$\dot{y}(t) = L(y_t) \tag{4.2}$$

be the linear part. For any characteristic root λ of (4.2) there exists a decomposition of C as $C = P_\lambda \oplus Q_\lambda$ where P_λ and Q_λ are invariant under the solution operator of (4.2) (see Hale [9, Chapter 20]). Call the projection operator defined by the decomposition π_λ, with $R(\pi_\lambda) = P_\lambda$.

THEOREM 4.2 (Chow-Hale). Suppose the following conditions obtain: (i) There is a characteristic root λ of (4.2) such that $\operatorname{Re}\lambda > 0$.

(ii) There exists a closed convex set $K \subset C$, $0 \in K$ and $\delta > 0$ such that $\inf\{\pi_\lambda\phi \mid \phi \in K, |\phi| = \delta\} > 0$.

(iii) There exists a bounded continuous function τ: $K\backslash\{0\} \to [\alpha, \infty)$ $0 \leq \alpha$, such that the map defined by $A\phi = x_{\tau(\phi)}(\phi)$, $\phi \in K\backslash\{0\}$, maps $K\backslash\{0\} \to K$ and is completely continuous.

Then 0 is an ejective point.

For the proof of this theorem, see Chow and Hale [4]. The idea of condition (i) is to ensure the existence of an eigenspace of positive eigenvectors. Condition (ii) implies that the projection of all the initial functions of norm δ on this eigenspace is non-zero.

To apply Theorem 4.1 we have to define K and A. Let $K = \{\psi = (\phi, p) \in C_0 \mid 0 \leq p \leq b/a,\ 0 = \phi(-r),\ \phi$ non-decreasing, $\phi(0) + kp \leq \pi - \epsilon\}$ where $k = a\pi/(a+1)b$ and $0 < \epsilon \ll 1$. Let $z(t) = (x(t), y(t))$ be a solution of (2.1) with delay r, $(a/b) < r_0 < r < (a/a + 1)\pi a/b$ and initial function $\psi \in K\backslash\{0\}$.

LEMMA 4.1. (i) There exists a continuous function $\tau_1(\psi)$: $K\backslash\{0\} \to (r, \infty)$ such that $z_{\tau_1(\psi)}(\psi) \in -K \stackrel{\text{def}}{=} \{-\psi \mid \psi \in K\}$.

(ii) There exist a continuous function $\tau_2(\psi)$: $-K\backslash\{0\} \to (r, \infty)$ such that $z_{\tau_2(\psi)}(\psi) \in K$.

(iii) The solution $z(t)$ is oscillatory, i.e., $x(t)$, $y(t)$ have infinitely many zeros.

Proof: If $\psi \in K$ and $z(\psi)$ is a solution of (2.1) then $-z(\psi) = z(-\psi)$ is also a solution (simply multiply by -1 both sides of the equation). Thus, (i) implies (ii). Also (i) and (ii) imply (iii).

We need only to prove (i). Refer to Fig. 4. Let $z(t)$ be a solution with initial function in K. Then at time $t = 0$ it would start at some point of the I quadrant, say the point 0 (see

Fig. 4). As long as it remains in I we have $\dot{x} > 0$ and $\dot{y} < 0$. Since by Lemma 2.2 it cannot leave the box G_ϵ, it has to cross the x-axis at some time t_1. At the crossing $y(t_1) = 0$ and so $\dot{x} = 0$. It crosses with vertical slope. Also, $\dot{y} = -(b/r) \sin x(t_1 - r) < 0$, and the solution cannot cross back to I.

Since it cannot cross back to I, nor get out of the box G_ϵ, it either approaches the origin or crosses to III. We will show later that it cannot approach the origin, so there is a time t_2 such that $x(t_2) = 0$ and $\dot{x}(t_2) < 0$.

In III, $\dot{x} < 0$, so the solution cannot approach the origin. Since it cannot leave the box, it will cross the x-axis at some time t_4. This implies $\dot{y}(t_4) > 0$, and so $\sin x(t_4 - r) < 0$ and $x(t_4 - r) < 0$. Therefore, there exists a time t_3 such that $x(t_3 - r) = 0$.

Using the fact that the solution depends continuously on the initial data, and the implicit function theorem, one can prove that the time t_3 such that $x(t_3 - r; \phi, p) = 0$ is a continuous function of $(\phi, p) \in K\backslash\{0\}$.

The function z_{t_3} belongs to $-K$, for $y(t_3) < 0$, x_{t_3} is decreasing, $x(t_3 - r) = 0$ and $|x(t_3) + ky(t_3)| \leq \pi - \epsilon$. Thus, we can define $\tau_1(\psi) = t_3$.

To finish the proof we need to prove that the solution $z(t)$ does not approach the origin in II. At the time of the crossing of the x-axis we have $y(t_1) = 0$ and $\dot{y}(t_1) = -(b/r) \sin x(t_1 - r) < 0$. By continuity $\dot{y}(t) < 0$ for some time. Let $t^* > t_1$ be such that $\dot{y}(t^*) = 0$ for the first time and let $y(t^*) = -\delta < 0$ be the corresponding value of y. We claim that there exists a ρ, $0 < \rho < \delta$ such that for $t \geq t^*$ and $z(t)$ in II, $y(t) \leq -\rho$. In particular, this implies that there exists a $t_2 > t^*$ such that $x(t_2) = 0$ and $y(t_2) \leq -\rho$.

Pick a $x^* > 0$ so small that:

(i) $x^* < \delta$,

(ii) $x^*/\sin x^* \leq 1 + \eta$, for some small $\eta > 0$ such that $(1 + \eta)(a/b) < r_0$,

(iii) $\sin x^* \leq \min \{\sin x(t_1 - r), \sin x(t_1)\}$.

As t increases, $x(t - r)$ increases from the value $x(t_1 - r)$ to the value $x(t_1)$, and then decreases approaching the y-axis. Thus, it is possible to choose a x^* which satisfies (iii) and

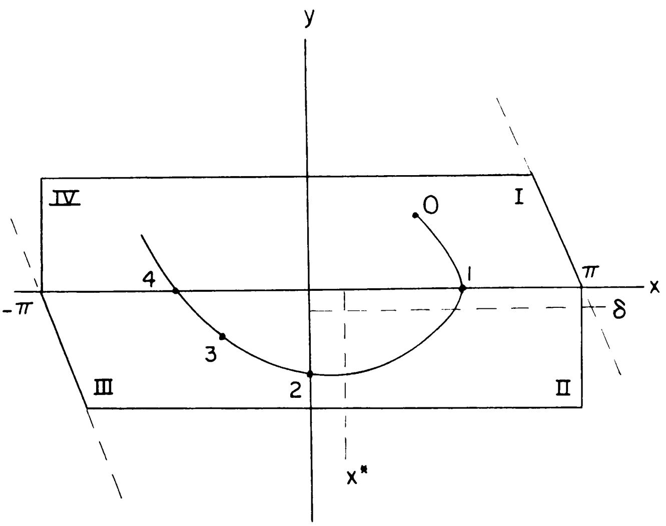

FIG. 4.

such that

$$\sin x^* \le \sin x(t-r) \quad \text{for} \quad t \ge t_1 \quad \text{and} \quad x(t-r) \ge x^*.$$

(see Fig. 5). From the second equation in (2.1) we observe that

$$|y| < (b/a) \sin x(t-r) \quad \text{implies} \quad \dot{y} < 0. \tag{4.3}$$

Let $\rho = (b/a) \sin x^*$. Note that $\rho < \sin x^* \le x^* < \delta$ since $(b/a) \le 1$. We want to prove that for $t \ge t^*$ and $x(t-r) \ge x^*$ we have $y(t) \le -\delta$. Indeed, $y(t^*) = -\delta < -\rho$, and for $t > t^*$ the solution cannot cross the line $y = -\rho$, since at that moment we have $|y| = \rho = (b/a) \sin x^* \le (b/a) \sin x(t-r)$, and by (4.3) $\dot{y} < 0$.

Thus, since $\dot{x} = y$, we have $|x(t) - x(t-r)| \ge \rho r$ or $x(t-r) - x(t) \ge \rho r = (b/a) \sin x^* r$. We are interested in values of the delay $r > (a/b)$. By the choice of η we have that $r > r_0 > (a/b)(1+\eta) \ge (a/b)x^*/\sin x^*$, and

$$x(t-r) - x(t) \ge \rho r > (b/a)(a/b)x^*(\sin x^*/\sin x^*) = x^*,$$

and so when $x(t-r) = x^*$ we have $x(t) < 0$ and the solution had crossed the axis at some time t_2, with $y(t_2) \le -\rho$. That proves the lemma.

We can now define $A\colon K\backslash\{0\} \to K$ by $A\psi = -z_{T(\psi)}(\psi)$. If ψ is a fixed point of A, i.e. if $A\psi = \psi$, then $z_t(\psi)$ is a periodic solution of period $2\tau(\psi)$. Indeed,

$$z_{2T(\psi)}(\psi) = z_{T(\psi)}(z_{T(\psi)}(\psi)) = z_{T(\psi)}(-A(\psi)) = z_{T(\psi)}(-\psi) = -z_{T(\psi)}(\psi) = A(\psi) = \psi.$$

The next step is to prove

LEMMA 4.2. The map $A\colon K\backslash\{0\} \to K$ is completely continuous.

Proof: A is continuous, for $A\psi = -z_{T(\psi)}(\psi)$ and the solution $z_t(\psi)$ is continuous in t and ψ. Also, $\tau(\psi)$ is continuous in ψ. Thus, $z_{T(\psi)}(\psi)$ is continuous in ψ.

To prove that A is compact, we prove that for all bounded sets $B \subset K$ the set AB is uniformly bounded and equicontinuous. AB is equibounded since $AB \subset K$ and K is bounded. Let $\psi \in B$; since $A\psi = -z_{T(\psi)}(\psi)$ and $z(t, \psi)$ is a solution of the equation its derivative satisfies the equation. The right-hand side of the equation is uniformly bounded, so we can find a uniform bound for the derivatives. Thus, the set of functions $\{A\psi \mid \psi \in B\}$ is equicontinuous.

It remains to prove that the trivial solution $\{0\}$ is an ejective point. To use Theorem 4.2, we have only to check condition (ii), since condition (i) is ensured by Lemma 3.2, condition (iii) by Lemmas 4.1 and 4.2.

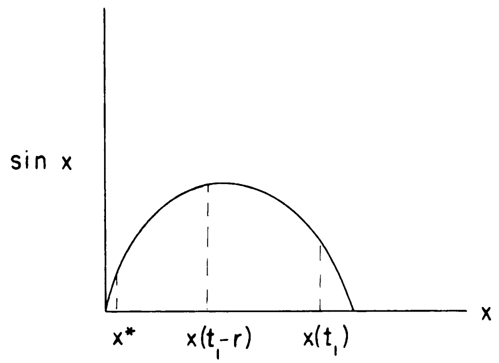

FIG. 5

LEMMA 4.3: Let $r > r_0$; then $\inf \{\|\pi_\lambda \psi\|, \psi \in K, |\psi| = 1\} > 0$.

Proof: The proof is essentially the same as in Lemma 31.5 in Hale [9, p. 173].

We can now prove

THEOREM 4.3. For each r such that $(a/b) < r_0 < r < (a/a + 1)\pi(a/b)$ Eq. (2.1) has a periodic solution.

Proof: Take K and A as above. By Lemma 4.2, A is completely continuous. By Lemmas 3.2, 4.1, 4.2, 4.3 and Theorem 4.2, $\{0\}$ is an ejective point. By Theorem 4.1, A has a fixed point in $K\backslash\{0\}$. Since there are no more equilibrium points, this fixed point corresponds to a non-trivial periodic solution.

5. Conclusions. We have proved that for a wide range of the parameters there exist periodic solutions. Thus the model reflects the experimental fact that there are periodic oscillations for a wide range of temperatures and for different experimental setups. Slight changes in the method of cultivation of the Helioanthus entrain changes in the period (see Andersen and Johnsson [1]).

An exhuastive numerical study of Eq. (2.1) had been made prior to the present work (see Casal and Somolinos [3]). The numerical and graphical results obtained via the computer provided an idea of the properties of the solutions for different ranges of the parameters. This insight proved invaluable for constructing the theoretical argument presented in this paper. In particular it was found that for values of the parameters $a = 4.8$, $b = 0.186$, all solutions tend to the origin as time increases, if the delay r is less than 35 minutes, but that for each value of r between 35 and 80 minutes there exists a periodic solution.

The value of r_0 in Theorem 4.3 is, for these values of a and b, $r_0 = 35$ minutes, in good agreement with the computer results. Our original proof of the theorem yielded periodic solutions only for $r < (a/b)\pi/2 = 40$. It was the desire to match the computer results which provided the motivation to improve the range of r to $r \leq (a^2/a + 1)\pi/b \simeq 76$ minutes, which agrees much better with the numerical results.

Johnsson and Karlsson [13] proposed also different weighting functions ("windows") for the description of the plant's memory. They lead to models with infinite time delays. It is possible to prove the existence of periodic solutions with small amplitude, using a Hopf bifurcation theorem for equations with infinite delay (see Lima [14]).

Finally, it would be interesting to study the phenomenon of entrainment [1]. The experiments suggest the existence of forced oscillations when the forcing frequency is not too different from the natural frequency.

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