

Water Uptake, Diameter Change, and Nonlinear Diffusion in Tree Stems

Received for publication May 30, 1974 and in revised form October 2, 1974

JEAN-YVES PARLANGE, NEIL C. TURNER,¹ AND PAUL E. WAGGONER

Department of Ecology and Climatology, The Connecticut Agricultural Experiment Station, New Haven, Connecticut 06504

ABSTRACT

A diffusion model for phloem swelling and contraction is proposed in which the rate of water movement changes markedly with moisture content. Good agreement between the actual swelling of the phloem of cotton stems and that predicted by the model was obtained. This result implies that water moves more readily into the phloem when it becomes wetter. This model also explains the lag of shrinkage of pine stems behind the water potential of the foliage and predicts that the lag is related to the thickness of the phloem.

The diameter of woody stems varies daily between a maximum near sunrise and a minimum 2 to 4 hr after noon (5). The shrinkage is caused by dehydration during transpiration (7), and the magnitude of this diurnal change is related to the weather (8). In a steady environment, the stem diameter is closely related to the water potential of the foliage (24), but in the field, the diurnal changes in diameter lag several hours behind the diurnal changes in the water potential of the foliage (6, 14, 21, 22).

Initially Haasis (5) suggested that the changes in xylem thickness were responsible for the changes in stem diameter, but because the xylem vessels are relatively incompressible, Turner and Waggoner (21) suggested that the phloem may also respond to changes in tension in the xylem. Recently Molz and Klepper (11) demonstrated that at least 92% of the change in diameter of cotton stems caused by water stress was located in the tissues outside the xylem, which they called "phloem" and suggested that the lag in stem diameter behind leaf water potential was caused by the gradual lateral diffusion of water from the phloem in response to deficits in the xylem (10). Significantly, their model for lateral water movement through the phloem, further elaborated by Molz *et al.* (12), is based on the simplifying assumption that a constant diffusion coefficient governs water movement through an aggregation of swelling or shrinking cells. A constant diffusion coefficient implies that water diffuses in paths that do not vary with water content, as may occur when water moves through a nonporous medium such as protoplasm. Because a constant diffusion coefficient leads to a linear diffusion equation, we shall

refer to the model used by Molz and Klepper (10) as the "linear" diffusion model.

Considerable evidence indicates that the chief pathway of water movement within the leaf mesophyll and root cortex is, in fact, in the porous cell walls (2, 4, 16, 19, 20, 23) although this is not certain (9). Evidence about the pathway of lateral water movement in the phloem is lacking, but it is reasonable to assume that water moves along or between the walls in this tissue, too. Our experience with other porous media has indicated that water movement is not governed by a constant diffusion coefficient, but that the rate of flow of water changes markedly with moisture content (17, 18). A variable diffusion coefficient causes a nonlinear equation, and we call the new model the "nonlinear" one. The purpose of our present paper is to show that the nonlinear model in which water diffuses faster as the medium becomes wetter fits the observations of phloem swelling of cotton equally as well as the linear model by Molz *et al.* (12). Moreover, we show that the nonlinear model explains the lag in the shrinking and swelling of red pine stems behind the hydration of the foliage.

THEORY

The new model assumes that water content can vary discontinuously through the phloem (Fig. 1). If the phloem has an initial moisture content, θ_0 , then, as water moves from the xylem through the vascular cambium to the phloem and swelling commences, the phloem near to the xylem will have a greater water content, θ_1 . The boundary between the phloem of greater water content θ_1 and that with the initial water content θ_0 is located by the radius of the front, r_f , which increases with time and with wetting. The radius of the outside of the phloem, r_p , varies with time from r_{p0} to $r_{p\infty}$ as the stem swells. The radius of the xylem, r_x , is assumed constant (11). The phloem is considered homogenous, and the thickness of the vascular cambium is considered negligible.

For a homogenous porous medium, Talsma *et al.* (18) show that when the rate of H₂O movement, *i.e.* the diffusivity (D), varies rapidly with moisture content, then the change in r_f with time is given by:

$$\ln \left(\frac{r_f}{r_x} \right) = \frac{g}{\theta_1 - \theta_0} \int_{\theta_0}^{\theta_1} D(\gamma) d\gamma \quad (1)$$

where g is a function of time given by

$$\frac{t}{r_x^2} = \left\{ \left[\frac{g}{\theta_1 - \theta_0} - \frac{1}{2A} \right] [\exp(2gA)] + \frac{1}{2A} \right\} \quad (2)$$

when A is the integrated diffusivity given by

¹ Present address: CSIRO Division of Plant Industry, P. O. Box 1600, Canberra City, A.C.T. 2601, Australia.

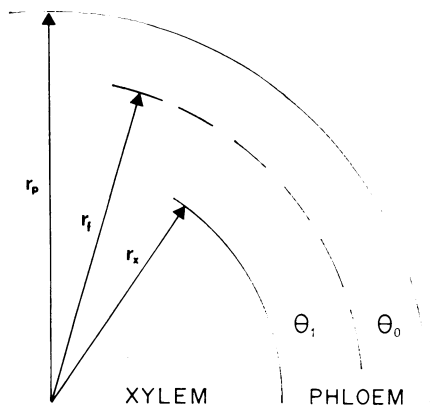


FIG. 1. Schematic diagram of a tree stem. The xylem has a constant radius, r_x . The radius of the phloem, r_p , and hence of the stem, increases as water diffuses from the xylem into the phloem increasing the water content from the initial θ_0 to θ_1 at the front r_f .

$$A \approx \int_{\theta_0}^{\theta_1} D d\theta / (\theta_1 - \theta_0) \quad (3)$$

Eliminating g from equation 1 gives

$$\frac{4tA}{r_x^2} = \left[2 \ln \left(\frac{r_f}{r_x} \right) - 1 \right] \frac{r_f^2}{r_x^2} + 1 \quad (4)$$

If the dependence of D upon θ could be measured in the phloem, then equations 3 and 4 could be used directly. Although this has not been done, equation 4 can still be used, but A must be determined empirically.

If the water moving into the phloem makes it swell by an equal volume, then

$$(\theta_1 - \theta_0) (r_f^2 - r_x^2) = (r_p^2 - r_{p0}^2) \quad (5)$$

When swelling ceases, the front r_f has reached the outer boundary of the phloem, $r_{p\infty}$, and

$$r_f = r_p = r_{p\infty} \quad (6)$$

At any intermediate time the uptake of water, u , as a fraction of the final uptake at an infinite time is

$$u = (r_p^2 - r_{p0}^2) / (r_{p\infty}^2 - r_{p0}^2), \quad (7)$$

or, by substituting from equation 5,

$$u = (r_f^2 - r_x^2) / (r_{p\infty}^2 - r_x^2) \quad (8)$$

Thus for a known A and r_x , equation 4 gives the boundary r_f for any time, and for any $r_{p\infty}$, equation 8 gives the fractional uptake, u , and stem radius, r_p .

EXPERIMENTAL

Molz *et al.* (12) measured the stem diameter of several 3-month-old, potted cotton plants (*Gossypium hirsutum* I. cv. 'Auburn 7-683') in a growth room with a linear variable displacement transducer attached to the stem a few centimeters above the soil. The soil was allowed to dry until the stem contracted and then plastic bags were tied around the plant to prevent further shrinkage. After a 2- to 5-hr equilibration, the stem was cut under water, and the expansion of the stem was measured for the following 140 min. The final stem diameter and phloem thickness were measured with a micrometer caliper. Subsequently, Molz *et al.* (13) observed the swelling for longer times. It should be remembered that here "phloem" is the tissues outside the xylem.

Turner and Waggoner (21) measured the diurnal changes in stem diameter and leaf water potential of the foliage of 15 m tall red pine (*Pinus resinosa* Ait.) in a forest. Some of the trees had been sprayed with phenylmercuric acetate to partially close the stomata (22). The stem diameter 140 cm above the ground was measured with a dendrometer (3) and the foliage potential with a pressure chamber (15). The phloem thickness was measured microscopically in cores taken at 140 cm from the ground. Here "phloem" is the living bark.

RESULTS AND DISCUSSION

Swelling of Cotton Stems. The swelling of a stressed cotton stem after severing under water is shown in Figure 2 (12). The diameter ($2r_x$) of the xylem of this stem was 0.4178 cm and Figure 2 shows that $2r_{p0}$ was 0.6195 and $2r_{p\infty}$ was 0.6360 cm.

The course of swelling predicted by the nonlinear model, using equations 4 and 8 and A of 1.2×10^{-6} cm² sec⁻¹ is shown by the solid line in Figure 2. Clearly, for the chosen value of A , the nonlinear diffusion model, which assumes that there is a sharp change in moisture content at a wetting front, agrees closely with the observations.

The stem increased less rapidly than predicted between 60 and 120 min because the transition from θ_0 to θ_1 in the phloem cannot, in fact, occur discontinuously, but must occur over a finite but short distance. Hence the observations suggest that after 60 min, as water begins to reach the outside of the stem, the wetting and swelling slows down. The discrepancy between the predictions and observations after this time indicates further that the transition from θ_0 to θ_1 occurs over a distance of 0.002 cm. *i.e.* the difference between the diameter at 60 min and 140 min. Because this 0.002 cm is only 14% of the total swelling of the phloem, it indicates that the transition from θ_0 to θ_1 is sharp and that use of a discontinuity is a justifiable approximation.

The dashed line in Figure 2 shows the swelling of the cotton stem predicted by Molz *et al.* (12) assuming linear diffusion and using an average diffusion coefficient, D , of 1.72×10^{-6}

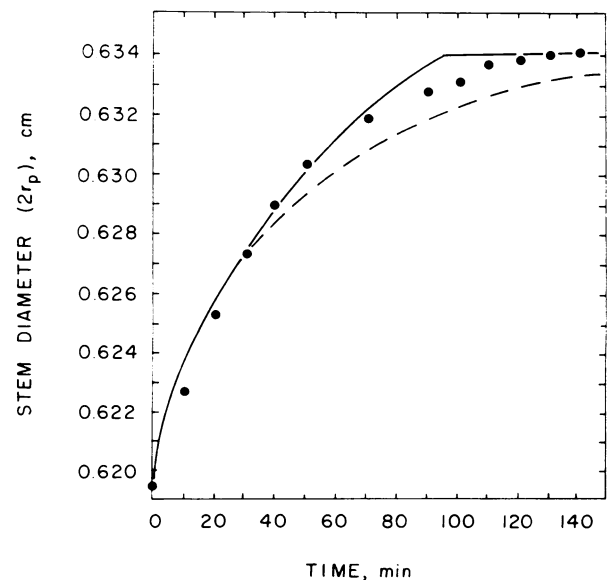


FIG. 2. Change in stem diameter after a desiccated cotton stem is severed under water at zero time. The points (●) are the observed swelling, the solid line the swelling predicted by our non-linear diffusion model and the dashed line by the linear diffusion model of Molz *et al.* (11).

cm² sec⁻¹. Clearly, the agreement between the predicted and actual swelling is adequate. In this case, however, the stem swells more rapidly than predicted. If the diffusivity is constant the outside of the stem reduces at once the amount of water diffusing into the phloem, hence reducing the predicted swelling below the swelling predicted when the diffusivity changes sharply with moisture (solid line, Fig. 2).

The values of A and \bar{D} were obtained independently by fitting the two models to observations for moderate times, *i.e.* 20 to 40 min. A and \bar{D} are not equal, but if the water intakes for very short times are equated, it can be shown that

$$\pi A = 2 \bar{D} \quad (9)$$

Molz *et al.* (12) took a value for \bar{D} of 1.72×10^{-6} cm² sec⁻¹. According to equation 9 this D corresponds to an A of 1.1×10^{-6} cm² sec⁻¹ which is only slightly less than the 1.2×10^{-6} cm² sec⁻¹ obtained by fitting the nonlinear model to the data. This agreement simply indicates that the two solutions which by construction yield the same result for moderate times differ slightly in the very short time limit. This is unimportant because the experimental data for very short times are probably less reliable.

Molz *et al.* (12) attributed the small discrepancy between observed and predicted swelling to growth during the 140 min of measurement. However, when swelling was measured for 1320 min in a subsequent study, growth did not contribute significantly to swelling during the first 240 min (11). Furthermore, since their model utilizes the final stem diameter, $r_{p\infty}$, reduction of this diameter to account for growth would also reduce the predicted values below the dashed curve in Figure 2 and maintain the discrepancy.

The linear diffusion model does reasonably predict swelling, but does not prove that the diffusion coefficient is constant as suggested by Molz *et al.* (12). Indeed the nonlinear model fits the observed swelling equally well, if not better than the linear diffusion model, and suggests that the diffusivity varies markedly with moisture. An analogous situation arises in soils: with a diffusivity measured *a priori* and known to vary rapidly with moisture content, linear diffusion models are often used to predict water intake with reasonable precision (17). However, the water profiles in the material predicted by a linear diffusion model are unrealistic. Clearly, for phloem the real nature of the material's wetting properties will be truly understood only when water profiles within the phloem are measured rather than the swelling alone.

Stem Contractions in Red Pine. The diurnal shrinkage of stems and decrease in water potential of foliage of red pine that had been sprayed with phenylmercuric acetate or left unsprayed are shown in Figure 3. Both changes were decreased by the spray that closed stomata. In both sprayed and unsprayed trees the shrinkage of the stem lagged 2 hr behind the water potential of the foliage in the crown (Fig. 4).

The phloem of the pines was about 0.2 cm thick, much less than the stem diameter of 18 cm hence r_x/r_f is close to 1, and equation 4 reduces to

$$2At \simeq (r_x - r_f)^2 \quad (10)$$

or

$$(r_f - r_x) \simeq (2At)^{1/2} \quad (11)$$

Substituting this expression in equation 8 yields

$$u \simeq (2At)^{1/2} / (r_{p\infty} - r_x) \quad (12)$$

where use has been made of the fact that $(r_{p\infty} - r_x) \simeq (r_{p\infty} - r_x)$ for the red pine phloem. Equation 12 shows that when the phloem thickness is much less than the stem diameter, the

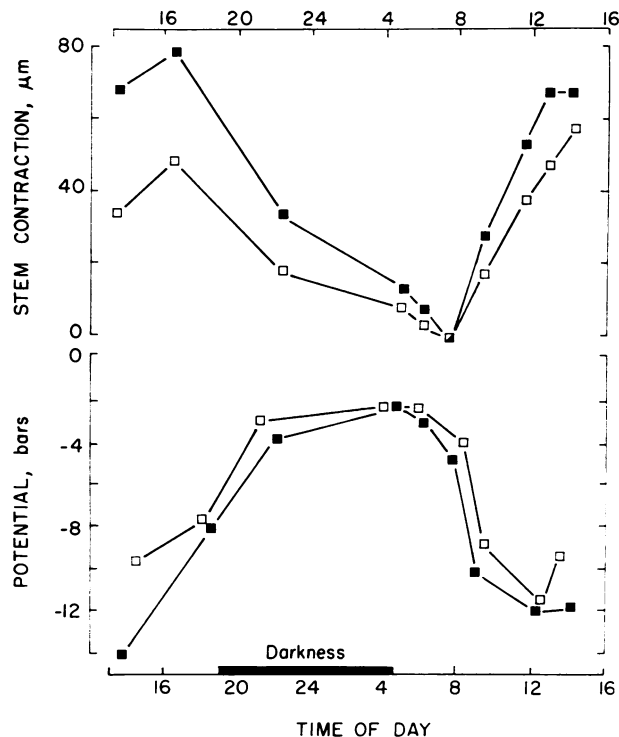


FIG. 3. Diurnal variation in the contraction of the stem and the water potential of foliage in red pines sprayed with a stomatal-closing compound (□) or left unsprayed (■).

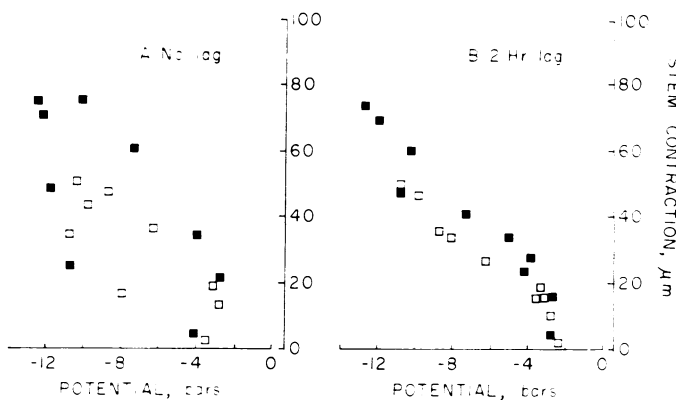


FIG. 4. Relation between the contraction of the stem and the water potential of the foliage of red pines sprayed with a stomatal-closing compound (□) or left unsprayed (■). A: Contraction related to the potential at the same time; B: contraction related to the potential 2 hr earlier.

water uptake by the phloem depends on the thickness of the phloem, but not on the stem diameter.

The driving force for the changes in water content in the phloem of the stem is the water potential in the adjacent xylem. The water potential in the stem xylem varies with the water potential of the foliage (1). Equation 12 indicates that when the water potential suddenly changes in the xylem, the phloem reaches its equilibrium state, *i.e.* $u = 1$, in a finite time, τ , where:

$$\tau \simeq (r_{p\infty} - r_x)^2 / 2A \quad (13)$$

However, under field conditions the potential in the xylem changes continuously rather than suddenly (Fig. 3). During a continuous change in potential, the equilibrium phloem radius,

$r_{p\infty}$, corresponding to a particular xylem potential at a given time is reached after a time lag, T .

According to Equation 12, a small potential change during and proportional to an interval dt of time will, after a longer time t , change the diameter of the phloem in proportion to $t^{1/2} dt$. The eventual change, after a time τ is then proportional to $\tau^{3/2} dt$. Thus, the eventual change in the diameter produced when the xylem potential is changing smoothly and continuously over many dt , as in Figure 3, can be obtained by summing each contribution $\tau^{1/2} dt$ over τ :

$$\int_0^T T^{1/2} dt = T^{3/2} \quad (14)$$

i.e. the diameter changes linearly with time with proportionality factor $\tau^{1/2}$. However, because of the lag in reaching an equilibrium diameter after a change in xylem potential, one of the small continuing changes in potential at time t during τ can change the diameter only for a time less than τ , namely $(\tau - t)$ and the consequence of each change is proportional to $(\tau - t)^{1/2}$ according to equation 12. Again summing each contribution $(\tau - t)^{1/2} dt$ over τ ,

$$\int_0^T (\tau - t)^{1/2} dt = 2/3 T^{3/2} \quad (15)$$

i.e., only $2/3$ of the change caused by continuing changes during τ is observed by the end of τ . Now the lag T is the additional time for the diameter to increase by the remaining $1/3$. Since the diameter changes linearly with time, the lag T is simply $1/3 \tau$.

From equations 13 and 15 it can be seen that T is 5556 sec or 1.54 hr for the red pine with 0.2 cm phloem, if we use the same A as obtained for cotton stems. This estimated lag is slightly less than that observed in Figure 4, but since the average diffusivity of cotton stems varied about a quarter (12), the observed lag is clearly within the range of the predicted lag. The reasonable agreement between the estimated and the measured lag in stem contraction during a change in water potential in the foliage suggests that the A in red pine is about the same as in cotton. If, as this analysis of cotton and pine suggest, diverse stems have similar diffusion characteristics, then the course of drying (equation 12) and hence of shrinkage, the time for reaching an equilibrium diameter (equation 13), and the lag of diameter behind potential are all related to the thickness of the phloem. This postulate, and the consistency with observation of a conception of water moving faster as the phloem moistens, are the chief outcomes of our analysis.

LITERATURE CITED

- BEGG, J. E. AND N. C. TURNER. 1970. Water potential gradients in field tobacco. *Plant Physiol.* 46: 343-346.
- CROWDY, S. H. AND T. W. TANTON. 1970. Water pathways in higher plants. *J. Exp. Bot.* 21: 102-111.
- DAUBENMIRE, R. F. 1945. An improved precision dendrometer. *Ecology* 26: 97-98.
- GAFF, D. F., T. C. CHAMBERS, AND K. MARKUS. 1964. Studies of extra-fascicular movement of water in the leaf. *Aust. J. Biol. Sci.* 17: 581-586.
- HAASIS, F. W. 1934. Diametrical changes in tree trunks. *Carnegie Inst. Wash. Pub.* 450.
- HELLKVIST, J., G. P. RICHARDS, AND P. G. JARVIS. 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. *J. Appl. Ecol.* In press.
- KOZLOWSKI, T. T. 1972. Shrinking and swelling of plant tissues. In: T. T. Kozlowski, ed., *Water Deficits and Plant Growth*, Vol. 3. Academic Press, New York: pp. 1-64.
- MACDOUGAL, D. T. 1921. Growth in trees. *Carnegie Inst. Wash. Pub.* 307.
- MILBURN, J. A. AND P. E. WEATHERLEY. 1971. The influence of temperature on the process of water uptake by detached leaves and leaf discs. *New Phytol.* 70: 929-938.
- MOLZ, F. J. AND B. KLEPPER. 1972. Radial propagation of water potential in stems. *Agron. J.* 64: 469-473.
- MOLZ, F. J. AND B. KLEPPER. 1973. On the mechanism of water stress-induced stem deformation. *Agron. J.* 65: 304-306.
- MOLZ, F. J., B. KLEPPER, AND V. D. BROWNING. 1973. Radial diffusion of free energy in stem phloem: an experimental study. *Agron. J.* 65: 219-222.
- MOLZ, F. J., B. KLEPPER, AND C. M. PETERSON. 1973. Dehydration versus growth-induced water uptake in plant tissues. *Plant Physiol.* 51: 859-862.
- NAMKEN, L. N., J. F. BARTHOLIC, AND J. R. RUNKLES. 1969. Monitoring cotton plant stem radius as an indication of water stress. *Agron. J.* 61: 891-893.
- SCHOLANDER, P. F., H. T. HAMMEL, E. A. HEMMINGSEN, AND E. D. BRADSTREET. 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proc. Nat. Acad. Sci. U.S.A.* 52: 119-125.
- STRUGGER, S. 1938-1939. Die Lumineszenzmikroskopische Analyse des Transpirationsströmes in Parenchymen. *Flora* 33: 56-68.
- TALSMA, T. AND J.-Y. PARLANGE. 1972. One dimensional vertical infiltration. *Aust. J. Soil Res.* 10: 143-150.
- TALSMA, T., J.-Y. PARLANGE, AND P. H. GROENEVELT. 1972. Soil moisture distribution during two-dimensional absorption from a cylindrical source. *Aust. J. Soil Res.* 10: 209-214.
- TANTON, T. W. AND S. H. CROWDY. 1972. Water pathways in higher plants. II. Water pathways in roots. *J. Exp. Bot.* 23: 600-618.
- TANTON, T. W. AND S. H. CROWDY. 1972. Water pathways in higher plants. III. The transpiration stream within leaves. *J. Exp. Bot.* 23: 619-625.
- TURNER, N. C. AND P. E. WAGGONER. 1968. Effects of changing stomatal width in a red pine forest on soil water content, leaf water potential, bole diameter, and growth. *Plant Physiol.* 43: 973-978.
- WAGGONER, P. E. AND N. C. TURNER. 1971. Transpiration and its control by stomata in a pine forest. *Conn. Agr. Exp. Sta. Bull.* 726.
- WEATHERLEY, P. E. 1963. The pathway of water movement across the root cortex and leaf mesophyll of transpiring plants. In: A. J. Rutter and F. H. Whitehead, eds., *The Water Relations of Plants*. Blackwell, London, pp. 85-100.
- WORRALL, J. 1966. A method of correcting dendrometer measures of tree diameter for variation induced by moisture stress changes. *Forest Sci.* 12: 427-429.