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ON STOCHASTIC GROWTH AND FORM

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Many models of biological development at the cellular level are deterministic;[1–6] i.e., the rules of growth contain no elements of probability, so that a given configuration of starting cells always yields a pattern which is the same in every detail. These patterns are usually highly symmetric[1, 2, 5, 6] or quite irregular.[3, 4] Probabilistic models have been considered for analogues of growth of bacterial colonies,[7, 8] theories of cellular movement in dissociated and reaggregated embryonic tissues,[9] and differentiation of hydroid colonies.[10] In most cases the over-all form is approximately circular,[7, 8, 10] spherical,[9] or occasionally elliptical[8] (due to an externally imposed nutrient gradient).

This article presents a simple model for the growth of a stochastically generated spiral (a "snail," if you wish), and the preliminary results of a computer program written to execute the rules of growth. A general viewpoint of a developing organism as an ensemble of interacting, probabilistic, decision-making units is outlined, and also a scheme for exploiting such models. If forms generated by stochastic growth rules may be shown to be reasonably stable, then the amount of information necessary to specify the development of an organism may be considerably less than has been estimated.[14]

Growth Rules for a Stochastic Spiral.—Two kinds of cells are assumed: type I (Inside), and type S (Shell). They grow on a square planar lattice. With one exception (to be mentioned later), all interactions are steric: the only thing that prevents a cell from growing is the other cells which may already occupy its nearest-neighbor sites. "Growth" of a cell means that the cell remains where it is, but produces another which then occupies an adjacent site that was previously empty. A cell cannot grow (or "reproduce") if it already has four nearest neighbors. One cell, I or S, grows at a time.

All I cells which are not completely surrounded (the "active" ones) have equal probabilities of dividing next. All empty sites around the chosen cell have equal probabilities of receiving the new I cell.

One S cell is designated the "leader." It is the only S cell that may divide. The cell it produces becomes the new leader. Growth is directional: the leader cell grows the new S cell into the site to its left (relative to the vector from the cell from which it grew, directed to itself), provided that site is available. If it is not available, growth is into the forward site. If *that* is not available, then growth is to the right. If the leading S cell is surrounded by other cells, then the cell it grew from becomes the new leader, and growth towards the left is attempted again by this cell. In other words, if the leading S cell becomes trapped by other cells, the first exposed cell down the chain of consecutive S cells resumes growth.

These growth rules are reasonably analogous to those which may be used by certain real cells. The random growth of I cells is similar to the growth of tumors. The behavior of S cells is reminiscent of apical meristem in plants, which only grows at the tip of a shoot, inhibiting growth further down. If the apical meristem is cut off, growth resumes at a lower point. Also, vines tend to spiral in one direction.[12]

The starting configuration of cells in this study was always ISZ, the Z cell on the right designating the initial leading S cell.

There is one free parameter for this system: the ratio r of the specific (per cell) growth rate of active I cells (the ones which are not surrounded), to that of the leading S cell. In other words, given i active I cells, the probability that a particular one of these will be the next cell to divide is $P_I = rP_S$ (where P_S is the probability that the leading S cell will divide). The total proba-

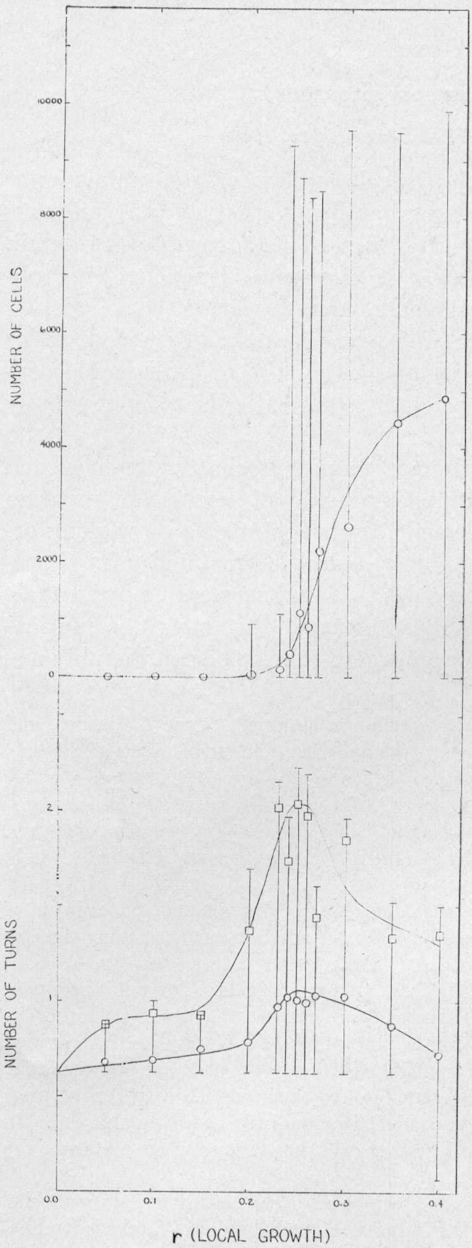

FIG. 1

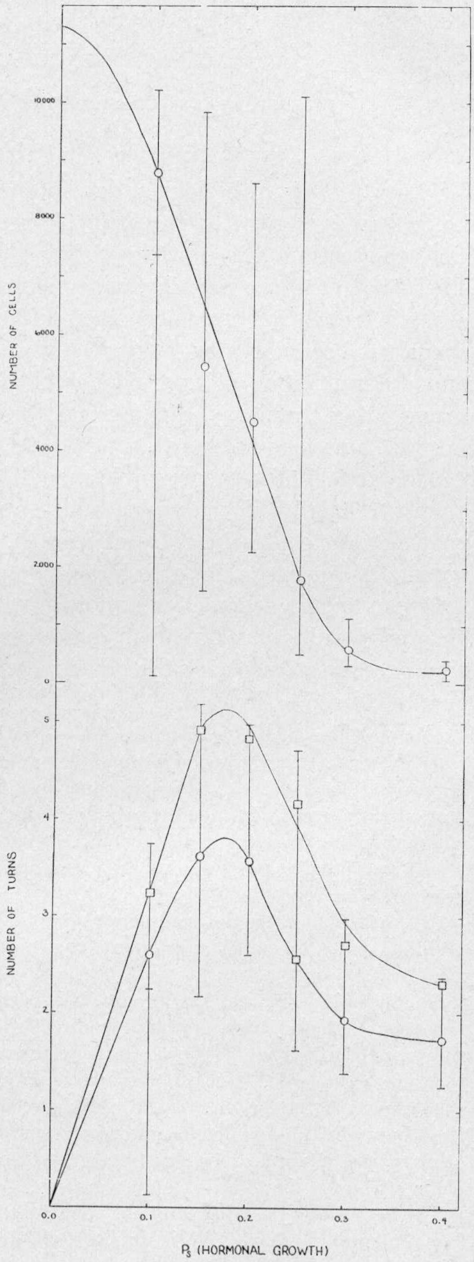

FIG. 2

FIGS. 1 AND 2.—○, Mean value; □, mean value of the three spirals with the most turns. Thirty to thirty-three cases were run for each value of r or P_S. The bars indicate extrema. The smallest 'spiral," which sets the lower limit in size, is $\overset{*}{*}\overset{***}{\underset{**}{ISZ}}$ (see Figs. 3–6). At $P_S = 0.1$ in Fig. 2, there was one case in which the S cells were completely surrounded early in growth. The extra bars indicate the minima of size and number of turns when this case is disregarded.