Plant Physiol. (1976) 57, 153-156

Water Uptake and Water Diffusivity of Seeds[1]

Received for publication May 5, 1975 and in revised form July 25, 1975

PAUL E. WAGGONER AND JEAN-YVES PARLANGE
The Connecticut Agricultural Experiment Station, New Haven, Connecticut 06504

ABSTRACT

When pea (Pisum sativum) seeds were wetted, a sharp front separated the wet and dry portions, the seeds swelled, and the water content in the wetted portion continued to increase for a long time. A model was proposed and tested that takes into account these three characteristics and in particular does not postulate a constant diffusivity. The parameters of the model are simply the rate of penetration of the wetting front and a swelling factor.

Recently the early water uptake and swelling of phloem has been examined. The uptake was interpreted in terms of both a constant diffusivity (5) and of a diffusivity that varied rapidly with water content (7). Although the variable diffusivity fitted the observations somewhat better, the total water uptake by the entire structure is insensitive to the effect of water content upon diffusivity, and the nature of diffusion in plant tissue can be solved only by observing the water profile in the tissue. The water content and profile vary smoothly when diffusivity is constant and abruptly when diffusivity increases rapidly with moisture. Because phloem or leaves are so thin that the water profile cannot be observed easily in them, we decided to observe water uptake and the profile of wetting in large seeds.

As in any other living tissue, water uptake in dry seed is first controlled by permeation and then by growth (1). Since permeation and growth in seed occur on different time scales, they are easily separated. In addition, dead seeds, *e.g.*, split peas (11), or swelling in water too cold for growth (4) can be observed.

The equation so far used (8, 10) to model uptake by spherical seed was derived from three assumptions: (*a*) constant diffusivity, (*b*) no swelling, (*c*) constant water content near the surface after the first wetting. These are not borne out by observations; thus, a variable diffusivity was required to fit observations (8, 10). The seeds swelled to about double their size (8, 10, 11), and such swelling requires a different definition of coordinates (9). Finally, the swelling makes more room for water, the flux through the surface scarcely changes for a long time (11), and the water content near the surface increases for a long time (6).

Our task is to observe the water profile in seed to show the inconstancy of the diffusivity and then to propose a model that does not require a constant diffusivity but does take into account swelling and the continuing change of water content as the surface expands.

THEORY

Fundamentally, our theory depends upon two things. First, see Figure 1, a location in the spherical seed is identified by its original distance $r(o)$ from the center and by a swelling factor λ:

$$\lambda = \delta r(t)/\delta r(o) \tag{1}$$

where $\delta r(o)$ and $\delta r(t)$ are the distances between nearby locations before and after wetting for time t. In general, λ varies with water content and temperature. Second, we visualize water moving into the seed behind a wetting front and replace the concept of a diffusion coefficient by the position $r_f(t)$ of the wetting front.

The water content θ at an original location of $r(o)$ is the volume of water per dry volume, and the volume of the wet seed relative to the dry is $1 + \theta$. The initial volume $4\,\Pi r(o)^2\,\delta r(o)$ of the dry shell of thickness $\delta r(o)$ swells to $4\,\Pi r^2(t)\,\delta r(t)$ after permeation of water for time t. The volume of wet relative to the dry shell is

$$1 + \theta = r^2(t)\delta r(t)/r^2(o)\delta r(o) = \lambda \left[r_f(t) + \int_{r_f(t)}^{r(o)} \lambda\, dr \right]^2 \Big/ r^2(o) \tag{2}$$

That is, $\delta r(t)/\delta r(o)$ is replaced by λ, and $r(t)$ is replaced by the dry length $r_f(t)$ plus the wet, swollen length. Note that the outward swelling λ is more than the circumferential stretching

$$\left[r_f(t) + \int_{r_f(t)}^{r(o)} \lambda\, dr \right] \Big/ r(o).$$

This is because the outward swelling is not constrained, while the circumferential stretching is constrained. We can say that the swelling is anisotropic.

Note that just behind the front, where the water content is θ_f, the location $r_f(t)$ is approximately $r(o)$, and the thickness of the wet, swollen layer is approximately zero, making

$$1 + \theta_f = \lambda(\theta_f) \tag{3}$$

Equation 2 defines θ at location $r(o)$ in terms of r_f and λ, which must now be estimated. The location r_f of the wetting front can be observed, but we must obtain λ in observable terms.

In practice, when the swelling factor λ is a slowly varying function of water content θ, then the average λ for the two extremes of θ_f at the wetting front and θ_s at the outer surface will be approximately the relative change in thickness of the wet layer:

$$\frac{r_s(t) - r_f(t)}{r_s(o) - r_f(t)} \simeq \frac{\lambda(\theta_f) + \lambda(\theta_s)}{2} \tag{4}$$

Since $\lambda(\theta_s)$ is nearly $\lambda(\theta_f)$ at short times, $\lambda(\theta_f)$ is calculated from equation 4 alone at short times. At any time, equation 4 then gives $\lambda(\theta_s)$, when the radius r_s of the seed and the location r_f of the wetting front are observed. The corresponding value of θ_s is then obtained by applying equation 2 at the surface. Since the stretched radius in brackets is $r_s(t)$, equation 2 becomes:

$$1 + \theta_s = \lambda(\theta_s) r_s^2(t)/r_s^2(o) \tag{5}$$

which yields θ_s.

A simple situation occurs when λ is approximately constant. Since λ certainly does not decrease with θ, the constancy of λ

[1] This investigation of water movement into seeds is dedicated to Leon Bernstein whose investigations, scholarship, and editing have advanced knowledge of how plants get water and exchange salt.

can be established by checking that λ (i) after the first or initial wetting is approximately equal to $\lambda(\infty)$ after a long time or equivalently that $\lambda(i)$ equals

$$[\lambda(i) + \lambda(\infty)]/2.$$

After a very long time, the left hand side of equation 4 becomes $r_s(\infty)/r_s(o)$, and the right hand side becomes

$$[\lambda(i) + \lambda(\infty)]/2.$$

Hence we check constancy of λ by checking whether

$$r_s(\infty)/r_s(o) \simeq \lambda(i) \quad (6)$$

In this simple case of constant λ, equation 4 becomes

$$r_f(t) \simeq [\lambda r_s(o) - r_s(t)]/(\lambda - 1) \quad (7)$$

and equation 5 yields

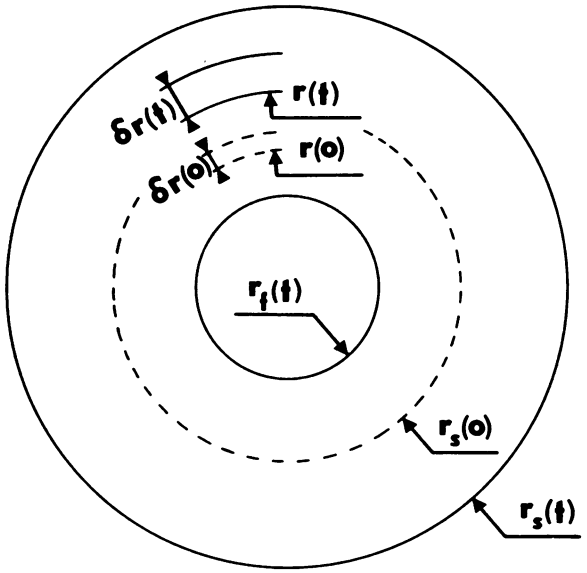

FIG. 1. Schematic diagram of a swelling pea. The outer radius of the pea swells from $r_s(o)$ to $r_s(t)$ during a time t, while the wetting front penetrates from $r_s(o)$ to $r_f(t)$. A location $r(o)$ in the dry pea moves to $r(t)$ on wetting, while an element $\delta r(o)$ stretches into $\delta r(t)$. The stretching factor is $\delta r(t)/\delta r(o)$.

$$1 + \theta \simeq \lambda[\lambda r(o) - (\lambda - 1)r_f(t)]^2/r(o)^2 \quad (8)$$

Equation 7 gives the location of the wetting front $r_f(t)$ when the swollen radius $r_s(t)$ is measured, and equation 8 specifies the water profile by giving θ as a function of $r(o)$.

Thus the purpose of the experiments is to test equation 6 to see whether λ is constant. Then use equations 7 and 8. If equation 6 does not hold, use the more complex equations 4 and 5 to obtain $\lambda(\theta)$ and obtain the profile with equation 2.

MATERIALS AND METHODS

Pea seeds (*Pisum sativum*) were chosen because of their sphericity. The average weight of a seed was 0.15 g, the density of oven-dried peas was 1.3, and they contained 13% water when air-dried.

The seeds were wet in a bath of distilled H_2O. The H_2O was at room temperature, 20 C ± 2 C, or maintained at 0 C by ice. At 0 C the effect of growth on H_2O uptake is minimal (4). At intervals, *e.g.*, every 15 min, the seeds were removed from the H_2O, dried with tissue paper, and weighed. The drying and weighing took less than 30 sec for a batch of 20 seeds. The seed coats were removed to decrease variability because they were usually cracked, and when the coats are wet, they tend to fall apart.

Some peas were killed by placing them overnight in an oven at 100 C. Although the peas tended to split in two toward the end of the experiment, increasing the area of contact with H_2O, the oven-dried peas tended to preserve their spherical shape. Water uptake in peas split before the experiments was also observed.

Besides H_2O uptake, the position of the wetting front was observed by two methods. The first method was cutting the pea in two, marking the wetted part with LiCl and photographing it (Fig. 2). The other method was to scrape the wet layer off with a blade, and to weigh it and the dry core both before and after drying in the oven.

RESULTS AND DISCUSSION

Figure 2 shows a wetting front as H_2O permeates a pea. The H_2O content varies abruptly at the wetting front rather than smoothly. This is the observation that could not be made in a thin phloem (7) and confirms that using a constant diffusivity in

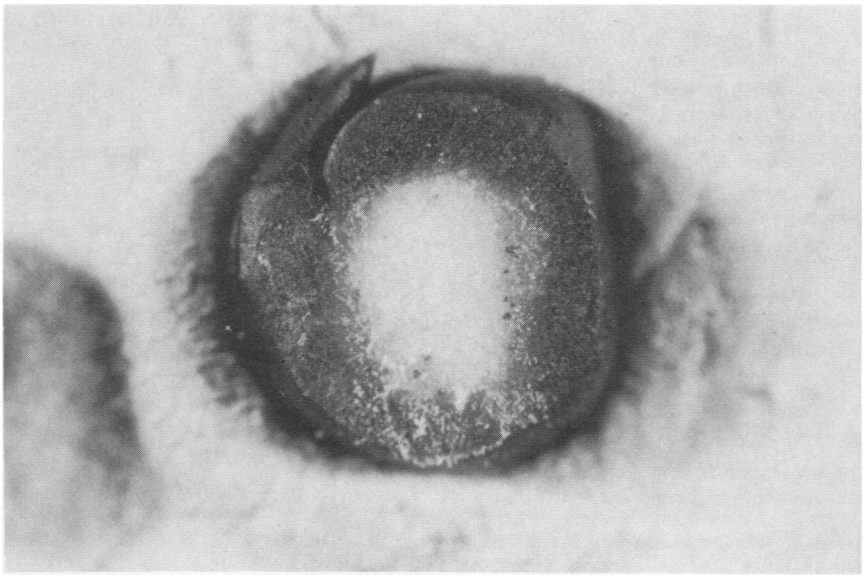

FIG. 2. Wetting front in a pea shown by LiCl strain.

a model is inappropriate, at least for peas and hence possibly for other plant tissues as well, such as phloem.

Figure 3 shows the course of water uptake by six batches of 20 peas. The curves have been normalized to represent the H_2O uptake per initial volume of seeds, *i.e.* $[r_s^3(t)r_s^{-3}(o) - 1]$.

The uptake of H_2O by the live peas essentially stopped after 300 min, but when they were left overnight they increased slowly in weight, showing some growth. The live peas tended to split visibly during the early stages of H_2O uptake. By comparison the H_2O uptake after a day by oven-dried peas was slightly less than by the live ones. Except for growth, the dead, oven-dried, split peas and live peas absorbed H_2O similarly.

On the other hand, the oven-dried, but unsplit peas took up H_2O more slowly. The ratio of the uptake rates by split and unsplit peas was about 1.55 and is essentially equal to the 1.5 ratio of the areas in contact with free H_2O.

The asymptotic H_2O uptakes at freezing and room temperature are about the same, suggesting that $\lambda(\theta_s)$ is not greatly influenced by temperature. On the other hand the rate of H_2O uptake is much slower at cooler temperatures, and at 0 C the rate is about a third the rate at 20 C. Thus $r_s(t)$ is greatly influenced by temperature.

In all cases, the intake curves are made of three components, a rapid initial intake, a long and nearly linear "main curve" and finally a slow increase before saturation. The initial transient phenomenon lasts about 30 min, which is of the order of the characteristic time for permeation of a single cell 100 μm in length, calculated from a conductivity through the cell membrane 5×10^{-7} cm/sec·bar (3) and a potential difference of 10 bars. The final portion may or may not include some growth, depending on whether the peas are alive. Different regimes of H_2O intake, *i.e.*, a transient behavior at first, followed by a more steady permeation later, are not unusual for porous media (2). This description agrees with Shull's observation (11), with our "main curves" being even more remarkably linear than Shull's. Note that "the effect of the initial rapid intake is to throw the main part of the curve upward from base line" (11). It is also interesting that all the main curves extrapolate to the same point at zero time.

Figure 4 shows a continuing increase in the average H_2O content of the wetted layer of the peas as a function of time in four experiments. Weighing the "dry" cores showed that they were slightly wet, but their H_2O content was rather less than the variability in the data in Figure 4 and the H_2O in the dry core was ignored. In addition, the removal of the wet layer was imperfect, and parts of it may have been left around the core, explaining some of the variability in Figure 4. This suggests that the measured content in the wet layer may be too large, since the parts left around the core would be the driest parts of the wetted layer.

Clearly the diffusivity is not constant since there is an abrupt change in H_2O content at the wetting front, and equations 4 and

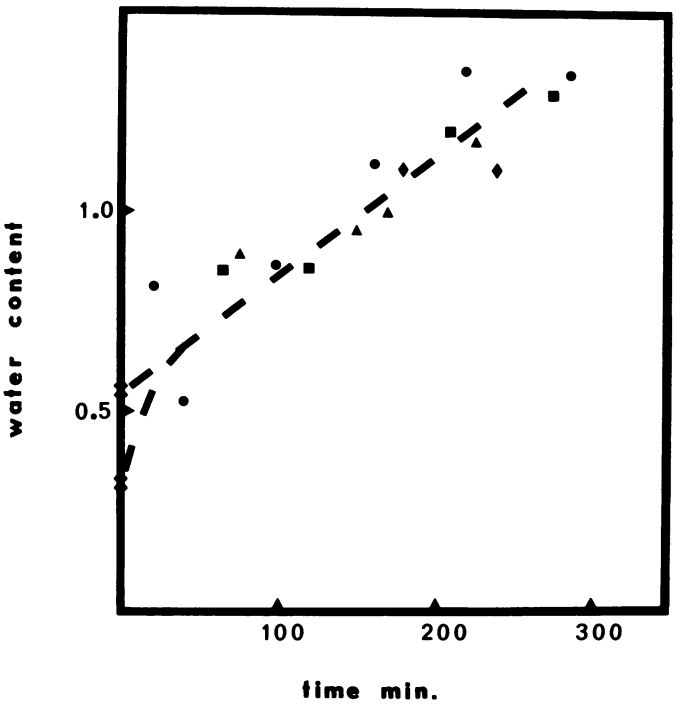

FIG. 3. Water uptake relative to the volume of the dry pea. Two batches of 20 live peas each (○); two batches of 20 dead, split peas (▲); one batch of 20 dead, whole peas (●). The foregoing were wet at room temperature. One batch of 20 dead, whole peas wet at 0 C (■).

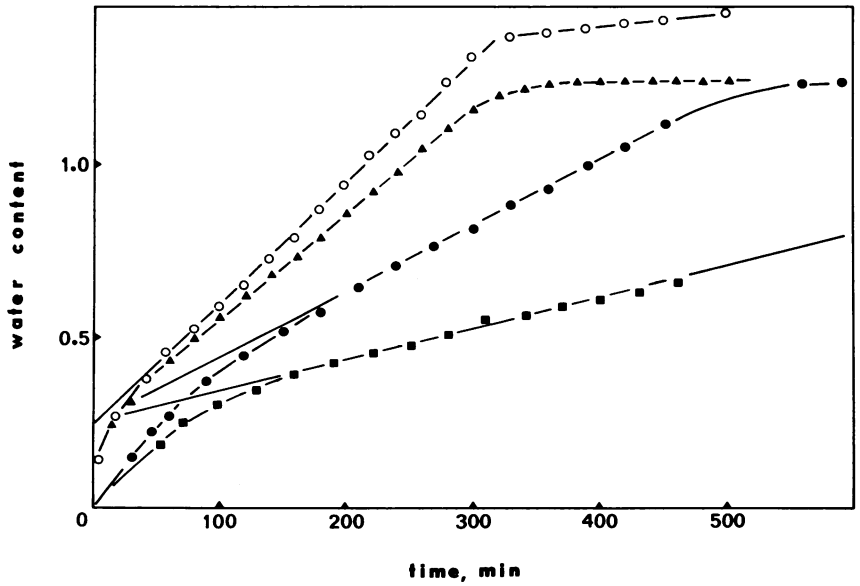

FIG. 4. Change in average H_2O content θ in the wet layers of four batches of 10 peas each. The H_2O content is the content per dry volume of the wet layer.

5 are to be used. Equations 4 and 5 require measurements of $r_s(t)$ and $r_f(t)$ to deduce $\lambda(\theta)$ and thus calculate wetting profiles by equation 2. The $r_s(t)$ can be obtained from Figure 3, and $r_f(t)$ can be obtained from Figures 3 and 4 together. If, however, λ happens to be constant, then its constant value plus $r_s(t)$ taken from Figure 3 defines the wetting profile by equation 7. To check whether λ is constant we must return to equation 6, measure its left and right hand sides, and verify that they are equal. The left hand side is estimated from Figure 3 as the cube root of the asymptotic H_2O contents plus 1, *i.e.*, $1 + \theta$, of the dead peas. The $r_s(\infty)/r_s(o)$ was $(1.22 + 1)^{1/3}$ or 1.3. The right hand side or $\lambda(i)$ is obtained from equation 5 when t approaches zero. By extrapolating the "main curve" of Figure 3, we find $r_s^2(t)/r_s^2(o)$ approaches $(0.26 + 1)^{2/3}$ or 1.17. The θ_s after initial wetting is required for equation 5, and is estimated to be 0.51 in Figure 4. Hence, equation 5 gives a $\lambda(i)$ of 1.51/1.17 or 1.3. Thus both the left and right hand sides of equation 6 equal about 1.3, proving that in these seeds λ is constant.

Thus, equation 7 describes the profile. In a simple example, the wetting front in the dead, spherical (*i.e.*, whole) peas will be 20% of the way to the center after 30 min and 90% of the way after 400 min.

In these particular seeds the equations were simplified by the observation that λ was constant. There is no reason why λ should be constant and no reason why the main portion of the H_2O uptake curve should be straight. Nevertheless, in all cases where there is a sharp wetting front and the material swells, equation 2 can be used. Further, the continuing increase in H_2O content of the wet shell, as shown in Figure 4, will always occur.

LITERATURE CITED

1. Blacklow, W. M. 1972. Mathematical description of the influence of temperature and seed quality on inhibition by seeds of corn. Crop Sci. 12: 643–646.
2. Jackson, R. D. and A. Klute. 1967. Estimation of dead-end pore volume in soils from transient steady state diffusion coefficients. Soil Sci. Soc. Am. Proc. 31: 122–123.
3. Kramer, P. J. 1969. Plant and Soil Water Relationships. McGraw Hill Book Co., New York. p. 37.
4. 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.
5. 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.
6. Parlange, J.-Y. 1972. One-dimensional infiltration with constant flux at the surface. Soil Sci. 114: 1–4.
7. Parlange, J.-Y., N. C. Turner, and P. E. Waggoner. 1975. Water uptake, diameter change, and nonlinear diffusion in tree stems. Plant Physiol. 55: 247–250.
8. Phillips, R. E. 1968. Water diffusivity of germinating soybean, corn and cotton seed. Agron. J. 60: 568–571.
9. Raats, P. A. C. and A. Klute. 1968. Transport in soils. The balance of mass. Soil Sci. Soc. Am. Proc. 32: 161–166.
10. Shaykevich, C. F. and J. Williams. 1971. Resistance to water absorption in germinating rapeseed. J. Exp. Bot. 22: 19–24.
11. Shull, C. A. 1920. Temperature and rate of moisture intake in seeds. Bot. Gaz. 69: 361–390.