Mathematical Model of Polar Auxin Transport[1]

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Summary. Polar auxin transport can be simulated by a model which achieves polarity through the preferential secretion of more auxin from the lower end than from the upper end of each cell. Solution of the model using a computer provides a possible explanation of the differences between the polarity expressed by different tissues and the differencs between pieces of different lengths, on the basis of small differences in the polarity of auxin secretion from individual cells. A method of estimating the polarity of individual cells is described.

The polarity of plant cells is a basic feature required for orderly growth and differentiation. The elongation of cells in the growth of a stem expresses a polarity; apical dominance relies on the polarity of a growth-regulating system. The transport of the auxin indoleacetic acid is unique in being the only known polar vector in natural growth-regulating systems, and a better knowledge of it should eventually lead us to a more intimate understanding of the polarity of cells and whole organisms.

The finding that the transport of auxin is apparently driven by a secretive action of the cells of stems or coleoptiles (5) permits one to conceive of polar transport as being a preferential secretion of auxin out of the lower end of the cell as compared with the upper end. With this concept, one may then ask how extensive the difference between the amounts coming out of each end would need to be for an experimentally determined net polarity of transport in a stem. The article demonstrates how this difference may be quantitatively approximated by computer manipulation of a mathematical model, even though direct measurement at the cellular level is not possible.

Methods

The transport experiment to be simulated is the classic system developed by van der Weij (12), in which a section of plant stem or coleoptile tissue from 2 to 10 mm long is placed between 2 agar blocks, a donor block which contains IAA and a receptor block. The preferential transport in the basipetal direction is the feature of polarity being examined. This differential may be explained by hypotheses that either all of the auxin leaves each cell by secretive action, or various amounts of auxin leave the cell by passive diffusion with secretion accounting for the preferential exit at the basal end. The system is represented in figure 1, showing 1 experiment to measure basipetal transport and another for acropetal transport.

A simple algebraic statement of the model, which assumes that all auxin is moved out of a cell in unit time, is an equation in which the auxin concentration, C, in any cell i at time t is the sum of the auxin which has moved into it from the next cell above, plus the auxin moving into it from the next cell below. The proportion of the auxin moving out of the basal end of a cell per unit time is designated as d, and that from the upper end is u. Thus,

$$C_{i,t} = d\ C_{i-1,t-1} + u\ C_{i+1,t-1} \qquad (I)$$

or, the concentration in cell i at time t equals $d \times$ the concentration of the cell above $(i-1)$ at the preceeding time interval $(t-1)$ plus $u \times$ the concentration of the cell below $(i+1)$ at the preceeding time interval.

The polarity of the cell can be expressed as the ratio of the auxin moving out of the basal and the apical ends.

$$\text{Cell polar ratio} = p = \frac{d}{u} \qquad (II)$$

Thus, a p value of 1.0 would indicate no polarity, with 50 % of the auxin coming out from each end of the cell. A cell which secretes 60 % from the basal end and 40 % from the apical end would have a cell polar ratio of 1.5.

Initial analyses were made with this model; however, study soon indicated that it might be desirable to allow retention of some auxin in each cell. Such a leakage from the transport system could allow for auxin that is metabolized by the cell, or enters into other reactions which result in its being not secreted. In experiments with ^{14}C-

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IAA, the distribution of radioactivity along the stem may not be a reflection exclusively of the auxin in transit (3).

This more complex model of the system expands on the basic relationship given in equation (I) by stating that the radioactive concentration in any cell is made up of 2 portions: A, that available for further transport, and E, that fixed within the cell.

$$C_{i,t} = A_{i,t} + E_{i,t} \qquad \text{(III)}$$

The total amount fixed at any time in a cell is the sum of that fixed within the cell at the previous time plus the incremental amount fixed during the last time interval. This increment, E′, is treated in this model as a proportion, f, of the transportable amount in the cell at the beginning of the interval. Thus,

$$E_{i,t} = E_{i,t-1} + E'_{i,t} \qquad \text{(IV)}$$

where $E'_{i,t} = fA_{i,t-1}$

To determine the amount of transportable auxin at any time, equation (IV) is incorporated into equation (I) as follows:

$$A_{i,t} = dA_{i-1,t-1} + uA_{i+1,t-1} + (1 - d - u - f)A_{i,t-1} \qquad \text{(V)}$$

This equation states that the transportable amount in any cell is the sum of the amounts coming from the cell above and the cell below, plus that left in the cell after removal for upward and downward transport and fixation.

To simulate the transport process, we assumed an amount of auxin in the donor block (100) and then calculated the amount moved to the cell below in 1 time interval. At each succeeding time interval (t) the donor block concentration is again set at 100 and the concentration in each cell down the file is calculated from the state of adjacent cells at $t - 1$. A computer program, written in Fortran IV and run on the IBM 7094, made practical the determination of the characteristics of the model system under a variety of cell polar ratios, time intervals and cell numbers.

The program sets up $2N + 2$ by 2 matrices, where N is the number of cells in the stem section being simulated. One matrix simulates basipetal flow, and the other simulates acropetal (fig 1). In each matrix the second column is the cell concentration values 1 time unit after reaching the values given in the first column. Before the calculations for the next time interval are made, the values in the second column of the matrix are transferred to the first.

The program permitted running any pre-set number of iterations, with a profile of cell concentrations given at specified times during the run. The program also printed out the cell polar ratio, a running record of concentrations in basipetal and acropetal receptor blocks, and the ratio of basipetal to acropetal receptor concentrations, termed the polarity quotient, Q. For most of the tests described here, the runs were made for 1000 time intervals, at cell polar ratios from 1.00 to about 1.08.

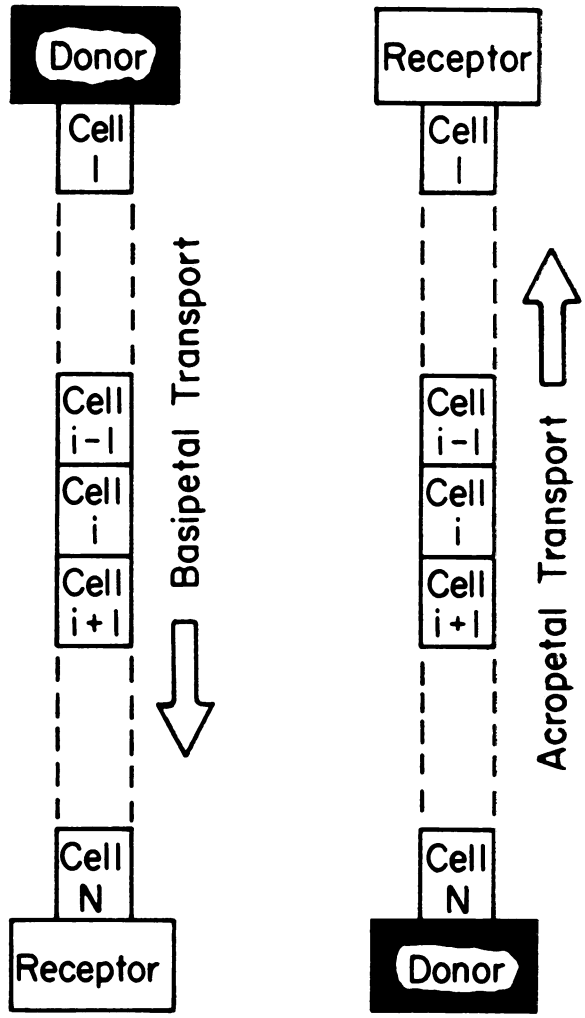

FIG. 1. Representation of the model for the transport of auxin, showing a donor block containing auxin applied either to the apical end of a file of cells or to the basal end.

Results and Discussion

After the computer had solved the equation for 1000 time units, the accumulation of auxin in the receptor block could be plotted as a function of time. The data in figure 2 show auxin arrival curves for the model system using 2 polar ratios; for $p = 1.00$ the arrival curve was identical for basipetal or acropetal transport, but for $p = 1.04$ it is observed that the arrival rate for basipetal transport is markedly greater than for acropetal transport. Thus, a very small preferential secretion of auxin out of the basal end of each cell can result in a marked polarity of transport through the multicellular model.

In contrast to the concave shaped arrival curves in figure 2, most biological experiments show linear

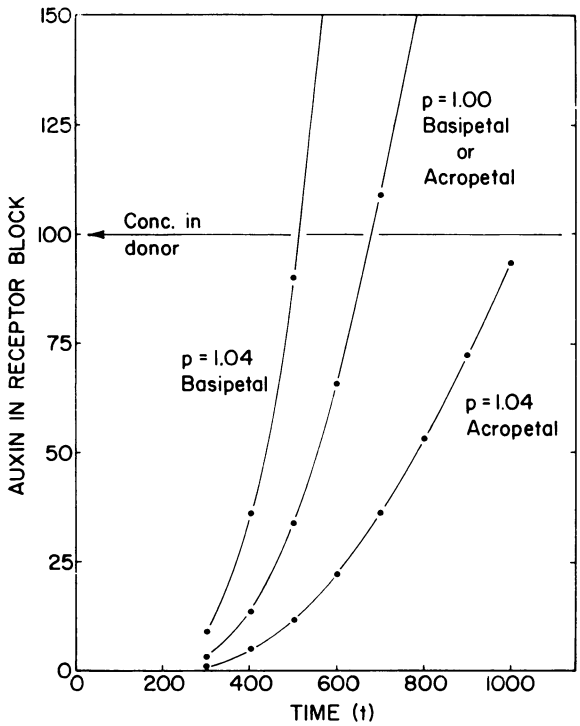

FIG. 2. Theoretical arrival of auxin in the receptor blocks after various intervals of time. When the cell polar ratio is unity the same amounts of auxin arrive for basipetal or acropetal transport, but with $p = 1.04$, a preferential arrival is achieved by basipetal transport in the model. N = 50 cells, $f = 0$.

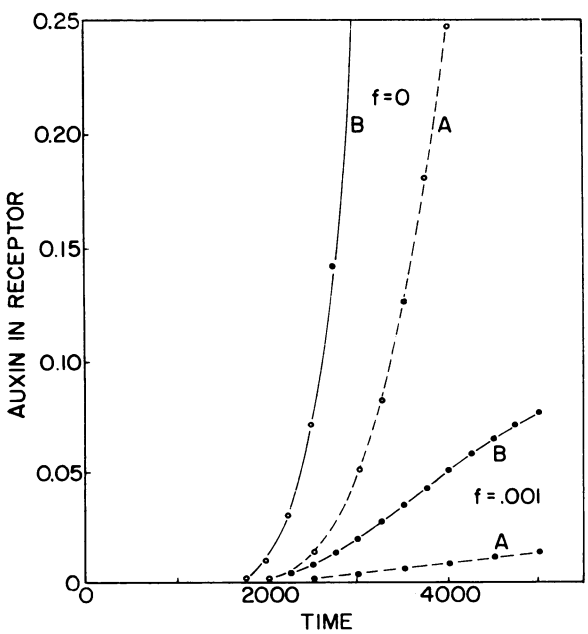

FIG. 3. Theoretical arrival curves for auxin in the receptor blocks may be concave when none is fixed in the cells en route ($f = 0$), but becomes nearly linear for both basipetal (B) and acropetal (A) transport with fixation ($f = 0.001$). N = 187, $p = 1.008$.

arrival curves, and linearity is generally assumed when such curves are utilized to calculate transport velocities (12). Examination of several variables in the mathematical model to determine what changes would alter the shape of the arrival curves led to the finding that increasing the proportion of auxin fixed as it passes through each cell gave a more linear trend. Some arrival curves for basipetal and acropetal transport with rather large amounts of fixation of the auxin are shown in figure 3 in comparison with curves with no fixation. Both the basipetal and the acropetal arrival curves become nearly linear with a fixation value of 0.001. When the basipetal curve was extended over longer periods of time it was found that this amount of fixation would even cause the arrival curve to become convex instead of concave, a feature which is just beginning to show in the basipetal curve in figure 3 for $f = 0.001$. Increases in f values above 0.001 resulted in increasingly convex arrival curves.

At the end of a transport period, the auxin concentration in representative cells along the section can be plotted as in figure 4. Under conditions of no fixation along the way ($f = 0$) it is evident

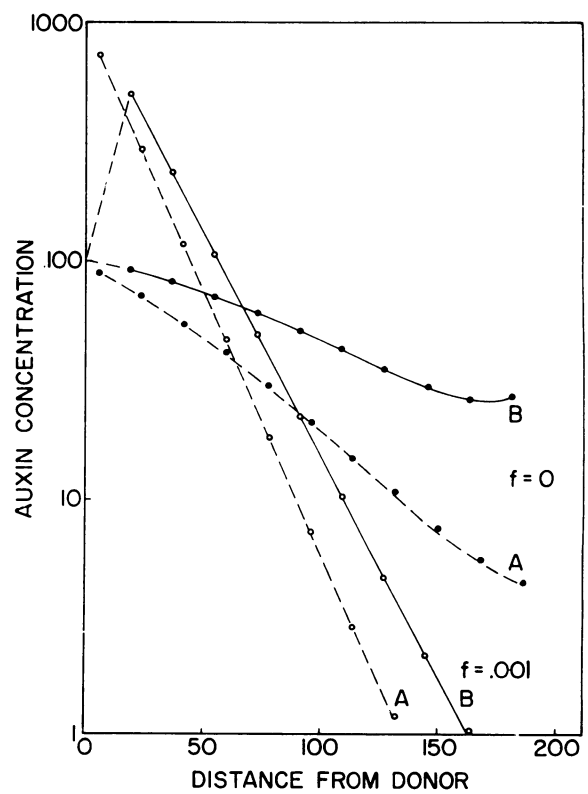

FIG. 4. Theoretical distribution of auxin along the transporting sections, showing a steeper gradient after acropetal transport (A) than after basipetal (B), and a strictly logarithmic decline in concentration when fixation takes place ($f = 0.001$). N = 187, $p = 1.008$, $t = 10\,000$.

that the distribution of auxin along the file of cells describes a much steeper gradient after acropetal than after basipetal transport. The most convincing data on the actual distribution of auxin along a piece of tissue at the end of a transport experiment (3) show a precise logarithmic decline in radioactivity with increasing distance in coleoptiles; in the case of the model, it was found that increases in the amount of fixation by the individual cells resulted in strictly logarithmic distribution curves as shown in figure 4 (f = 0.001). That auxin is withdrawn from the transport system during transport in coleoptiles has been well documented (2, 3).

From the final concentration of auxin in the 2 receptor blocks after 1000 time units, one can calculate the polarity quotient (Q), the quotient of basipetal to acropetal transport. This has been done in figure 5 for 4 values of p, and for 3 different numbers of cells. The number 187 was selected as representative of a long section since this is the number of cells counted in a single file through the pith of a 5 mm section of *Coleus* stem, a material commonly utilized in auxin transport measurements (e.g. 6). From figure 5 it is seen that the degree of polarity achieved increases exponentially with increasing numbers of cells traversed. It might be noted that varying the values of f from 0.0 to 0.01 had negligible effects on the values of Q obtained.

According to this model, then, for a tissue with any given cell polar ratio, the polarity quotient observed should vary with the length of section through which transport is being measured.

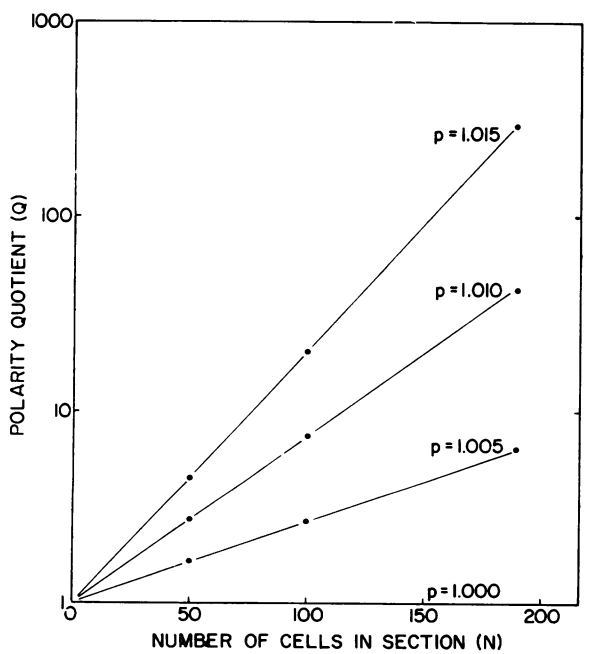

FIG. 5. Theoretical changes in the polarity quotient as a function of the numbers of cells in the transporting piece. Data for 4 different values of cell polar ratios (p) are plotted. f = 0, t = 1000.

The logarithmic relationship in figure 5 suggests a general equation for estimation of any one of the 3 variables, given the other 2. Such an equation was derived for the data shown in figure 5.

$$p = 1 + \frac{\log Q}{.872\ N}$$

As a working basis, this equation may be used to estimate the cell polar ratios for biological materials. For example, Jacobs (6) reported a polar quotient for 3.0 of a 5 mm *Coleus* stem piece. This represents a file of 187 pith cells, and solution of the equation yields a value of p = 1.003; that is, 50.15 % of the auxin secreted from the basal end of each cell and 49.85 % from the apical end would account for the polarity quotient observed. A polarity quotient of 100 would indicate a p = 1.012.

This model has 4 principal properties which seem relevant to the biological problem of auxin transport:

A) A small differential in the secretion of auxin out of the basal end of each cell is capable of imparting polarity to the overall transport by the model. Small increases in the extent of this differential secretion can raise the polarity from a quotient of 2 or 3 to values far above 100 (fig 5). Further increases in the differential secretion would result in an apparent complete polarity; for example, in a file of 100 cells, if 52.5 % of the secreted auxin were to come out of the basal end of each cell (p = 1.025), a polarity quotient in excess of 10,000 would be achieved, and essentially no auxin would reach the receptor block after transport in an acropetal direction. In other words, small differences in secretion of auxin from each end of the cell can be amplified into large differences in overall transport through tissues, producing the apparent basipetal polarity.

B) Not only would the extent of polarity be expected to increase exponentially with the cell polar ratio, but it would be expected to increase exponentially with the number of cells in a section (fig 5). That the extent of transport varies between types of plant tissue has been noted by Jacobs (6), and by workers in this laboratory (5, 8, 10), but the extent of polarity has been compared in only a few cases (e.g. 4, 6, 9, 11, 13). That the polar quotient does in fact increase with the length of stem pieces has been shown in a preliminary report by de la Fuente and Leopold (1).

C) The model would predict that the distribution of auxin along the transporting section could be either logarithmic with distance from the donor block, or curvilinear on a log scale (fig 4), and would be less steep for the basipetal transporting section than the acropetal.

D) The model presents a method of approximating cell polar ratios of the cells of various plant materials. The method will be applied to 4 types of plant materials in the following paper.

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