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A MODEL OF WATER FLOW THROUGH GROWING PLANTS*

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ALM D. M., HESKETH J. D., STOLLER E. W., and WAX L. M. *A model of water flow through growing plants*. BIOTRONICS 23, 11–34, 1994. A set of differential-algebraic equations was derived and a computer model called PSIRC (pronounced “surk”) is presented to study the flow of water through growing annual plants. The model employs an electrical analogy whereby water potential corresponds to voltage, water flow corresponds to current, and resistances and capacitances are defined accordingly. The effects of diurnal changes in organ water uptake on turgor pressure and osmotic potential are modeled using capacitance functions; and the effects of organ growth on these processes are modeled using the logic of water supply and demand. For a seven-day field test during a drying period after an irrigation event, the model performed well when realistic parameters were obtained for *Abutilon theophrasti* L., *Datura stramonium*, L., and *Xanthium strumarium* L. Both measurements and simulations showed that *A. theophrasti* displays distinctly different behavior for supplying the transpiratory demand for water than does *D. stramonium*. In particular, *A. theophrasti* has: 1) a much higher root hydraulic resistance; 2) a larger hydraulic resistance between the xylem and the leaf symplast; and 3) a much lower saturated leaf osmotic potential than the other species. All else being equal, 1), 2), and 3) force *A. theophrasti* to operate at lower leaf water potentials than *D. stramonium* or *X. strumarium*. Simulations also suggest that diurnal osmotic adjustment and diurnal variation in root resistance are necessary to prevent wilting in all three species. Further implications, potential uses and extensions of the model are discussed.

Key words: *Abutilon theophrasti* L.; *Datura stramonium* L.; *Xanthium strumarium* L.; water relations; electrical analog; osmotic adjustment.

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INTRODUCTION

Water stress in plant tissues can affect plant establishment, which is an important factor determining the structure of a competitive plant community, such as a weed-crop field. Plant establishment is a complex of processes, best defined as: possibly competitive early growth under conditions of stochastic, ephemeral resource availabilities (our definition). This complex of processes can be defined as being complete, operationally—the plant is established—when it grows to a size sufficient to sustain continued growth that results in some measurable reduction in the fitness of one or more of its neighbors. Due to the central role of leaf area expansion to total growth rate (10, 18), to the extreme reduction in leaf area expansion due to water stress (6, 12), and to the potentially large fluctuations in soil water availability in the rooting zone of young plants, small interspecific differences in water relations early in the season may result in large interspecific differences in the share of canopy leaf area during late flower and fruit set—periods of substantial fitness (yield) reduction. Therefore, because yield losses in weed-crop communities will be determined partly by the availability of and possibly competition for water during weed establishment, we have derived a mathematical model and developed a computer simulation tool called PSIRC (pronounced “surk”) to investigate the dynamic effects of interspecific variation in measurable water relations characteristics for three annual weeds.

Although diurnal variation in water storage within annual plants is generally negligible compared to succulents (20), small, rapid changes in storage can result in large and rapid changes in water potential. The controls acting on the processes determining carbon partitioning to leaf area (10, 18) and interspecific differences in vertical movement of leaf area (4) may be influenced subtly by leaf and stem water relations. Defining organ water relations in the form of a predictive model that includes details such as water storage transients would therefore aid investigations into the effects of water relations parameters on leaf area development.

Much has been revealed concerning the effects of water storage, osmotic adjustment and other factors on the water relations of desert succulents using a resistor-capacitor analogy (25) and electrical circuit simulation software (SPICE, Intusoft Corporation, Berkley, CA). A hand-coded simulation model called “Plant Water Dynamics” (PWD), was recently used to show the effects of diurnal water storage on maize water relations (9). The PWD model used an iterative procedure (28) to adjust the leaf water potential until uptake, storage and transpiration were balanced. While the SPICE software relieves the modeler from having to hand-code the numerical algorithms, it is difficult to interface with more extensive plant growth models. In contrast, the PWD approach is easily coupled with existing plant growth models but represents a loss of mathematical rigor compared to the SPICE models. As we will describe, experiments similar to those necessary to parameterize the SPICE or PWD models can be used to parameterize the more flexible system of equations

presented here.

Specifically, we report an extension of the electrical analog approach (8, 19, 21, 22, 25) to simulating diurnal changes in water storage by growing plants. Our PSIRC model has the advantage of being operational, in that all but one parameter, a root-soil contact factor, can be measured directly in the field. In addition, off-the-shelf electrical circuit simulation software (e. g., SPICE) can be used to check the correctness of the derived equations and computer code, which, unlike SPICE, can be easily incorporated into existing plant growth models. Apparent strategic differences in the water relations behavior of three annual dicotyledonous weeds are highlighted by this approach, both by the simulations and the required measurements.

MATERIALS AND METHODS

Plant Material

Seeds of *Abutilon theophrasti* (L.), *Datura stramonium* (L.), and *Xanthium strumarium* (L.), were planted 2.5, 2.5, and 5 cm deep on 6 June 1991 at the University of Illinois Agronomy/ Plant Pathology Research Farm. The soil is a Flanagan silt loam (Aquic Argiudolls; fine montmorillonitic mesic). The seeds were planted at random nodes of a 1.25 m rectangular grid and the resulting 15, widely-space seedlings of each species were irrigated every-other day until emergence and then weekly thereafter with 2.5 cm of the public water supply. The measurements began on 18 July when *A. theophrasti*, *D. stramonium*, and *X. strumarium* were 0.14, 0.10, and 0.10 m tall, with 12, 10, and 9 mainstem leaves (greater than 1 cm²), respectively. No branches were present at the beginning but a few were visible by the end of the experiments.

Model Development

The input (driving) variables for the model are soil water potential (Ψ_{soil} , MPa), osmotic potential of the leaf at full turgor (Π_{sat} , MPa), root conductance *per unit leaf area* (L_{root} , m s⁻¹ MPa⁻¹), and transpiration *per unit leaf area* (I_{trans} , m s⁻¹). Expressing root conductance on a leaf area bases allowed for removing the effects of variation in plant size without having to determine root surface areas in the field, which is an extremely difficult task. Making transpiration an input (instead of stomatal resistance) eliminated the need to measure the variability of the boundary layer resistance, air temperature and dew point throughout the day (25), thereby eliminating the associated error. An electrical circuit analog that includes a current (transpiration) source is shown in Figure 1. The hydraulic units corresponding to voltage, resistance, and capacitance are water potential (MPa), hydraulic resistance (MPa s m⁻³), and hydraulic capacitance (m⁻³ MPa⁻¹), respectively; and these units apply whenever we use the terms potential, resistance or capacitance. Electrical analogs, including Figure 1, typically depict the osmotic potentials (Π) as independent sources (25). The equations derived herein, however, represent Π as a capacitor, resulting in a more flexible and representative model.

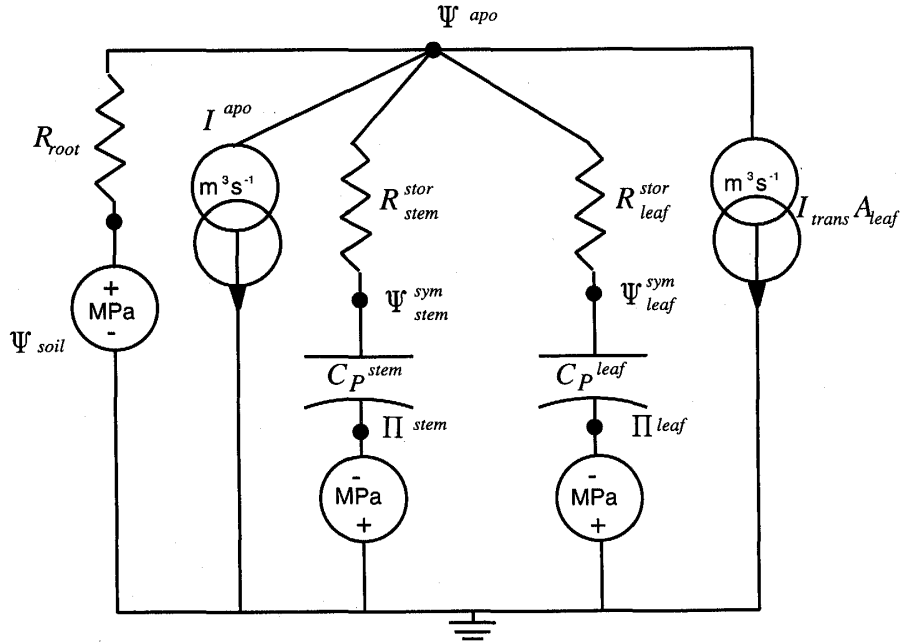


Fig. 1. An electrical circuit analog for plant hydraulics. The circuit inputs include independent current sources (double circles): transpiration (I_{trans}) and water accumulation in the growing apoplast (I_{apo}); and an independent potential source (single circle): soil water potential (Ψ_{soil}). Although this analog shows the osmotic potentials (Π) as independent sources, our "PSIRC" model uses the saturated osmotic potential as an input and Π is a state variable (eqn [8]).

To avoid duplicate equations, we neglect the "leaf" and "stem" subscripts (Fig. 1) for eqns [1–16] and discuss both as organ groups. An important variable in plant water relations is the relative water content of the organ group (θ), having a value between 0 and 1 and representing the ratio of water in the organs (Q , m^3) to that at saturation (Q_{sat} , m^3), or $\theta = Q/Q_{sat}$ (26, 27). The organ water consists of water in the living symplast tissue (Q^{sym} , m^3) plus water in the apoplast (Q^{apo} , m^3). Q^{sym} can also be expressed as a relative quantity, the relative symplast water content, or

$$\theta^{sym} = \frac{Q^{sym}}{f^{sym} Q_{sat}} = \frac{Q^{sym}}{Q_{sat}} \quad [1]$$

where f^{sym} represents the fraction of symplastic water when the organ is saturated, or Q_{sat}^{sym}/Q_{sat} . Under the traditional model of potential-driven water flow in plants (2, 20), the change in the relative water content of the symplast can be described by

$$\frac{d\theta^{sym}}{dt} = (\Psi^{apo} - \Psi^{sym}) L_{\theta} \quad [2]$$

where Ψ^{apo} represents the water potential of the apoplast (xylem), Ψ^{sym} represents the water potential of the symplast, and L_θ represents the relative hydraulic conductance ($\text{MPa}^{-1} \text{ s}^{-1}$) between the symplast and the xylem. Multiplying eqn [2] by Q_{sat}^{sym} yields the rate equation for the absolute amount of water in the organ symplast, or

$$\frac{dQ^{sym}}{dt} = \frac{\Psi^{apo} - \Psi^{sym}}{R^{stor}} \quad [3]$$

where $Q_{sat}^{sym} L_\theta$ is expressed as its inverse representing the "storage" resistance, R^{stor} (21), the derivation of which is described later.

Ψ^{sym} represents the sum of symplast turgor pressure (P , MPa) and symplast osmotic potential (Π), or $\Psi^{sym} = P + \Pi$. (Π is conventionally used to represent the osmotic pressure, or the *negative* of the osmotic potential, which is usually written as Ψ_Π ; however, to avoid double subscripts we are using Π to represent the osmotic potential). Just as the supply of water (dQ^{sym}/dt) tends to increase P , the demand for water tends to reduce P :

$$\frac{dP}{dt} = \left(\frac{1}{C_P} \right) \left(\frac{dQ^{sym}}{dt} - r_Q Q^{sym} \right) \quad [4]$$

where r_Q represents the relative growth rate of the water (s^{-1}) necessary to meet the relative growth rate of the organ tissue, and C_P represents the turgor-based hydraulic capacitance (25), or

$$C_P = \frac{dQ^{sym}}{dP} = \frac{Q^{sym}}{\varepsilon} \quad [5]$$

where ε , itself a function (described in the *Parameterization* section) of P , is the bulk organ volumetric elastic modulus, or $\Delta P / (\Delta Q^{sym} / Q^{sym})$, (22). Unlike P , changes in Π result not only from water supply and demand but also from changes in the amount of osmotically-active solutes. The relationship between Π , Q^{sym} , and Q_{sat}^{sym} can be described (24) by

$$\Pi = \frac{\Pi_{sat}}{\theta^{sym}} = \frac{\Pi_{sat} Q_{sat}^{sym}}{Q^{sym}} \quad [6]$$

which, when solved for Q^{sym} and differentiated with respect to Π gives the osmotic-based hydraulic capacitance:

$$C_\Pi = \frac{dQ^{sym}}{d\Pi} = - \frac{\Pi_{sat} Q_{sat}^{sym}}{\Pi^2} \quad [7]$$

A change in Π_{sat} also affects Π , both directly, *via* change in solute concentration and indirectly, because the osmotic force increases the saturated volume. The rate equation for Π is then determined by both hydraulic and solute effects, or

$$\frac{d\Pi}{dt} = \left(\frac{1}{C_{\Pi}} \right) \left(\frac{dQ^{sym}}{dt} - r_Q Q^{sym} \right) + \left[\frac{1}{\theta^{sym}} + \left(\frac{\Pi_{sat}}{Q^{sym}} \right) \frac{dQ^{sym}}{d\Pi_{sat}} \right] \frac{d\Pi_{sat}}{dt} \quad [8]$$

where the term inside the brackets is the derivative of eqn [6] with respect to Π_{sat} , $d\Pi_{sat}/dt$ is calculated by numerical differentiation of the input signal, Π_{sat} , and $dQ^{sym}/d\Pi_{sat}$ is derived as follows. When the leaf is saturated, $\Psi^{sym}=0$ and the turgor pressure is equal to the negative of the osmotic potential, or

$$P_{sat} = -\Pi_{sat} \quad [9]$$

Production of osmotica will therefore decrease Π_{sat} , increase P_{sat} and consequently increase Q^{sym}_{sat} . Applying the logic behind eqn [5] yields

$$\frac{dQ^{sym}_{sat}}{d\Pi_{sat}} = -\frac{dQ^{sym}_{sat}}{dp_{sat}} = \frac{-Q^{sym}_{sat}}{\varepsilon_{sat}} \quad [10]$$

where ε_{sat} is the elastic modulus function (described in the *Parameterization* section) evaluated at P_{sat} . Organ growth also increases Q^{sym}_{sat} , resulting in the rate equation

$$\frac{dQ^{sym}_{sat}}{dt} = \left(\frac{dQ^{sym}_{sat}}{d\Pi_{sat}} \right) \frac{d\Pi_{sat}}{dt} + r_Q Q^{sym}_{sat} \quad [11]$$

We now return to the storage resistance (Fig. 1; eqn [3]), which would be very difficult to derive theoretically; however, an empirical estimation method has been described (21), whereby R^{stor} can be defined as in the electrical case (Fig. 1), with a time constant (τ , s), as

$$R^{stor} = \frac{\tau}{C_{\Psi}} \quad [12]$$

where C_{Ψ} represents the potential-based hydraulic capacitance, which can be written

$$C_{\Psi} = \frac{dQ^{sym}}{d\Psi^{sym}} = \frac{dQ^{sym}}{\left(\frac{d\Pi}{dQ^{sym}} + \frac{dP}{dQ^{sym}} \right) dQ^{sym}} = \left(\frac{1}{C_P} + \frac{1}{C_{\Pi}} \right)^{-1} \quad [13]$$

revealing the serial linkage of P and Π as shown in Figure 1.

Finally, organ growth increases water in the apoplast, where $Q^{apo}_{sat} = Q^{apo}$, $d\theta^{apo}/dt = 0$, and $\theta^{apo} = 1$. The rate equation is simply

$$\frac{dQ^{apo}}{dt} = r_Q Q^{apo} = I^{apo} \quad [14]$$

where the " I^{apo} " designates that when the plant is growing the increase in Q^{apo} is represented as a current source (Fig. 1).

For completeness,

$$f^{sym} = \frac{Q_{sat}^{sym}}{Q_{sat}^{sym} + Q^{apo}} \quad [15]$$

and

$$\theta = \frac{Q_{sat}^{sym} + Q^{apo}}{Q_{sat}^{sym} + Q^{apo}} \quad [16]$$

While the principle state variables are described by differential equations (eqns [1–14]), resistor networks (Fig. 1) are governed by algebraic equation systems (3, 5, 7). Since there is only one unknown (interior) potential in the resistance “tree” of Figure 1, Ψ^{apo} is constrained by a single algebraic equation resulting from the application of Kirchoff’s Voltage Law (3). Because there is no direct current path through the capacitors (Fig. 1) they can be ignored, and temporarily ignoring the transpiration ($I_{trans}A_{leaf}$) and I^{apo} current sources ($m^3 s^{-1}$), the xylem water potential (assumed uniform throughout the shoot; Fig. 1), is

$$\Psi^{apo} = \frac{\Psi_{soil} R_{stem}^{stor} R_{leaf}^{stor} + \Psi_{stem}^{sym} R_{leaf}^{stor} R_{root} + \Psi_{leaf}^{sym} R_{stem}^{stor} R_{root}}{R_{stem}^{stor} R_{leaf}^{stor} + R_{leaf}^{stor} R_{root} + R_{stem}^{stor} R_{root}} \quad [17]$$

where Ψ_{soil} is the soil water potential and R_{root} is the total root system hydraulic resistance. The application of Kirchhoff’s Voltage Law, however, does not tolerate $I_{trans}A_{leaf}$ or I^{apo} because an ideal current source term has no resistance from which to calculate a voltage drop. To maintain the mass balance, the current source effects are therefore collapsed into an independent “voltage” source (7), the soil water potential term, as:

$$\Psi^{apo} = \frac{[\Psi_{soil} - (I_{trans}A_{leaf} + I^{apo})R_{root}] R_{stem}^{stor} R_{leaf}^{stor} + \Psi_{stem}^{sym} R_{leaf}^{stor} R_{root} + \Psi_{leaf}^{sym} R_{stem}^{stor} R_{root}}{R_{stem}^{stor} R_{leaf}^{stor} + R_{leaf}^{stor} R_{root} + R_{stem}^{stor} R_{root}} \quad [18]$$

The determinations of the parameters τ , ϵ , and r_Q ; of the driving (input) variables R_{root} , I_{trans} , and Π_{sat} ; and of the initial values for state variables are described below.

Model Parameterization.

All parameters were determined in the field using plants from the experimental population for which the model was validated.

All leaf water potential measurements (Ψ_{leaf}^{sym}) were made using a pressure-bomb (Soil Moisture Equipment). The bulk organ volumetric elastic moduli, $\epsilon = \theta^{sym} \Delta P / \Delta \theta^{sym}$, were determined using a non-linear regression computer program (24), or when the program failed to converge, from visual, graphic analysis of modified Hofler diagrams (P plotted against θ^{sym} ; Figure 3, inset), which were constructed after Π_{sat} and f^{sym} were estimated using pressure-volume (PV) curves, or $1/\Psi^{sym}$ plotted against $1-\theta$. Both PV curves and Hofler diagrams are derived from repeated measurements of (Ψ_{leaf}^{sym}) as a leaf is dehydrated on the

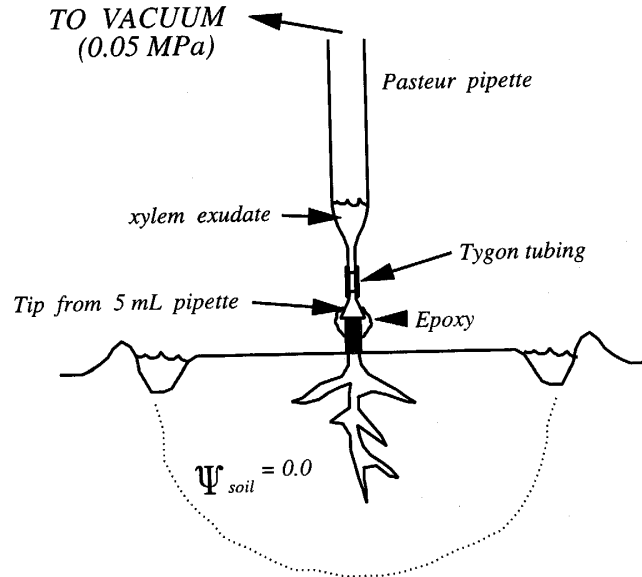


Fig. 2. A technique for measuring root system hydraulic conductivity (L_{root} eqn [19]) in the field. Fifteen minutes after saturating the soil, the stem was cut at about 5 cm above the soil. The cut stem was blotted dry and the tip of a 5 mL disposable pipette was attached using quick-setting (5-minute) epoxy resin.

laboratory bench (26, 27). Specifically, ε was estimated at $P=0.5$ MPa and assumed to be proportional to P (24) with $\varepsilon=0$ at $P=0$, which prevents negative turgor pressures from developing (2).

The time constant, τ , of the leaf was also measured using a pressure bomb and the method of Nobel and Jordan (21), but ignoring the osmotic potential of the apoplast. Elastic moduli were determined for both leaves and internodes, but τ was determined only for leaves and assumed to be the same for stems. At the beginning and end of a seven day validation period, A_{leaf} was measured and a relative expansion rate calculated as $r_A = \ln(A_{leaf, end}/A_{leaf, begin})/(t_{end}-t_{begin})$, where t =time (s). Leaf expansion in the model was then calculated as $dA_{leaf}/dt = r_A A_{leaf}$. We also assumed that both the relative growth rate of the stem and r_Q were equal to r_A .

All simulations were initialized with time=0 at midnight. The initial saturated water content, Q_{sat} , was estimated from a linear extrapolation of early-morning PV data (16) for representative leaves and internodes and scaled to the total leaf area A_{leaf} and stem (internode+petiole) volume, V_{stem} , which was measured with a micrometer (for diameter) and a ruler (for length) at dawn. The initial values of Q were set to $0.95Q_{sat}$ and Ψ^{sym} values for both leaf and stem were initialized at Ψ_{soil} (Table 2).

Root resistance was measured by saturating the soil around the root, 15 minutes later cutting the stem near the soil surface, attaching tygon tubing and

pulling water through the root system for 20 minutes using a 0.05 MPa vacuum pump (Fig. 2). The xylem sap collected during the first 5 minutes was discarded, whereas that collected during the latter 900 s was used to calculate root conductivity. Root resistance is presented as its intensive inverse, root conductance per unit organ size, or root conductivity (L_{root} ; $\text{m s}^{-1} \text{MPa}^{-1}$), because conductance is proportional to organ size; and proportionalities are easier to conceptualize than inverse proportionalities. [The reader should note that the term conductance (the inverse of resistance) is usually defined as $\text{m}^3 \text{MPa}^{-1} \text{s}^{-1}$, regardless of the extensive variable used to represent organ size; whereas “conductivity” can refer to various units, such as $\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$ or $\text{m s}^{-1} \text{MPa}^{-1}$, depending on the extensive variable used as a reference; i. e., conductance equals the product of conductivity and some extensive variable representing organ size.] Typically, root hydraulic conductivity is expressed on a root surface area or root length basis; however, as we did not measure root system sizes, L_{root} is expressed per unit leaf area, A_{leaf} , or

$$L_{root} = \frac{1}{A_{leaf}} \left(\frac{Vol}{(0.05 - \pi_{vol})(900)} \right) \quad [19]$$

where Vol is the amount of xylem exudate collected (m^3 ; Fig. 2) and π_{vol} is the osmotic potential of that sap (MPa), measured with a Wescor psychrometer.

Calibration, Validation and Verification

The leaf area-based root conductivity (eqn [19]) must be multiplied by the leaf area of the plant and then the inverse taken to yield R_{root} . When the soil is less than saturated, however, and the plant is withdrawing water from the soil, uptake can be limited by the soil conductivity (II, 28) as well as the contact between the root and the soil (II). Therefore, R_{root} in the model was adjusted to include an effective root-soil resistance, i. e., the product of the measured root resistance and the root-soil contact factor, cf , or

$$R_{root} = \frac{cf}{A_{leaf} L_{root}} \quad [20]$$

The model was calibrated by adjusting cf until the predicted values of Ψ^{sym} agreed with the measured values of (Ψ_{leaf}^{sym}) . During the calibration day (22, 18, and 23 July for *A. theophrasti*, *D. stramonium*, and *X. strumarium*, respectively), (Ψ_{leaf}^{sym}) was measured about every 3 h on the same plants for which I_{trans} , Π_{sat} , and L_{root} were measured (in the order presented, the last being a plant-destructive measurement), also about every 3 h. I_{trans} was measured using an LI-1600 steady state porometer (LiCor) and Π_{sat} was calculated using eqns [6] and [15] with psychrometric measurements of Π (26), gravimetric measurements of θ (26), and f^{sym} values estimated from previous PV curves (Fig. 3; refs 26, 27). Tissue psychrometry was performed using an SC-10 thermocouple psychrometer (Decagon). Ψ_{soil} was measured gravimetrically at a depth of 0.1 m, which was

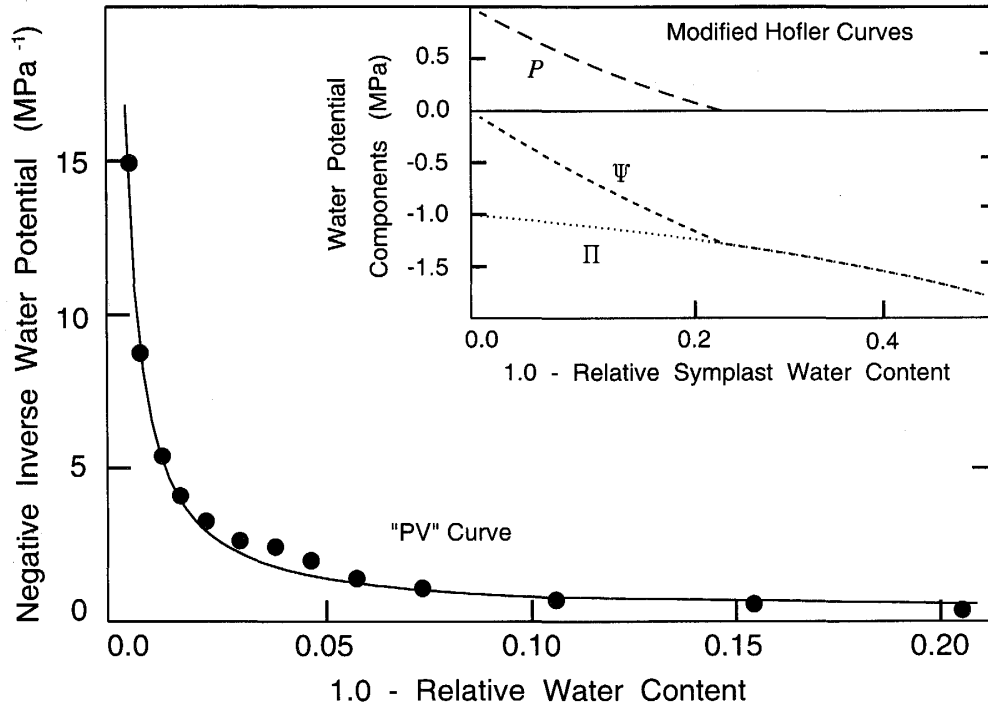


Fig. 3. A pressure-volume (PV) curve and the resulting modified Hofler curves (inset) for a leaf of *Abutilon theophrasti*. The relative water content was calculated as $(\text{fresh_weight} - \text{dry_weight}) \div (\text{saturated_weight} - \text{dry_weight})$. Linear extrapolation of the nearly-horizontal portion of the PV curve to the y-intercept yields the negative inverse of the saturated osmotic pressure (Π_{sat}); extrapolation to the x-intercept yields the fraction of symplast volume at saturation (f^{sym}); see turner (26). Given Π_{sat} and f^{sym} , the modified Hofler curves (inset) can be calculated using eqn [21] and $P = \Psi - \Pi$.

assumed to be the mean water extraction depth (see 15, 23).

After calibrating as described above, a week-long (24–30 July) validation was performed after stopping irrigation. In addition, based on the results from the calibration day, we assumed that the effective root-soil conductivity (L_{root}/cf) and Π_{sat} were proportional to I_{trans} (Table 3), and then only I_{trans} was measured for input. This approach was judged to be rational in that the effective root-soil conductance is in fact calibrated, and the measurements of L_{root} were used only to establish the diurnal pattern. ($\Psi_{\text{leaf}}^{\text{sym}}$) was measured at about 8, 12, and 16 h for seven days and compared with simulations. Input (driving) variables were calculated at each time step using linear interpolation between observed or estimated values.

A simplified version of the model (eqns [1–18] without growth or variation in Π_{sat} corresponding to Figure 1) was programmed on a microcomputer using Turbo Pascal version 6.0 (Borland International, Scotts Valley, California) with standard floating point ("real") variables, an Eulerian integration algorithm and a variable time step of $\text{MIN}(\tau_{\text{leaf}}, \tau_{\text{stem}})/3$. The precision was checked by comparison with a commercial electrical circuit simulation package (SPICE,

Intusoft Corporation, Berkley, California) and agreement for all state variables was within 0.5%. The complete analysis (eqns [1-20]) was verified by comparing the simulations with the additional constraint (24) of

$$\Pi = \frac{\Pi_{sat}}{1 - \frac{1-\theta}{f^{sym}}} \quad [21]$$

RESULTS

Model Input.

The parameters derived from the pressure-volume (PV) and modified Hofler curves (Fig. 3) were similar among species (Table 1). For all three species, the elastic moduli of internode segments at a turgor pressure of 0.5 MPa ($\epsilon_{stem}^{P=0.5}$, MPa) were more than twice the respective leaf values ($\epsilon_{leaf}^{P=0.5}$) whereas differences among species were smaller. The leaf time constant (τ , eqn [12]), increased non-linearly as leaf water potential (Ψ_{leaf} , MPa) decreased (Fig. 4), the non-linearity being strongest for *A. theophrasti* and weakest for *D. stramonium*.

The relative leaf area growth rate (r_A , s⁻¹) was highest for *D. stramonium* and lowest for *A. theophrasti*. (Table 1). Organ sizes differed among species, with *D. stramonium* having the most leaf water at initial saturation ($Q_{sat, leaf}$, m³) and *A. theophrasti* the least, whereas the stem water ($Q_{sat, stem}$, m³) was not as variable (Table 2).

All three of the driving variables showed a distinct diurnal pattern, with leaf area-based root conductivity (L_{root} , m s⁻¹ MPa⁻¹) showing a positive and osmotic potential at full turgor (Π_{sat}^{leaf} , MPa) showing a negative correspondence to transpiration (I_{trans} , m s⁻¹, Fig. 5). Both I_{trans} and L_{root} were highest for *D. stramonium* whereas Π_{sat}^{leaf} was most negative for *A. theophrasti*. For a particular species, all three driving variables displayed peaks or valleys near 15 h solar time (Fig. 5). Linear Regressions of the effective root-soil conductivity (L_{root}/cf , see eqns [19] and [20]) or of Π_{sat}^{leaf} against I_{trans} had generally high correlation coefficients (Table 3).

The osmotic effects on the L_{root} measurements (π_{Vol} , eqn [19]) varied among

Table 1. Leaf and stem values for elastic modulus at a turgor pressure of 0.5 MPa, $\epsilon^{P=0.5}$, and relative leaf area growth rate, r_A .

Parameter	Units	Species		
		<i>A. theophrasti</i>	<i>D. stramonium</i>	<i>X. strumarium</i>
$\epsilon_{leaf}^{P=0.5}$	MPa	4.6 (.28)	5.2 (.21)	5.7 (.35)
$\epsilon_{stem}^{P=0.5}$	MPa	10.2 (.16)	10.5 (.29)	16.3 (.22)
r_A	s ⁻¹	3.92×10^{-7} (.12)	8.54×10^{-7} (.17)	4.18×10^{-7} (.17)

Values in parenthesis represent the coefficient of variation for n=4.

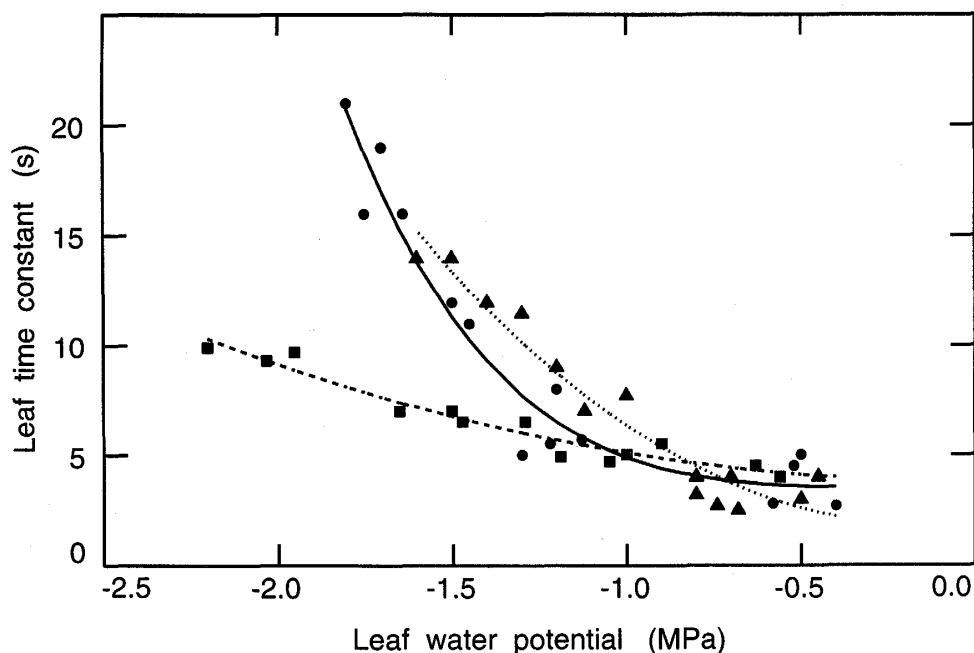


Fig. 4. The leaf hydraulic time constants (τ , eqn [12]) derived from the transient response of leaf water potential after a 0.1 to 0.3 MPa step-change in the pressure-bomb balance pressure, (see Nobel and Jordan, 1983; 21), for *Abutilon theophrasti* (circles, —), *Datura stramonium* (squares, ...) and *Xanthium strumarium* (triangles, ...). The curves represent the equation $\tau = a + b(-\Psi^{\text{sym}})^c$, where $a = 3.52, 3.78$ and 1.60 ; $b = 1.34, 1.30$ and 4.74 ; and $c = 4.34, 2.04$ and 2.25 for the three species, respectively, with r^2 of 0.94, 0.95 and 0.94.

Table 2. Initial values for the auxillary and state variables.

Variable	Units	Species		
		<i>A. theophrasti</i>	<i>D. stramonium</i>	<i>X. strumarium</i>
Auxillary variables				
$Q_{sat, leaf}$	$m^3 (\times 10^6)$	9.40 (.26)	21.52 (.19)	18.45 (.18)
$\Omega_{sat, stem}$	$m^3 (\times 10^6)$	7.06 (.14)	7.85 (.21)	7.30 (.20)
f_{leaf}^{sym}	—	0.58 (.18)	0.57 (.17)	0.46 (.26)
f_{stem}^{sym}	—	0.50 (.21)	0.48 (.25)	0.42 (.27)
$\theta_{leaf} \theta_{stem}$	—	0.95	0.95	0.95
State variables				
A_{leaf}	m^2	0.050 (.20)	0.052 (.16)	0.049 (.13)
$Q_{leaf}^{sym}, Q_{stem}^{sym}, Q_{apo, leaf}, Q_{apo, stem}, Q_{sat, leaf}^{sym}, Q_{sat, stem}^{sym}$		Calculated using auxillary variables and eqns (15) and (16).		
Π_{leaf}, Π_{stem}		Calculated using eqn (6)		
P_{leaf}, P_{stem}		Calculated as $P = \Psi_{soil} - \Pi$		

Values in parenthesis represent the coefficient of variation for $n=4$.

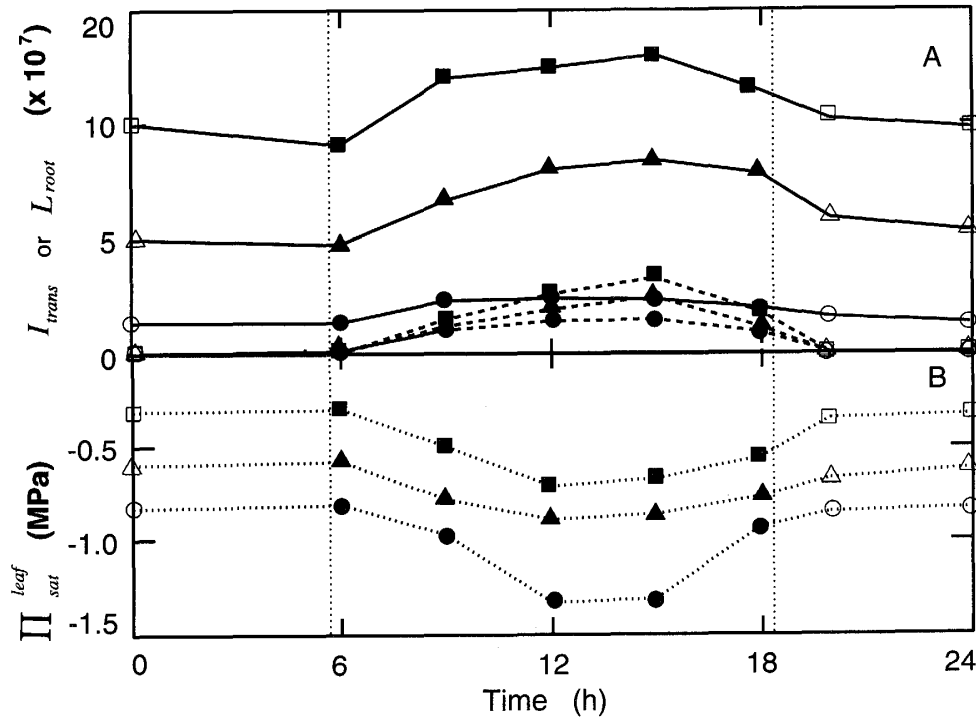


Fig. 5. Interpolation curves for input variables: Leaf area-based root hydraulic conductivity (L_{root} , $\text{m s}^{-1} \text{MPa}^{-1}$; —), leaf area-based transpiration rate (I_{trans} , m s^{-1} , ---), and saturated osmotic potential (Π_{sat} , MPa ; ...) for the model calibration day. Daytime (closed) symbols represent observation means ($n=1, 4$, and 3 for L_{root} , I_{trans} , and Π_{sat} , respectively) and night-time (open) symbols represent best-guess estimates for the linear interpolation algorithm (lines) used in the model to simulate continuous-time input. Symbols are by species as in Figure 4.

species and throughout the day (Fig. 6). Unlike the L_{root} data (Fig. 5), *A. theophrasti* had the lowest π_{vol} while *D. stramonium* had the highest (Fig. 6). Hence, the species with the lowest L_{root} (*A. theophrasti*, Fig. 5) had the largest driving force during the measurement ($0.05 - \pi_{vol}$, eqn [19]).

Model Output.

The values of storage, uptake, and transpiration must balance, where

$$\text{storage} = \frac{dQ_{leaf}^{sym}}{dt} + \frac{dQ_{leaf}^{apo}}{dt} + \frac{dQ_{stem}^{sym}}{dt} + \frac{dQ_{stem}^{apo}}{dt} \quad [22]$$

and

$$\text{uptake} = \frac{\Psi_{soil} - \Psi^{apo}}{R_{root}} \quad [23]$$

In all cases, uptake equaled transpiration plus storage with a relative error of less than 10^{-6} . In addition, the model satisfied eqn [21] indicating that eqns [1–18] were derived correctly.

Table 3. Linear equation parameters for Π_{sat} and L_{root}/cf as functions of I_{trans}

Parameter	Species		
	<i>A. theophrasti</i>	<i>D. stramonium</i>	<i>X. strumarium</i>
Saturated osmotic potential, Π_{sat}			
Slope($\times 10^{-7}$)	-0.189	-0.074	-0.093
Intercept	-0.970	-0.382	-0.913
r^2	0.81	0.91	0.84
Root-soil hydraulic conductivity, L_{root}/cf			
Slope	0.097	0.194	0.163
Intercept($\times 10^7$)	0.534	3.152	1.143
r^2	0.74	0.90	0.84

Π_{sat} is the osmotic potential (MPa) at full turgor; L_{root}/cf is the effective root-soil hydraulic conductivity per unit leaf area ($m^{-1} MPa^{-1}$); and I_{trans} is the transpiration per unit leaf area ($m s^{-1}$). The actual data ($n=5$) are the daytime (closed) symbols in Figure 5.

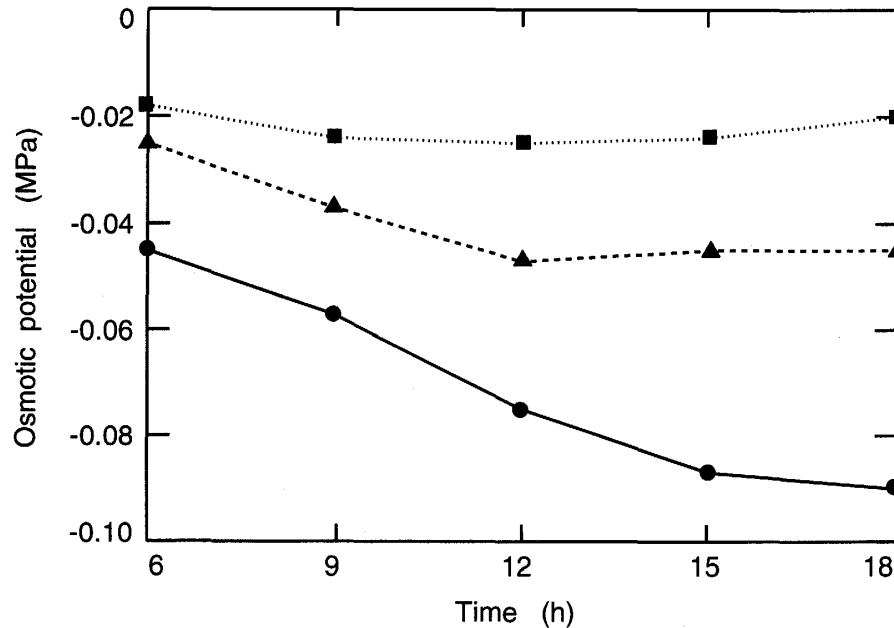


Fig. 6. Osmotic potential of the xylem exudate collected during measurements of root hydraulic conductivity (π_{vol} in eqn [19]), as depicted in Figure 2. Symbols are by species as in Figure 4.

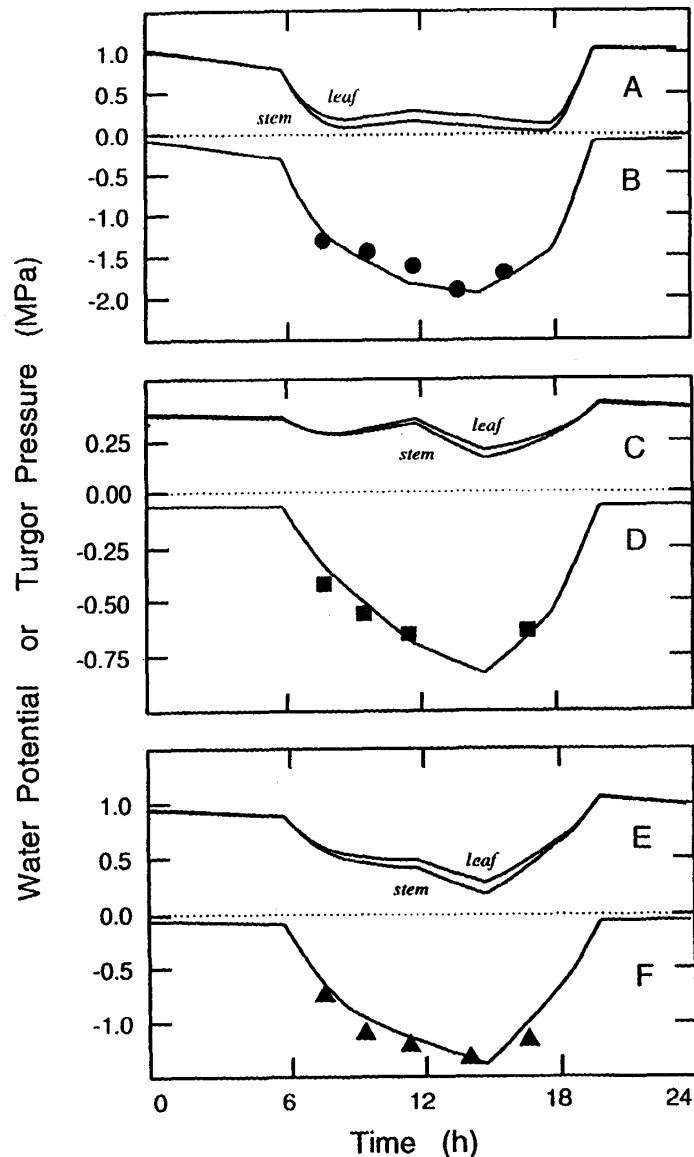


Fig. 7. Calibrated water potentials (curves in B, D, F), predicted turgor pressures (curves in A, C, E) and observed water potentials (symbols in B, D, and F) for *A. theophrasti* L. (A, B), *D. stramonium* (C, D), and *X. strumarium* (E, F). The model was calibrated by adjusting cf in eqn [20]. The soil water potential was -0.07 MPa. The stem and leaf water potentials were essentially indistinguishable in all cases.

As described in the *Materials and Methods* section, a root-soil contact factor, cf , was used to adjust root resistance (eqn [20]) to calibrate the model against measurements of Ψ_{leaf} following the day of parameter measurements. The values of cf required to obtain agreement were 1.5, 1.5, and 2.2, for *A. theophrasti*, *D. stramonium*, and *X. strumarium*, respectively. When Ψ^{sym} agreed with the Ψ_{leaf} measurements, the simulations suggested that approximately 75, 50 and 75% diurnal fluctuation in turgor pressure (P , MPa) occurred for *A. theophrasti*, *D.*

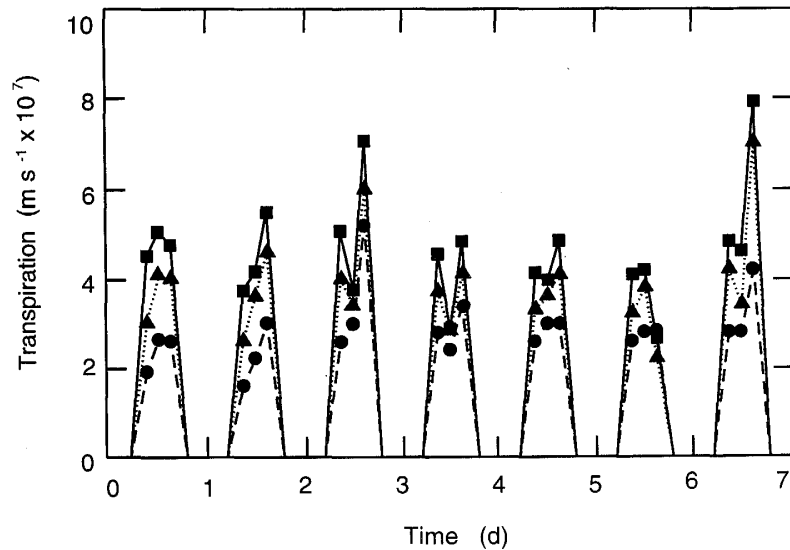


Fig. 8. Transpiration inputs for the simulation shown in Figure 9. Symbols and lines are by species as in Fig. 6.

stramonium, and *X. strumarium*, respectively (Fig. 7); and mid-day depressions in P_{stem} were greater than for P_{leaf} . Also, (Ψ_{leaf}^{sym}) and Ψ_{stem}^{sym} were essentially indistinguishable (Fig. 7). A sensitivity analysis (not shown) revealed that fixing Π_{sat} at the morning values caused *X. strumarium* to wilt at mid-day and the other two species to wilt for most of the day; and fixing R_{root} at the morning values caused all species to wilt for most of the day.

To validate the model, Ψ_{leaf} was measured at morning, noon, and evening over a seven-day period as the soil dried after irrigation. During this period, only I_{trans} was measured for input (Fig. 8), whereas L_{root}/cf and Π_{sat}^{leaf} were assumed to be proportional to I_{trans} (Fig. 5; Table 3). The relative species differences were predicted well for 21 measurements of Ψ_{leaf} while P , which was calculated as $\Psi_{leaf} - \Pi$, was occasionally overestimated (Fig. 9). As with Figure 7, leaf and stem water potentials were indistinguishable.

The ratio of storage (eqn [22]) to uptake (eqn [23]) is informative. While the simulated storage is generally less than 0.5% of uptake, the early morning and late evening values can be as high as 3% and are in fact asymptotic (Fig 10). This behavior reflects primarily the lag of uptake behind transpiration. Negative storage ratios were largest and occurred most often for *A. theophrasti* (Fig. 10A) and were the smallest and occurred least often for *D. stramonium* (Fig. 10B). Sharp directional reversals of the storage ratio coincided with mid-day depressions in the transpiration rate [compare Figs. 9 and [10]. Also, the symplast fractions of the leaf and stem (eqn [15]) increased during the day by 2 to 3% for each species and all simulations (data not shown).

The output of the model can also be examined in the water potential domain rather than over time. The behaviors of the simulated relative potential-based

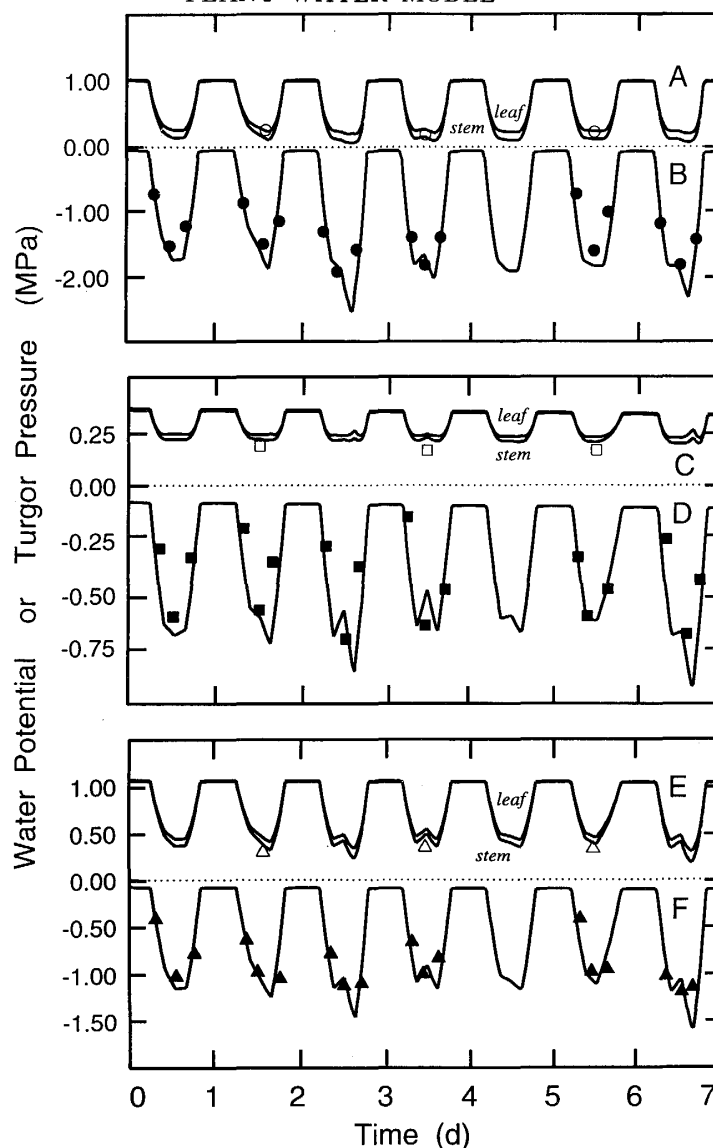


Fig. 9. Predicted (curves) and observed water potentials (closed symbols) and turgor pressures (open symbols) for a seven-day period after calibration as in Figure 7. Panels and symbols by species as in Figure 7. Only transpiration (Fig. 8) was a measured input, whereas effective root-soil conductivity and saturated osmotic potential were assumed to be proportional to transpiration (Table 3). Soil water potential was -0.07 MPa at the beginning and -0.11 MPa at the end of the period and was assumed to decline linearly with time.

capacitance (C_{Ψ}/Q^{sym} , eqn [13]) and the simulated relative storage conductance ($L_{\theta} = R^{stor} Q_{sat}^{sym})^{-1}$, eqns [2] and [3]) reveal major interspecific differences (Fig. 11). The C_{Ψ}/Q^{sym} generally increased as Ψ^{sym} decreased, whereas the L_{θ} displayed the opposite behavior (Fig. 11). The patterns were slightly sigmoidal for *A. theophrasti* and *X. strumarium*, but parabolic for *D. stramonium*. Nearly all values were highest for *D. stramonium* and lowest for *X. strumarium*. In addition, *D. stramonium* displayed more hysteresis than the other two species, as C_{Ψ}/Q^{sym}

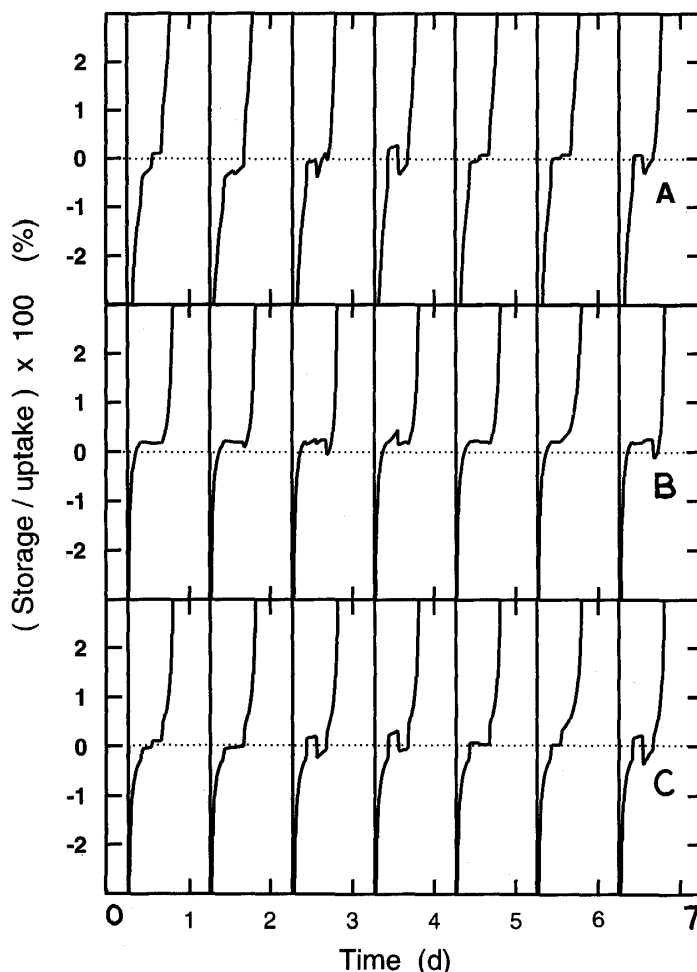


Fig. 10. The ratio of storage (eqn [22]) to uptake (eqn [23]) for *A. theophrasti* (A), *D. stramonium* (B), and *X. strumarium* (C), for the simulations of Figure 8.

increased notably with time (Fig. 11).

A key feature of our PSIRC model is the incorporation of growth effects on water accumulation *via* potential-driven flow. The growth component of the system of equations does in fact perform as expected (Fig. 12), indicating that the growth demands were correctly transduced to water potential gradients.

DISCUSSION

A system of differential-algebraic equations was derived and a simulation model called "PSIRC" was constructed to simulate the dynamics of plant water movement in growing plants. By adding supply and demand terms to the electrical analog, or "resistor-capacitor" approach (8, 19, 21, 22, 25), the growth-induced demand for water was converted in PSIRC to a water potential gradient which in turn drives the uptake of the water for growth. The model

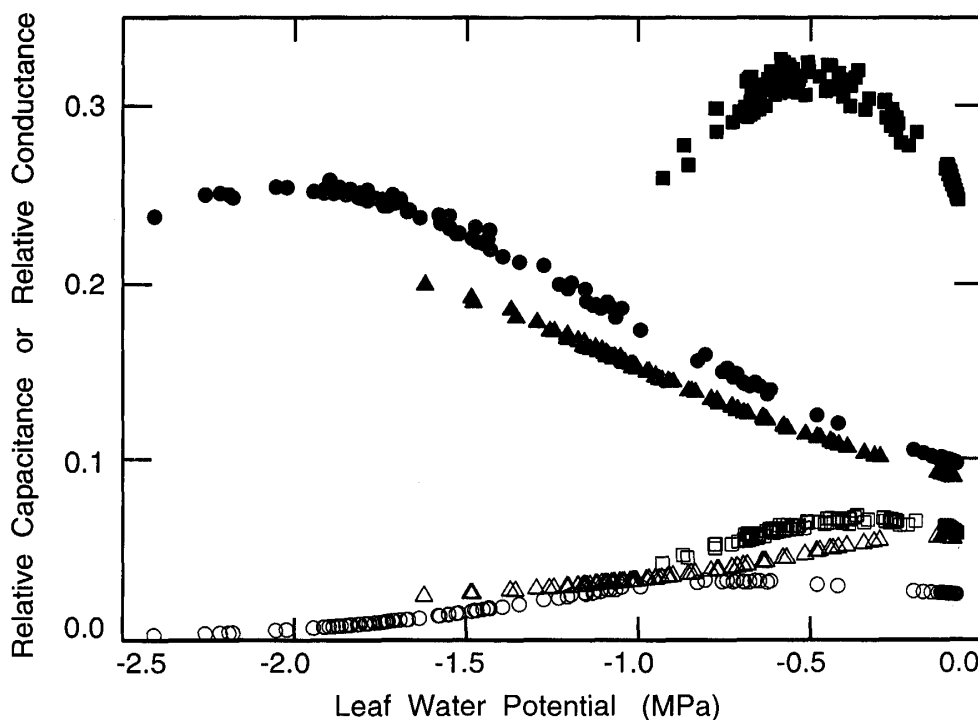


Fig. 11. Relative water potential-based capacitance of the symplast (closed symbols; C_{ψ}/Q^{sym} , eqn [13]) and relative hydraulic conductance between the symplast and the xylem [open symbols; $L_{\theta} = (R^{stor} Q_{sat}^{sym})^{-1}$, eqns (2) and (3)] for leaves of *A. theophrasti* (circles), *D. stramonium* (squares), and *X. strumarium* (triangles). Data are hourly values from the simulations shown in Figure 9.

parameterization experiments for three dicotyledonous annual weeds revealed that *Datura stramonium* has a much lower root hydraulic resistance than *Xanthium strumarium* and *Abutilon theophrasti*. Our simulations suggest that this low root resistance enables *D. stramonium* to simultaneously sustain high transpiration rates and a higher daytime amount of plant-stored water than the other two species. *Xanthium strumarium* and especially *A. theophrasti* are more opportunistic, increasing stored water faster when transpiratory demand is low (Figs. 8 and 9). Simulations also suggest that diurnal osmotic adjustment and diurnal variation in root resistance are necessary to prevent the wilting of all three species.

The behavior of electrical analog models is in part related to their hydraulic time constants (τ , eqn [12]), analogous to the electrical time constants in resistor-capacitor circuits (19, 21). The measured hydraulic time constants for all three species were non-linear functions of leaf water potential, giving rise to fluctuating values for the simulated leaf and stem relative capacitances and relative storage resistances (21). The water potential-based capacitance and storage resistance are indeed dynamic as indicated directly by eqns [5], [7] and [13] and observed in the measurement of the leaf time constant (Fig. 4). The biological interpretation of this behavior (Fig. 11) is that as the organ is

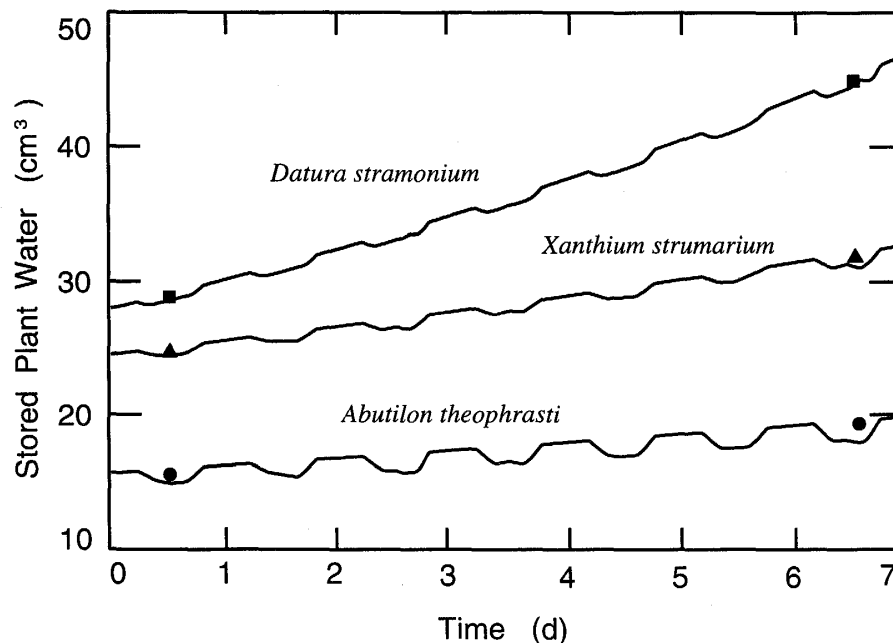


Fig. 12. Simulated (curves) and observed (symbols) growth in stored plant water for *A. theophrasti* (circles), *D. stramonium* (squares) and *X. strumarium* (triangles).

dehydrated, the symplast membranes offer less resistance to water flow while the amount of water loss required to decrease the water potential increases; these are mutually compensatory tendencies with respect to preventing organ water loss. A component of the water potential-based capacitance is the turgor-based capacitance (eqn [5]), which is inversely proportional to the bulk organ elastic modulus (20). Because the elastic moduli were higher for the stems than for the leaves, the stems tended to have larger mid-day depressions in turgor pressure (Figs. 7 and 9).

The root hydraulic conductance fluctuated substantially and the saturated osmotic potential fluctuated by at least 50% for all species. Simulations revealed that without this fluctuation, the plants would have wilted. The importance of diurnal osmotic adjustment for maintaining turgor in photosynthetic tissue has been demonstrated for maize (1, 12) and observed and simulated for CAM plants (25); and in both cases the adjustment is linked with accumulation of photosynthetic products: free sugars and crassulacean acids, respectively. In addition, the osmotic component of the driving force for root water uptake during our measurements of root hydraulic conductivity (Fig. 2) fluctuated on a diurnal basis. These patterns suggest that there may be a functional tradeoff among these species for mid-day decrease in saturated osmotic potential vs. mid-day increase in root hydraulic conductance.

Like PSIRC, the PWD model (9) includes diurnal plant water storage, but many parameters must be assumed because experimental parameterization would require an extensive effort or has otherwise not been done. The authors of

PWD conclude that the ability to match transpiration and leaf water potential directly indicates that three independent, non-linear parameters (as well as many auxillary parameters) were well estimated; however calibrating such a comprehensive model by adjusting many parameters in non-linear equations—even as few as three—can result in biologically incorrect calibrations due to mutually-correcting errors. For instance, it has been observed that the water potential gradient between the shoot and the soil can increase or remain constant as the transpiration rate decreases (23); the PWD model assigns all of this effect to increased xylem resistance due to cavitation. While cavitation is significant during drought, the observation could also be explained by dynamically-varying extraction zones (15, 23) or by the non-linear equations governing root resistance itself (5). In addition, diurnal variation in saturated osmotic potential was not included in PWD while such behavior is likely in all plants (1, 12, 25; this report). However, being an algorithmic rather than a mathematical model, PWD has the advantage of allowing time steps four orders of magnitude larger than does PSIRC.

Our PSIRC model also has assumptions that may be incorrect. The effects of the root-soil contact factor (cf) could be misplaced. Although soil and root-soil contact factors are typically necessary for accurate predictions (14), we did not measure cf directly, but calculated it using field calibration. Direct measurement of cf for a complex root system is not feasible. Anyhow, our measurements of root resistance were used to establish the diurnal pattern, which is perhaps more important than the absolute magnitude of root resistance. A second assumption we made was that the stem hydraulic resistance was negligible (Fig. 1), when in fact it may not have been (9). The plants were only about 0.1 m tall, however, and even with reasonably high axial resistivities, the stem would not represent much of a resistance. In addition, introducing xylem resistance terms explicitly begs a detailed consideration of plant architecture for both shoots (4, 25) and roots (5), i.e., inclusion of the topology of connections between organs, resulting in a much more complicated model. In such a model, eqn [18] would be a system of equations (cf. 5) and the differential equations would be duplicated for each phytomer. A number of the basic questions for such an approach remain unanswered, such as what is the resistance to flow between adjacent xylem traces and how does it vary along the stem? How does the resistance behave at trace junctions? These questions and others need to be addressed experimentally before such a complex model could be tested. Alternatively, if the cf factor does indeed reflect root-soil contact effects, then what can be inferred from interspecific differences? Another assumption we made was that the effects of the osmotic potential of the apoplast were subsumed by the measurements of τ (for predictions) and of leaf water potential (for observations), where in both cases the apoplast osmotic potential was not measured. Again, including apoplast osmotic effects will result in a much more complicated model (see the "Solutes" chapter in 20).

Notwithstanding the above considerations, PSIRC is a useful model. The model may be particularly useful in exploring the feedback between itself and

models of stomatal conductance (13), resource partitioning (18), or leaf expansion (5, 10). It is not clear to us, however, how the model would be validated at the appropriate temporal and spatial scales for these investigations. The major obstacle to a meaningful marriage of such models lies in the knowledge gaps at their interfaces. The relative growth rate (r_Q , s^{-1}) was an input for PSIRC and generated a "growth-induced water potential," (6); whereas an alternative approach is to predict r_Q . We assumed that r_Q was constant throughout the day, but this is known generally not to be, as some species grow thier leaves more during the day and some grow more during the night. According to the theory of Lockhart (17), the relative growth of the symplast should be proportional to the turgor pressure in excess of a cell wall-yield threshold, or

$$\left(\frac{1}{Q^{sym}}\right)\frac{dQ^{sym}}{dt}=\Phi(P-Y) \quad [24]$$

where Φ is the cell wall extensibility ($MPa^{-1} s^{-1}$), P is the turgor pressure (MPa), and Y is the yield threshold (MPa). Boyer (6) notes that plant cells solve eqns [24] and [3] simultaneously and that the potentials driving wall extension and water uptake are additive. In the context of PSIRC, these effects can be viewed as wall extension and water uptake adding to determine the water potential components; and to predict the relative growth rate, the right-hand-side of eqn [24] could be substituted for r_Q in eqns [4], [8] and [11]. Nevertheless, wall extensibility is still controlled by metabolism. And just as biological systems must obey the postulates of thermodynamics, thermodynamic systems must obey the laws of biology: compartmentalization and gene- and enzyme regulation dictate ultimately the controlling parameters Φ and Y . Interspecific variation in Φ or Y was apparent in the current study because the species with the highest relative growth rate (*D. stramonium*) did not have the highest turgor pressure. Both Φ and Y can be measured (6) but we know of no model for thier prediction. Perhaps a merger of physicochemical models (20) and phenological models (4) is needed.

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REFERENCES

1. Acevedo, E. (1979) Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. *Plant Physiol.* **64**, 476-480.
2. Acock, B. and Grange, R. I. (1981) Equilibrium models of leaf water relations. Pages 29-46 in D. A. Rose and D. A. Charles-Edwards (eds) *Mathematics and Plant Physiology*. Academic Press, London.
3. Adby, D. P. (1980) *Applied circuit theory: matrix and computer methods*. Halsted Press, a division of John Wiley and Sons, New York.
4. Alm, D. M., McGiffen, M. E. and Hesketh, J. D. (1991) Weed Phenology. Pages 191-218.

- in T. Hodges (ed) *Predicting Crop Phenology*. CRC Press, Boca Raton, Florida.
5. Alm, D. M., Cavalier, J. and Nobel, P. S. (1992) A finite-element model of radial and axial conductivities for individual roots: development and validation for two desert succulents. *Ann. Bot.* **69**, 87–92.
 6. Boyer, J. S. (1987) Hydraulics, wall extensibility and wall proteins. Pages 109–21 in D. J. Cosgrove and D. P. Knievel (eds) *Physiology of Cell Expansion During Plant Growth. Proceedings of the Second Annual Penn State Symposium in Plant Physiology*. The American Society of Plant Physiologists, Rockville, MD.
 7. Cellier, F. E. (1991) *Continuous System Modeling*. Springer-Verlag, New York.
 8. Cowan, I. R. (1972) An electrical analogue of evaporation from, and flow of water in plants. *Planta* **106**, 221–226.
 9. Fernandez, C. J. and McCree, K. J. (1991) Simulation model for studying dynamics of water flow and water status in plants. *Crop Sci.* **31**, 391–398.
 10. Hesketh, J. D. and Baker, D. N. (1969) Relative rates of leaf expansion in seedlings of species with differing photosynthetic rates. *J. Arizona Acad. Sci.* **5**, 216–20.
 11. Huck, M. G., Klepper, B. and Taylor, H. M. (1970) Diurnal variations in root diameter. *Plant Physiol.* **45**, 529–30.
 12. Hsiao, T. C., Acevedo, E., Fereres, E., and Henderson, D. W. (1976) Water stress, growth, and osmotic adjustment. *Phil. Tran. Roy. Soc. of Lon.* **B-273**, 479–500.
 13. Johnson, I. R., Melkonian, J. J., Thornley, H. M. and Riha, S. J. (1991) A model of water flow through plants incorporating shoot/root 'message' control of stomatal conductance. *Plant, Cell Environ.* **14**, 531–544.
 14. Jung, Y-S and Taylor, H. M. (1984) Differences in water uptake rate of soybean roots associated with time and depth. *Soil Sci.* **137**, 341–350.
 15. Karamanos, A. J. (1980) Response in plant water status to integrated values of soil matric potential calculated from soil water depletion by a field bean crop. *Aust. J. Plant Physiol.* **7**, 51–66.
 16. Kubiske, M. E. and Abrams, M. D. (1990) Pressure-volume relationships in non-rehydrated tissue at various water deficits. *Plant, Cell Environ.* **13**, 995–1000.
 17. Lockhart, J. A. (1965) An analysis of irreversible plant cell elongation. *J. Theor. Bio.* **8**, 264–275.
 18. McNaughton, S. J. (1974) Developmental control of net productivity in *Typha latifolia* ecotypes. *Ecology* **55**, 864–870.
 19. Molz, F. J., Kerns, D. V. Jr., Peterson, C. M. and Dane, J. H. (1979) A circuit analog model for studying quantitative water relations of plant tissues. *Plant Physiol.* **64**, 712–716.
 20. Nobel, P. S. (1991) *Physicochemical and Environmental Plant Physiology*, Academic Press, San Diego.
 21. Nobel, P. S. and Jordan, P. W. (1983) Transpiration stream of desert species: resistances and capacitances for a C_3 , a C_4 , and a CAM plant. *J. Exp. Bot.* **34**, 1379–1391.
 22. Powell, D. B. B. and Thorpe, M. R. (1977) Dynamic aspects of plant-water relations. Pages 259–279 in J. J. Landsberg and C. V. Cutting (eds) *Environmental Effects on Crop Physiology*. Academic Press, London.
 23. Reid, J. B. and Huck, M. G. (1990) Diurnal variation of crop hydraulic resistance: a new analysis. *Agron. J.* **82**, 827–834.
 24. Schulte, P. J. and Hinckley, T. M. (1985) A comparison of pressure-volume curve data analysis techniques. *J. Exp. Bot.* **36**, 1590–1602.
 25. Schulte, P. J. and Nobel, P. S. (1989) Responses of a CAM plant to drought and rain fall: capacitance and osmotic pressure influences on water movement. *J. Exp. Bot.* **40**, 61–70.
 26. Turner, N. C. (1981) Techniques and experimental approaches for the measurement of plant water status. *Plant Soil* **58**, 339–366.
 27. Tyree, M. T. and Hammel, H. T. (1972) The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *J. Exp. Bot.* **23**, 267–282.

28. Van Bavel, C. H. M., and Ahmed, J. (1976) Dynamic simulation of water depletion in the root zone. *Ecol. Model.* **2**, 189–212.