T1988PRO20

A COMPUTER PROGRAM TO CREATE THE FIBONACCI FLORET PATTERN OF THE SUNFLOWER HEAD.

L. F. Hernández and J. H. Palmer
Department of Botany, University of New South Wales, Sydney, 2033, Australia.

SUMMARY

A computer model is presented that generates floret patterns which closely resemble those commonly found in mature sunflower capitula. Using the graphics routine of a desk-top computer, "heads" bearing as many as 3200 "florets" and with any row numbers can be created. The range of Fibonacci systems produced by the model can be used for developmental studies of phyllotaxis in compositae in general.

INTRODUCTION

In the head of the sunflower the florets and fruits normally form two sets of spiral rows of "contact parastichies" the numbers of which generally conform to the Fibonacci series, 21, 34, 55, 89 with 55,89 being the most common numbers. The arrangement of floret parastichies observed in the capitulum can be regarded as a geometrical phenomenon (Thompson, 1952) and the Fibonacci angle of divergence observed between consecutive emerging primordia, as a natural consequence of locating each primordium or "sets" of consecutive developing primordia in the available space left at the level of the "generative front" (Palmer and Steer, 1985).

The creation of the sunflower floret and fruit pattern has received a great deal of study (Church, 1904; Mathai and Davis, 1974; Vogel, 1979; Ridley, 1982a; 1982b; Palmer and Marc, 1982; Williams and Brittain, 1984). Several theories have been presented and computer-generated patterns of the head have been developed attempting to explain the control mechanism for Fibonacci phyllotaxis in the sunflower (Vogel, 1979 ; Ridley, 1982a, 1982b). The variables used in these models have generally been related either to the area occupied by each fruit at maturity, the packing efficiency of the fruits in a defined circular surface (Mathai and Davis, 1974; Vogel, 1979; Ridley, 1982a), or the diffusion of chemical promoters or inhibitors controlling the position of new floret primordia in the capitulum surface (Berding et al., 1983).

Some of the geometric laws that are involved in the construction of the phyllotactic pattern seen in the sunflower head have been incorporated into a computer program. The model assumes that the location of each floret primordium starts from the outermost part of the theoretically final capitulum radius and then calculates the plane coordinates for each consecutive "floret centre" at a specified angle of divergence. If this angle is the Fibonacci angle, then this automatically divides the available area between older primordia in the golden section (Dixon, 1981), generating the characteristic Fibonacci arrangement of points in a plane.

METHODS

1. Geometry of the model

The calculation of the location of each "floret" starts from the limit of the theoretically maximum radius (R) reached by the reproductive apex once it has been fully differentiated into floret primordia. It is also assumed that each "floret" is located centripetally. The spacing (ΔS) between primordia is calculated as a percentage (P) of the floret radius (r) both preselected as input constants. ΔS is a constant related to the spacing between the centres of consecutive primordia (Fig. 1) and is calculated by assuming that the first "angular nearest neighbour" (the 21^{th} primordium) is encountered after 8.02 turns of the genetic spiral, with a divergence of 7.67°. This spacing value will determine the number of clockwise and anticlockwise conspicuous parastichies that can be seen in the final pattern (Fig. 1). The step by step decrease in the radius (D_i) varies proportionally in relation to the actual radius (R_i), so that for each point with respect to its predecessor, the variables take the form:

$$\Delta S = r \cdot P/100$$
$$R = R_i - D_i \qquad [R_i \leq R]$$

where:

$$D_i = (\Delta S/R_i) \cdot 100$$

The radius decrease can be also set to a constant value, when:

$$D_i = (\Delta S)$$

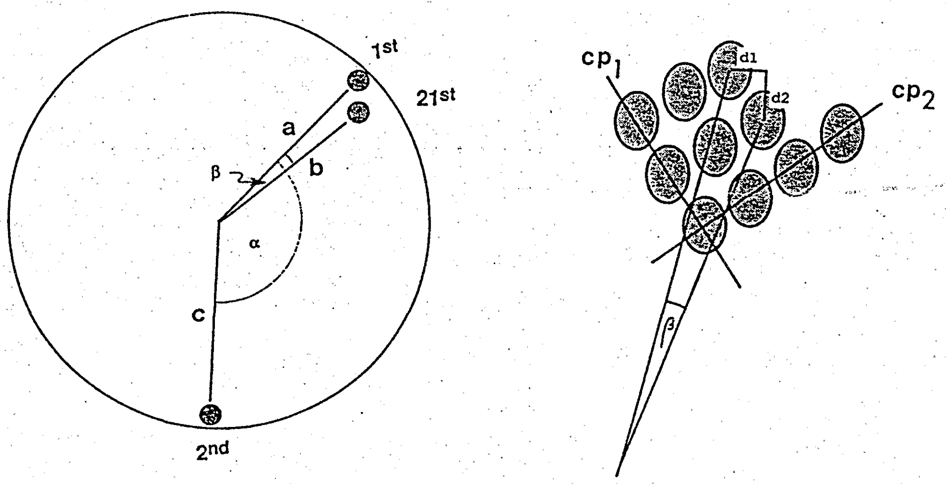

Figure 1: Schematic representation of the geometry of the computer model. If the divergence angle (α) = 137.5°, then the nearest angular neighbour (β = 7.67°) is encountered after 21 turns and the spacing between consecutive points is :

$$a = \text{Initial radius}$$
$$b = a - \Delta S \qquad [b = d2]$$
$$c = a - (b/21)$$

CP_1 and CP_2 show a pair of oppositely-oriented contact parastichies, determined by the spacing d1 and d2 between the nearest angular primordia, with a divergence (β) = 7.67°.

2. Program algorithm

<u>Constants</u>:

pi: 3.1416
XS: Position in the centre of the screen for X
YS: Position in the centre of the screen for Y
Rad1: Floret radius
Diverg1 = 0

Variables:

Diverg: Divergence angle
Rad2: Final capitulum radius
Spacing: Spacing between consecutive primordia as a percentage of Rad1

Graphic loop:

Diverg2 = Diverg1 - Diverg
Calculation of screen floret polar coordinates:
[XS - (Rad1 · SIN (Diverg2))], [YS - (Rad1 · COS (Diverg2))]
Diverg1 = Diverg2
Proportional radius decrease:
Rad2 = Rad2 - ((Spacing/Rad2)*100)
Constant radius decrease:
Rad2 = Rad2 - Spacing

Return to Graphic loop

The program has been written in basic for the Apple Macintosh desk top computer using Microsoft Basic (Fig. 2), but it can be easily adapted to be used in any computer with graphics facilities. The program is available on request.

RESULTS AND DISCUSSION

The model can create "heads" with any range of row number sequence and is a simple and deductive approach to the geometrical generation of contact parastichies in the sunflower capitulum. The floret patterns most commonly found in mature sunflower capitula are shown in Fig. 3. The "cyclotron generative spiral" model proposed by Vogel (1979) agrees with the patterns produced by the computer program described here. The "cyclotron" or "proportional" generative spiral is mainly a product of the surface expansion of the receptacle.

The program is interactive and can be used as a practical tool for a comprehensive generation of the phyllotactic patterns of compositae capitula.

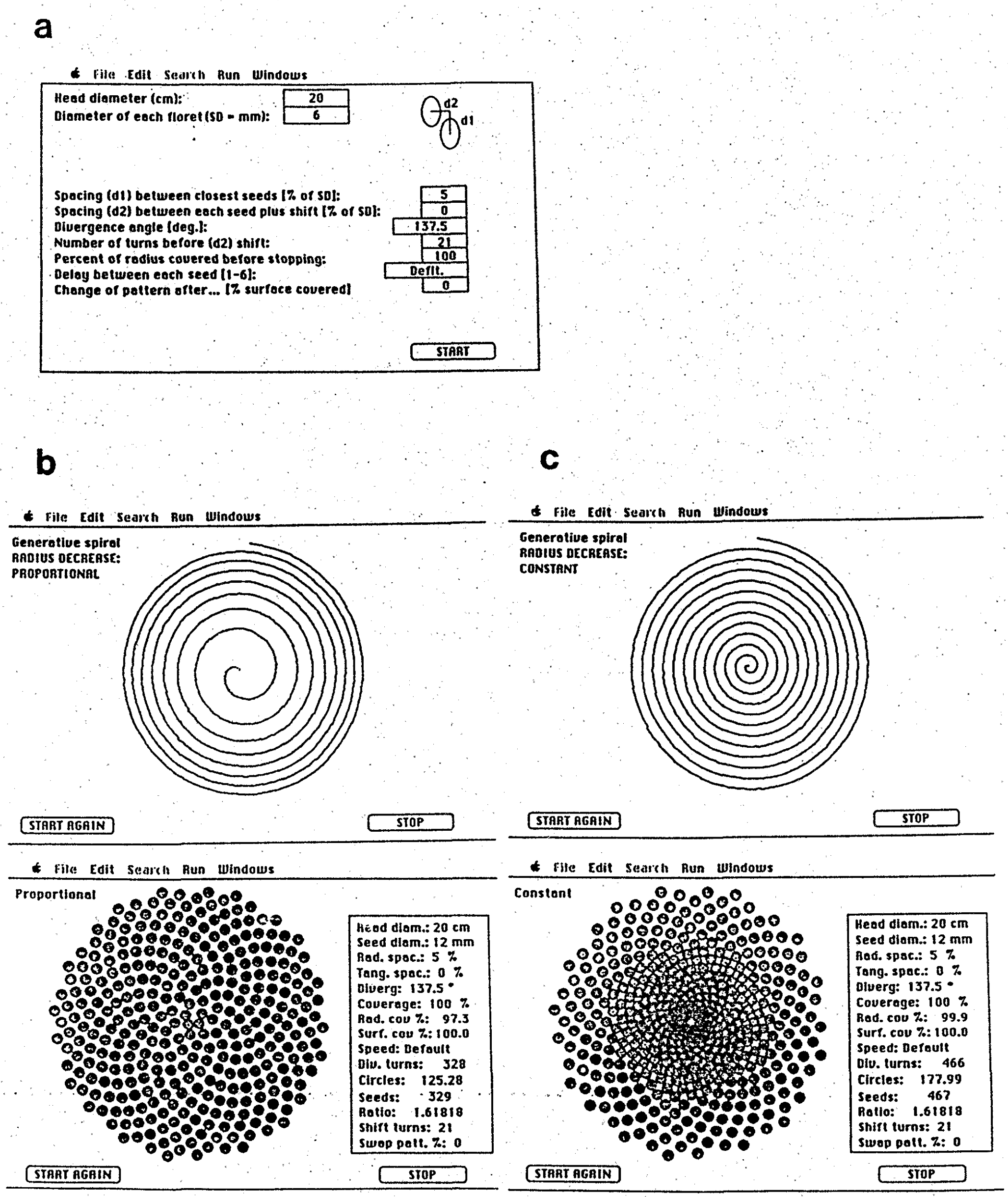

Figure 2: Format of the input variables (a) and output of the computer program using the options for radius decrease either (b) proportional or (c) constant. Note in each case the pattern of the generative spiral.

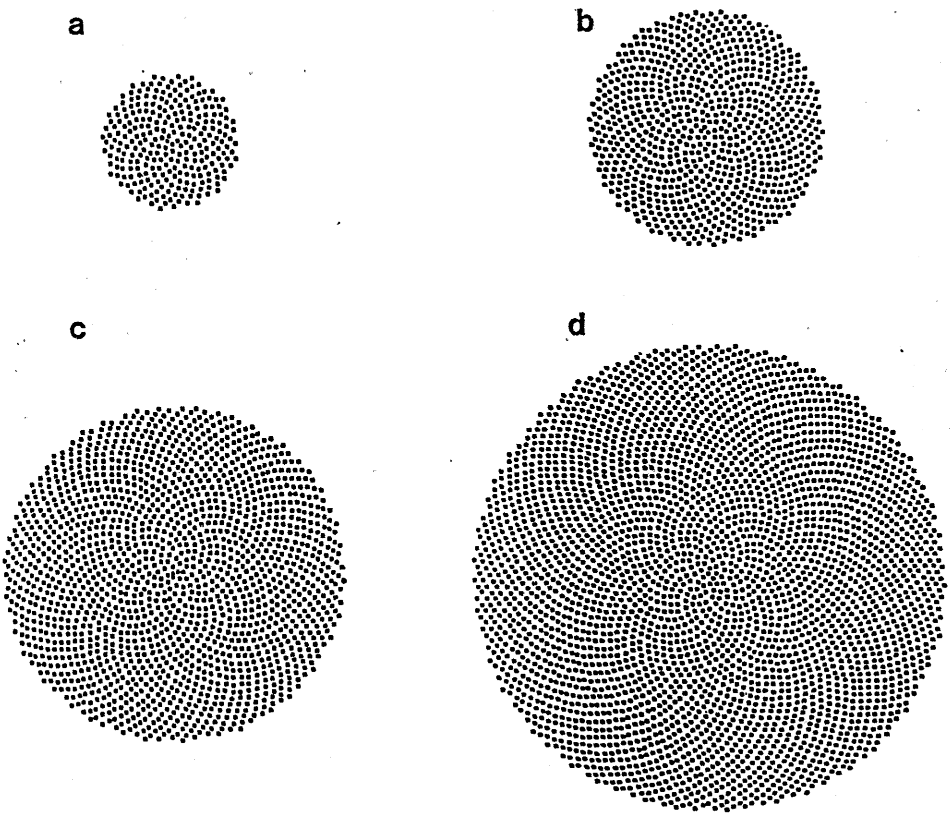

Figure 3: Ideal "capitula" created by the model. The number of rim parastichies are in each case: (a) 21/34; (b) 34/55; (c) 55/89; (d) 89/144.

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T1988PRO21

TECHNIQUES TO CHANGE THE NUMBER OF FLORET AND SEED ROWS IN THE SUNFLOWER CAPITULUM.

J. H. Palmer and L. F. Hernández.
Department of Botany, University of New South Wales, Sydney, 2033, Australia.

In the sunflower capitulum (head), disc florets and seeds are organised into distinct left and right turning spiral rows. The number of rows conform to the Fibonacci series, 21, 34, 55, 89, 144, with 55 and 89 being the most common in cultivated oilseed lines. The row number is not constant but decreases from the head rim to the centre, through 2 or 3 steps, with a common number linking the pairs together and forming the interlocking Fibonacci pattern that characterises the mature seed head (Fig.1). Environmental factors, for example, daylength and mineral nutrition can change disc floret row number although the Fibonacci pattern is always maintained (Palmer J. and Steer B.,1985. Field Crops Research, 11; 1-12). Three methods are described to remove the Fibonacci control of row number, without affecting disc floret initiation or seed production. Lines and hybrids used comprised Hysun 30, Sunfola 68-2, Suncross 150 and a Yugoslav Hybrid NS 44. The experiments were carried out on shoot apices of intact potted plants reared in a controlled environment cabinet under optimal growing conditions, during an 11 hr (SD) or 18 hr (LD) photoperiod.

(1). **Cytokinin Application.** Treatments commenced 18-25 days from sowing, when the shoot apex was 300-500 µm in diameter in the early dome stage of flower initiation, floral stage (FS) 3, prior to floret production (Marc J. and Palmer J.,1981. Field Crops Research, 4; 155-164). The cytokinin, benzyladenine (BA), was dissolved in 30% aqueous ethanol at a concentration of 0.5 mg ml^{-1}. This solution was applied directly to the terminal bud to give a daily dose of 50 µg, over a 5 day period. In 5 replicates, the control plants produced normal heads with 55/89 floret rows at the rim. 46% of BA treated plants showed no response; 54% produced heads showing varying degrees of irregularity in floret row organisation. 60% of these showed an increase in the number of disc floret rows to numbers which did not conform to the Fibonacci series (Fig. 2).The disc florets produced in the BA treatment appeared normal and gave fertile seeds.

(2). **Isolation of a Receptacle Segment.** The capitulum was used at FS 4 or 5, when the receptacle was a flat undeveloped disc, with a diameter ranging from 1.4-2.8 mm. A cylindrical wound was made in the receptacle surface with a sterile hypodermic needle to create a cylindrical plug of undifferentiated receptacle tissue 1 mm in diameter, which was isolated from lateral contact with the rest of the receptacle by a circular wound 50 µm wide and 200 µm deep, while retaining continuity with the subapical meristem. 96 plants were treated in in 4 replicates. Similar results were obtained in SD and LD. In LD, 3-6 days after creation of the plug, regularly spaced initials appeared around the plug rim. These rapidly formed involucral bracts and were followed by others which developed into either ray or disc florets (Fig.3). Similar floral organ initiation occurred around the outer rim of the wound. On the plug surface the disc florets were arranged in short spiral rows which extended to occupy the whole of the plug surface in about 9-12 days. The involucral bracts, ray and disc florets induced on the plug surface appeared to be normal in all respects. The base of the plug developed into a green stem-like structure and by the time of anthesis the plug resembled a miniature capitulum (Fig. 4), except that the disc florets were not organised into long spiral rows and the number of rows did not conform to the Fibonacci series. The disc florets produced fertile seeds.

(3). **Removal of Involucral Bracts in FS3.** Hysun 30 plants reared in LD were used. At FS 3, the first row of involucral bract primordia situated on the flank of the apical meristem, comprising about 30% of the final number, were removed. 30 plants were treated in this way in two replicates. This treatment caused a significant increase in capitulum diameter and in 55% of cases the capitula produced a new disc floret row pattern resulting from a number sequence called the "Lucas" sequence. This being the numbers generated by the fraction 47/76 and produced if the new disc floret primordia are theoretically arising with a divergence angle of approximately 99.5° (Jean R., 1986. Math. Biosci., 79; 127-154).