A Circuit Analog Model for Studying Quantitative Water Relations of Plant Tissues

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ABSTRACT

Using arrays of resistors and capacitors, a lumped circuit analog of plant tissue is developed. The circuit elements of the analog are identified in terms of physiological variables (hydraulic conductivities, water capacities, and cell dimensions) which can be measured in the laboratory. With the aid of a circuit simulation subroutine, the model was solved to predict water potential distributions as a function of position and time in plant tissues of three, six, and nine cells. Results presented for the six-cell case indicate that local equilibrium may or may not occur depending on the actual values of tissue hydraulic conductivities, water capacities, and the rate of change of water potential at the tissue boundaries. However, present measurements and estimates of tissue parameters suggest that local equilibrium is more the rule than the exception. Membrane resistance is an especially important parameter because it serves to isolate the vacuoles from the cell walls in addition to increasing the natural vacuole response time to changes in water potential.

The proposed model should be useful in studying water transport processes in roots, stems, and leaves. Nonhomogeneity can be taken into account easily. Nonlinearity (changes in circuit parameter values with potential) which is known to occur in plant tissues could be incorporated also if the required information were available.

It is now generally accepted that there are several pathways which water can follow while traversing plant tissue (Fig. 1). In the early part of this century, pathway A was favored (the vacuolar pathway). This viewpoint held that water movement occurred from vacuole to vacuole, traversing the cytoplasm and membranes of each cell (17). At a later date, pathway B (the cell wall pathway) was suggested, whereby water moves in the porous cell walls, bypassing the cell membranes (22). The discovery of plasmodesmata led to still another possible pathway, the symplasm pathway, which is labeled pathway C. Thus, the major water transport routes in Figure 1 are labeled with the capital letters A, B, and C. It is also possible for water to be exchanged between the vacuole and cell walls, and these subpathways are labeled with the lower case d and e.

To our knowledge, Philip (18–20) was the first investigator to present a detailed quantitative theory of water transport through plant tissues. Although Philip's development did not consider water flow in the cell walls, it was applied in a useful manner to certain aspects of water transport in the soil-plant-atmosphere system (21) and to the radial flow of water in cotton stems (12, 13) and leaf discs (14, 15). In recent years, more elaborate theories have been developed which describe water transport in cell walls and plasmodesmata (8, 11). These theories have been applied to water transport in the soil-root system (7) and to growing soybean hypocotyls (9).

The developments and applications discussed above are all based on the solution of one or more differential equations which embody the basic transport theory. There are advantages to this so-called distributed parameter approach, but the development of the equations can be relatively complex as discussed by Dainty (2). An alternative to a distributed parameter model is a lumped circuit analog. In such an analog model, the water resistance and water storage properties of the tissue are located at discrete positions and not spread out uniformly along the flow path. One advantage of the lumped parameter approach is that it generally is more obvious how the model represents the system of interest.

Circuit analog models have been reported previously. Cowan (1) used the concept in his description of whole plant water relations and Molz and Inkberry (11) introduced a circuit analog model along with their differential equations to describe the water relations of plant cells and cell walls. More recently, Ferrier and Dainty (3) used the analog approach, in a conceptual sense, in their analysis of water transport in beet storage tissue. The purpose of the present paper is to reduce the complexities of the various water flow paths to the simplest conceptual framework and test the effects of variations in the hydraulic properties of these paths using a circuit model of plant tissue which is more detailed and flexible than that previously available. Such an endeavor has been made more attractive by the recent development of sophisticated circuit simulation computer programs capable of solving complex, transient, electric circuit problems (24). These programs are generally available and provide circuit analog models with essentially the same flexibility as analytical models. The model we propose here will be used to study the water relations between the vacuole and cell walls of several plant cells in series.

DEVELOPMENT OF ANALOG MODEL

Table I lists the quantities which are analogous in the electrical and plant tissue systems, along with a typical set of units. The water potential is commonly expressed in bars and the analogous unit for electrical potential is the volt. A potential difference causes some quantity to flow from regions of higher potential to regions of lower potential. In the biological system, the quantity flowing is water with the flow rate measured in cm2 s⁻¹, while in the electrical system the flowing quantity is electric charge and the flow rate is given in coulombs s⁻¹ or amps (1 coulomb is equivalent to approximately 6 × 10⁸ electrons). The ratio of potential difference to the resulting flow rate is called resistance which is the inverse of conductance. Electrical resistance has the unit of v coulomb⁻¹ s which is commonly called an ohm. In the biological system the resistance unit is similarly bar cm⁻² s (i.e. the units of potential divided by the units of flow rate). The final
quantity to be identified is a measure of how water or electric charge is stored or released in the respective systems. For the water potential of a vacuole to decrease water must move out of a cell (loss from storage) if the solute mass remains constant. A rising water potential implies an inward flow of water which results in a storage increase. The ratio of the change in volume of water stored to the corresponding change in water potential is called water capacity and has units of cm³ bar⁻¹. Electrical capacity, the ratio of the change in charge stored on a capacitor to the voltage change across the capacitor, has units of coulomb volt⁻¹, or the farad.

Figure 2 shows the circuit analog of a plant cell constructed according to the concepts discussed previously. In the cell wall (Fig. 2A), water (electrical charge) can be both stored and transmitted. The total water capacity of the cell wall is 12Cw, where Cw is the capacitance of each wall capacitor. Each wall resistor has a value Rm, and the resistance from one side of the cell to the other (i.e. from aa to bb) is 3Rm/2. The interior of the cell (Fig. 2B) is represented as a vacuole with a total water capacity of Cc, surrounded by an effective membrane (plasmalemma plus cytoplasm plus tonoplast) of total resistance Rm/8, where Rm is the value of each membrane resistor. Part C of Figure 2 shows the complete analog of a plant cell composed of cell wall, membrane, and vacuole. More elaborate models could be constructed using larger numbers of resistors and capacitors.

A tissue can be constructed by placing two or more cells in series. Figure 3 shows a three-cell combination; and, obviously, the combination could be extended to as many cells as desired.

As indicated in the figure, the connection can be modified to represent the effect of plasmodesmata. To accomplish this, a resistance Rw is used to connect the vacuole of each cell to that of its neighbor. This allows water (charge) to flow directly from the vacuole of one cell to the vacuole of another without traversing plasmalemmas and entering the cell walls.

In order actually to use the circuit analogs in Figures 2 or 3 to represent plant cells or tissue, values based on the biological system must be obtained for the various resistors and capacitors. To accomplish this we will make use of Figure 2 along with the idealized cells shown in Figure 4. We will consistently call units of cm⁻¹ second⁻¹ permeabilities while units of cm² second⁻¹ bar⁻¹ will be referred to as conductivities.

If Km is the permeability of the cell membrane to water (cm⁻¹ second⁻¹), then according to the model of Figure 4 the membrane conductance between two adjoining cells is AKm/2, where A is the membrane surface area and the factor of 2 enters because water must traverse two effective membranes to get from one vacuole to the next (Fig. 4). The resistance is simply the inverse of this quantity, (AKm/2)⁻¹, which, in terms of circuit parameters, is given by 2Rm/2 = Rm. Equating the two expressions for the resistance yields Rm = 2/(AKm).

If P is the hydraulic conductivity of the cell wall material (cm² second⁻¹ bar⁻¹), then the resistance to water flow from one side of a cell to the other is (AP/Δx)⁻¹ where Δx is the length of the cell and A is the area of the cell wall perpendicular to flow. In the analog

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**Table 1. Analogous Quantities in the Electrical and Plant Tissue Systems**

<table>
<thead>
<tr>
<th>Entity</th>
<th>Electrical Unit</th>
<th>Biological Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potential</td>
<td>Volt</td>
<td>Bar</td>
</tr>
<tr>
<td>Flow</td>
<td>Coulombs s⁻¹ (amp)</td>
<td>cm² s⁻¹</td>
</tr>
<tr>
<td>Resistance to flow</td>
<td>Volt coulomb⁻¹ s (ohm)</td>
<td>Bar cm⁻³ s</td>
</tr>
<tr>
<td>Capacitance</td>
<td>Coulombs v⁻¹ (farad)</td>
<td>cm² bar⁻¹</td>
</tr>
</tbody>
</table>

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**FIG. 1.** Idealized diagram of a linear aggregation of plant cells. Each cell consists of a central vacuole surrounded by cytoplasm and a rigid cell wall. The cytoplasm is bounded on the outside and inside by semipermeable membranes and connected to the cytoplasm of contiguous cells through plasmodesmata. Various water pathways are indicated by letters and arrows. For purposes of illustration, the thickness of the cell walls and the diameter of the plasmodesmata are exaggerated.

**FIG. 2.** Circuit analog models of a cell wall (A), a membrane-surrounded vacuole (B), and complete cell (C) composed of cell wall, membrane, and vacuole. Water storage properties are represented by capacitors and water transmission properties by resistors.

**FIG. 3.** Circuit diagram showing how cells are linked together to form a tissue. Also included for illustration purposes are resistors, Rω, which can be used to represent the effects of plasmodesmata.

**FIG. 4.** Diagram showing how cells similar to those shown in Figure 1 are idealized for modeling purposes. The major approximation is to assume that the interior of a cell is separated from the cell wall by an effective membrane of plasmalemma, cytoplasm, and tonoplast. Also, the major resistance to plasmodesmata transport is assumed to occur in the plasmodesmata themselves.
system the same quantity is given by $3R_\infty/2$. Equating these two resistances yields $R_m = 2Ax/3AP$.

In a similar manner, values can be obtained for $C_w$ and $C_c$. If the specific water capacity of the cell wall material is given by $S\text{(cm}^2\text{cm}^{-3} \text{bar}^{-1})$, then the wall water capacity per cell becomes $W_s S\text{(cm}^2\text{bar}^{-1})$, where $W_s$ is the volume of wall material for a given cell. This is equivalent to saying that for every bar of water potential change, the wall material of a given cell absorbs (rising potential) or releases (falling potential) $W_s S\text{cm}^2$ of water. The analog version of the water capacity of a cell wall has already been identified as $12 C_w$. Thus, $C_w$ can be identified as $W_s S/12$.

In his analysis of the water relations of plant cell vacuoles, Philip (19) showed that to a first approximation the relationship between the water potential of a vacuole and the volume of water stored in the vacuole is given by $\phi = V(\epsilon + \eta)/V_0 - (\epsilon + 2\eta)$. In this equation, $\phi$=water potential (bar), $V$=volume of water stored in the vacuole (cm$^3$), $\epsilon$=elastic modulus of the cell wall (bar), $\eta$=osmotic pressure of cell contents at zero turgor pressure (bar) and $V_0$=volume of water stored in the vacuole at zero turgor.

Since water capacity is defined as the change in water storage with respect to potential, one can differentiate the previous equation to obtain $C_w=dV/d\phi = V_0/\epsilon + \eta_0$. Although $C_w$ can be defined in a more general manner, the previous equation is consistent with the assumptions made in this study.

The final circuit parameter that needs to be identified is $R_p$. Tyree (23) indicated that the array of plasmodesmata connecting neighboring cells can be viewed as a type of membrane with cross-sectional area $A$. (Note that $A$ is total membrane area, not just pore area.) If the permeability of this plasmodesma membrane is measured to be $K_p$ (cm$^2$ s$^{-1}$ bar$^{-1}$), then $R_p$ will be given as $(AK_p)^{-1}$. Table II summarizes the relationships that have been obtained between the circuit parameters and the plant tissue parameters. The parameters identified are those that are fundamental to an understanding of transport processes in plant tissue.

**APPLICATION OF THE ANALOG MODEL**

For a variety of parameter values, the model shown in Figure 3 was applied to groupings of three, six, and nine cells in series.

Table II. Relationships between the Circuit Parameters in Figures 2 and 3 and Plant Tissue Parameters Which in Principle, Could Be Determined Experimentally

<table>
<thead>
<tr>
<th>Units of cm s$^{-1}$ bar$^{-1}$ are consistently referred to as permeabilities while units of cm$^2$ s$^{-1}$ bar$^{-1}$ are called conductivities.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_m = 2/ AK_m$</td>
</tr>
</tbody>
</table>

$R_m$ = Membrane resistor (ohm)

1 $A$ = Cross-sectional area of vacuole-to-vacuole pathway (cm$^2$)

$K_m$ = Membrane permeability (cm$^2$ s$^{-1}$ bar$^{-1}$)

$R_p$ = Cross-sectional area of cell wall pathway (cm$^2$)

$K_p$ = Hydraulic conductivity of cell wall material (cm$^2$ s$^{-1}$ bar$^{-1}$)

$C_c$ = Permeability of a plasmodesmata array (cm$^2$ s$^{-1}$ bar$^{-1}$)

$C_m$ = Wall capacitance (farad)

$W_c$ = Volume of cell wall per cell (cm$^3$)

$S$ = Specific volumetric storage capacity of cell wall material (cm$^3$ cm$^{-3}$ bar$^{-1}$)

$C_v$ = Vacuole capacitance (farad)

$V_0$ = Cell volume at zero turgor pressure (cm$^3$)

$\epsilon = $ Elastic modulus of the cell wall (bar)

$\eta_0$ = Osmotic pressure of cell contents at zero turgor pressure (bar)

Initially, the water potential was assumed to be zero everywhere. Then at time zero, the potential of the left wall of the left-most cell was lowered to $-10$ bars, usually in a 30-s time period. This is fairly rapid, but not unreasonable for a laboratory situation. The model was then used to predict water potential as a function of position and time throughout the series of cells. Water potentials were calculated using an IBM 370 computer and the circuit simulation program called SPICE (16). This program is currently available from the University of California at Berkeley. A computer run for nine cells in series (the circuit was simplified somewhat before analysis) required approximately 10 s of central processing unit (CPU) time and minimal data preparation time. A convenient feature of SPICE is that it allows the coding of subcircuits. Thus, a single cell can be entered as a subcircuit, and then to stimulate tissue, this subcircuit is repeated as often as necessary.

Figure 5 shows a plot of water potential as a function of position and time for six cells in series. Since little information is available concerning the resistance of plasmodesmata to water flow, such effects, if any, were not considered explicitly. Thus, the computational portion of this paper applies to a tissue that has negligible plasmodesmatal water transport. Values for the parameters $C_w$, $R_m$, $R_p$, and $C_c$ were obtained from data used by Molz and Boyer (9) in their study of growth-induced water transport in soybean hypocotyls. Those data agree reasonably well with the latest measurements of $\epsilon$ and $K_m$ (3, 5, 6), and the over-all behavior of the resulting tissue (half-times, times to equilibrium, etc.) compares favorably with experimental measurements (4). The parameter values actually calculated and shown as the first line of Table III were $C_w = 5.3 \times 10^{-12}$, $R_m = 8.9 \times 10^9$, $R_p = 2.5 \times 10^9$, and $C_c = 1.9 \times 10^{-9}$. The situation shown in Figure 5 closely approximates what Molz and Ikenberry (11) called local equilibrium. This occurs when the tissue parameters and boundary conditions are such that only small water potential differences exist between the vacuole and cell wall for a given cell. When local equilibrium occurs, the water potential of a tissue can be characterized to a useful approximation by a single potential distribution that varies fairly smoothly from point to point.

A sensitivity analysis was performed using the data in Table III, line 1 as a reference. Each value for $C_w$, $R_m$, $R_p$, and $C_c$ was first increased and then decreased by a factor of 10. For the eight different parameter sets which were obtained, the problem represented by Figure 5 was solved. Results indicated that the most important parameter was $R_m$ which is used in parallel with seven other resistors to represent the membrane resistance. Shown in
Table III. Summary of the Results of All Computer Runs Indicating Whether Local Equilibrium Occurred in Groups of Six Cells in Series

<table>
<thead>
<tr>
<th>Local Equilibrium</th>
<th>Cw</th>
<th>Cv</th>
<th>Rw</th>
<th>Rm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approximated</td>
<td>1.9 x 10^-9</td>
<td>5.3 x 10^-12</td>
<td>8.9 x 10^9</td>
<td>2.8 x 10^10</td>
</tr>
<tr>
<td>No</td>
<td>1.9 x 10^-9</td>
<td>5.3 x 10^-12</td>
<td>8.9 x 10^9</td>
<td>2.8 x 10^11</td>
</tr>
<tr>
<td>Yes</td>
<td>1.9 x 10^-9</td>
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<td>8.9 x 10^10</td>
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<td>5.3 x 10^-12</td>
<td>8.9 x 10^10</td>
<td>2.8 x 10^10</td>
</tr>
</tbody>
</table>

No 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^12 |
No 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^11 |
No 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^11 |
Yes 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^10 |
Yes 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^11 |
Yes 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^10 |
Yes 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^11 |
No 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^12 |
Yes 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^12 |
Yes 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^12 |
Yes 1.0 x 10^-9 | 9.6 x 10^-12 | 1.3 x 10^10 | 1.7 x 10^12 |

A variety of models and modeling approaches now exist which can serve as a quantitative aid in studying the water relations of plant tissue. The circuit analog model discussed herein is able to include explicitly some of the discrete cellular geometry and anatomy of the tissue being studied, while in the differential equation models the tissue anatomy is approximated as one or more continua with smoothly varying water potential. For some applications the continuum approximation is appropriate but would be relatively bad for a tissue composed of only two or three cells in series. Both approaches are able to handle the effect of nonlinear behavior which occurs when parameters such as the cell wall elastic modulus are allowed to become functions of water potential. Obviously, the best model type for a particular situation must be chosen carefully.

Based on our present qualitative knowledge of the water relations of plant tissues, it can be argued that models such as the ones presented in this paper are oversimplified and, therefore, of limited use in a truly predictive sense. This is undoubtedly true. The present development does not allow for reflection coefficients less than 1, variable wall elasticity, growth, or other metabolically driven water transport. It would be possible, in a formal mathematical sense, to extend either the analog or differential equation models to include such effects, and to a very limited extent this has already been attempted with the differential equation models (9, 10). Further extensions will depend on the availability of additional quantitative data involving the fundamental parame-
ters (K_m, P, K_p, S, and e) for higher plant cells and the role of plasmodesmata. Recent advances in experimental technique suggest that such data will become increasingly available (3, 5, 6). At their present stage of development, quantitative models of plant tissue offer a means for gaining an insight into the dynamics of tissue water relations. The tissue properties controlling the processes are identified clearly, and a framework is defined within which to plan experiments.

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