

MODEL OF MOISTURE UPTAKE BY WHEAT SEEDS GERMINATING IN FREE WATER

M. Josiah, J. Favier, I. Yule

Department of Agricultural and Environmental Science, University of Newcastle upon Tyne, NE1 7RU, United Kingdom

A b s t r a c t. Viable, non-dormant seeds will germinate in the presence of sufficient oxygen once a certain level of hydration is reached. The rate of uptake of moisture is critical in determining the period between the start of hydration and the initiation of germination. The increase in moisture content of wheat seed set to germinate on filter paper with excess water was measured, at intervals during incubation at temperatures ranging from 12 °C to 30 °C, for seeds of 25 to 50 % initial moisture content (dry basis), until all seeds had germinated. The rate of uptake of moisture is described using a liquid diffusion model where the maximum moisture content attained at germination replaces the equilibrium or saturation moisture content used in similar absorption models. The maximum moisture content attained at germination is defined as the average of the mean seed moisture content immediately before germination (i.e. no seeds germinated) and the mean moisture content after the majority of seeds (>90 %) have germinated, where germination is defined as appearance of at least 1 mm of radicle. The model predicts the observed seed moisture content equally well for seeds from low to high initial moisture content. The diffusion coefficient was best described by an Arrhenius temperature function and was found to be almost twice as high as the values found in previous studies of water absorption by non-germinating seeds.

K e y w o r d s: moisture uptake, germination, wheat seed

INTRODUCTION

Seeds need to attain a certain level of hydration in order to germinate. As well as an adequate amount of water, they require suitable conditions of temperature, aeration, and light before germination will occur. These conditions are interrelated and depend on seed species, age and some-

times genotype [17]. At harvest, and in storage, the moisture content (dry basis) of wheat seed is generally less than 25 %. At this moisture content the seed is not capable of germinating. Given that a minimum level of hydration is required before germination is initiated, then, assuming other environmental conditions are conducive, the rate of uptake of water by a dry seed will determine the time period between the start of hydration and the start of germination.

The rate and extent of water uptake depends on the permeability of the seed coat to moisture, the moisture absorbing capacity of the seed embryo and endosperm and the availability of moisture either in liquid or gaseous form. Early studies of water uptake by germinating seeds used empirical models [3,22], while later studies usually used diffusion models [5,20,21] to describe the imbibition phase. In most of the above studies seeds were germinated either on the surface of water saturated medium such as filter paper or in aerated water ensuring a free supply of water and oxygen. When seeds are germinated in soil or soil surrogate other factors such as soil water potential and soil/seed surface contact influence the rate of seed moisture uptake [6,9,12].

Diffusion models have also been used to describe water absorption by non-germinating seed, including wheat [1,4,11,15], rice [10] and soybean [14]. These studies involved soaking the seeds until saturation

moisture content was reached. It has been shown that low oxygen tension inhibits germination of wheat seed [25]. Given a difference of six in order of magnitude between the diffusivity of oxygen in air ($\sim 0.2 \text{ cm}^2/\text{s}$) and water ($\sim 2 \cdot 10^{-6} \text{ cm}^2/\text{s}$) [8] it is probable that germination did not occur in the soaking experiments on wheat seeds due to insufficient oxygen reaching the embryo [13].

Most models of liquid diffusion in seeds assume a constant coefficient of diffusion (seed diffusivity) throughout the absorption period. This hypothesis would appear to be adequate for starchy seeds such as wheat, maize and rice [1,10,11,20] but a variable diffusivity has been observed in oily seeds such as rapeseed [21] and soybean [14,20]. Most diffusion models also describe increase in water content relative to initial and saturation moisture content. When seeds germinate during hydration the definition of saturation moisture content must be replaced with the maximum moisture content at germination [20] since the rate of water uptake will increase after germination due to water uptake through the seed radicle.

The purpose of this investigation was to develop a model that will describe the dynamics of moisture uptake by germinating wheat seeds. An analogy is made with an exponential model of seed drying and the concept of a wetting constant is introduced.

MODEL DEVELOPMENT

The seed is assumed to be a porous, solid, isotropic material, spherical in shape with uniform moisture content at the start of hydration. It is also assumed that the resistance to water transfer from the medium outside the seed is negligible and diffusion is radial into seed. The theoretical model based on Fick's law of diffusion described in spherical coordinates is:

$$\frac{\partial m}{\partial t} = \frac{\partial^2 m}{\partial r^2} + \frac{2}{r} \frac{\partial m}{\partial r} \quad (1)$$

where m is the mass of water absorbed at time, t , and r is the direction of diffusion. Applying the method of solution of Crank [7] and assuming a constant diffusion coefficient, the fraction of total absorbable water absorbed by the seed after time, t , is given by:

$$\frac{m}{m_\infty} = 1 - \frac{6}{\pi^2} \sum_{n=1}^{\infty} \frac{1}{n^2} e^{(-Dn^2\pi^2 t/a^2)} \quad (2)$$

where m is the mass of water absorbed at saturation, D is the diffusion coefficient or seed diffusivity, and a is the seed radius.

Differentiating Eq. (2) with respect to time gives:

$$\frac{dm}{dt} = \frac{m_\infty 6D}{a^2} \sum_{n=1}^{\infty} e^{(-Dn^2\pi^2 t/a^2)} \quad (3)$$

which converges for high values of t .

Considering only the first term of Eq. (3):

$$\frac{dm}{dt} = \frac{m_\infty 6D}{a^2} e^{(-D\pi^2 t/a^2)} \quad (4)$$

Shaykewich and Williams [21] eliminated m by finding the ratio of the rates of seed water uptake at different times. Thus,

$$\frac{dm_{t_1}/dt}{dm_{t_2}/dt} = \frac{a_2^2 e^{(-D\pi^2 t_1/a_1^2)}}{a_1^2 e^{(-D\pi^2 t_2/a_2^2)}} \quad (5)$$

where a_1 and a_2 are the radius of the seed at time t_1 and t_2 , respectively.

If the rate of water uptake at any time during hydration is assumed to depend on the potential for water absorption [19,23] then change in seed moisture content with time can be said to be proportional to the difference between the seed moisture content, M , at any time before germination and the maximum moisture content obtained prior to the emergence of the radicle, M_g , expressed mathematically:

$$\frac{dM}{dt} = -A(M - M_g) \quad (6)$$

where A is a rate constant. Since the rate at which the seed mass will increase with time depends on the rate of water uptake, from Eq. (4):

$$\frac{dm}{dt} = -A(M - M_g) \quad (7)$$

and at the start of hydration,

$$\frac{dm_o}{dt} = -A(M_o - M_g) \quad (8)$$

Substituting Eqs (7) and (8) into Eq. (5) gives:

$$\frac{M - M_g}{M_o - M_g} = \frac{a_o^2}{a^2} e^{(-D\pi^2 t/a^2)} \quad (9)$$

It can be calculated from the data of Chung *et al.* [4] that, at the extremities of the range of experimental conditions reported here, i.e., lowest initial seed moisture content and highest germination temperature, the maximum probable increase in seed radius is approximately 10%. Treating this increase in radius as negligible allows Eq. (9) to be written in the form:

$$\frac{M - M_g}{M_o - M_g} = Ce^{-kt} \quad (10)$$

where $k = D^2/a^2$ (h^{-1}) and C is a constant. Eq. (10) is analogous to the commonly used exponential drying equation with the L.H.S. equivalent to the moisture ratio and k now being called the 'wetting' constant. The rate of moisture uptake after differentiation of Eq. (10) is given by:

$$\frac{dM}{dt} = -kC(M - M_g) \quad (11)$$

where kC is equivalent to the rate constant A from Eq. (6). The constant C is in effect an error constant resulting from variability in time to germination among seeds. Dif-

ferences in time to germination from time of wetting of seeds from the same population may be due to differences in the structure of the endosperm starch/protein matrix [24] and variation in the time of synthesis of rate-limiting enzymes [2].

Linearizing Eq. (10) gives:

$$\ln(M_R) = \ln C - kt \quad (12)$$

where

$$M_R = \frac{M - M_g}{M_o - M_g}$$

is termed the seed moisture ratio.

MATERIALS AND METHODS

Wheat seed (v. Riband) was used for the experiment. The seed lot was dried to 10% dry basis (db) in a layer 20 mm deep with air at 40 °C, 10% r.h. using a drying rig designed for drying particulate crops [26]. The germinative capacity of the seed was determined following the method recommended by the I.S.T.A. [16] viz. eight replicates of 50 seeds were germinated on a double layer of moistened filter paper (Whatman No. 9) in the dark at 20 °C and the number of germinated seeds counted after seven days. The criteria used for a germinated seed was appearance of at least 1 mm of radicle. The germinative capacity of the seed lot was 98%.

Samples of different initial moisture contents (25, 30, 35, 40, 45, 50% db) were obtained by adding the required amount of water and equilibrating in a tumbler for 48 h. Samples were taken after equilibration and the moisture content determined by the oven method. Four hundred seeds of each moisture content were weighed and placed on a double layer of filter paper (Whatman No. 9) in Petri dishes at a density of 50 seeds/dish. The Petri dishes were then filled with sufficient water to cover the filter paper (6 ml per dish) and placed on a corrugated platform above 20 mm of water at the bottom

of a covered plastic container. The container was then placed in an incubator controlled to $\pm 0.5^\circ\text{C}$. Experiments were carried out at incubation temperatures of 12, 15, 18, 21, 24, 27 and 30°C .

At intervals after the container was placed in the incubator, the moisture content of the seeds was determined by removing the seeds from the Petri dishes, quickly blotting on a cotton towel to remove excess water, and weighing. Immediately after weighing the seeds were replaced on the wet filter paper in the Petri dishes and returned to the incubator. The process was continued for each dish of seeds until 90% or more of the seeds had germinated. In order to estimate the maximum moisture content attained before germination it was assumed that this moisture content was attained at a time halfway between no germination and 90% or greater germination being observed. Thus the maximum moisture content before germination was calculated as the average of the moisture content just prior to any germination being observed and the moisture content after 90% or more germination was observed.

RESULTS AND DISCUSSION

A typical seed water uptake curve is shown in Fig. 1. It can be seen that after an initial phase of rapid hydration the rate slows

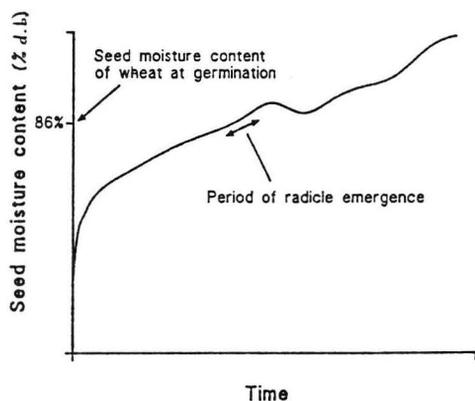


Fig. 1. Typical water uptake curve for germinating wheat seed.

until just after all seeds have germinated. In the initial stages of radicle emergence the seed takes up no moisture and then, as the coleoptile emerges and the roots extend, more moisture is taken up. In all samples, 90% or greater germination was achieved during a 12 h period following the last observation of little or no germination. The mean maximum moisture content attained before germination, M_g , calculated from thirty-six samples was 86% db (s.e. = 2.6%). The water uptake curve for seeds of varying initial moisture contents germinated at 12°C and 30°C are shown in Figs 2a and 2b, respectively. The time from wetting to germination at 12°C is approximately double that at 30°C .

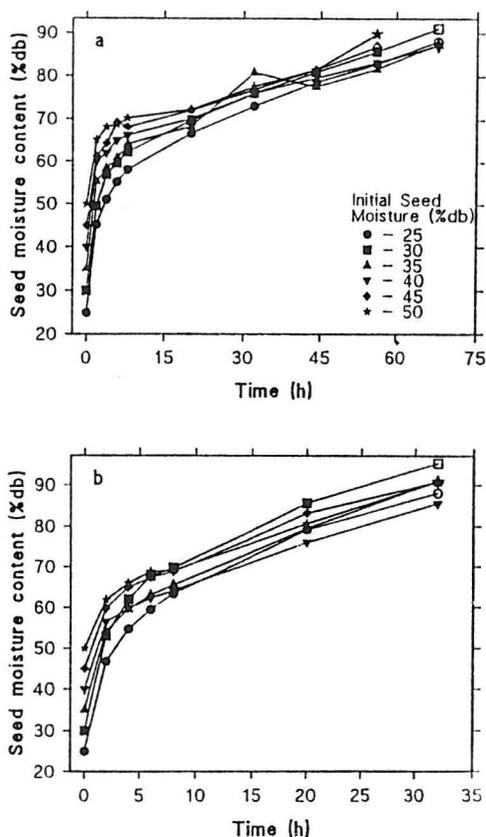


Fig. 2. Water uptake curves for wheat seed of different initial moisture content germinated at two temperatures: 12°C (a) and 30°C (b). Open symbols indicate 90% seeds germinated.

The wetting constant, k , can be determined for each initial seed moisture content/germination temperature combination by plotting moisture ratio on a logarithmic scale against hydration time. Fig. 3 shows the plot of moisture ratio against hydration time for the water uptake curves at 12°C. It can be seen that the initial moisture content of the seed has no significant effect on the relative rate of water uptake. The independence of wetting constant from initial moisture content was found at each germination temperature (Table 1). This validates the analytical technique of expressing relative water uptake in the form of a mois-

ture ratio based on maximum moisture content before germination.

The mean value of the wetting constant at each germination temperature, k_{mean} , is shown plotted against the reciprocal of absolute temperature in Fig. 4. The good fit of a linear regression on a log scale of k_{mean} values against the reciprocal of absolute temperature ($r=0.9526$) indicates that the wetting constant is an Arrhenius function of temperature. The equation for the wetting constant is:

$$k_{\text{mean}} = 288660 \exp\left(\frac{-4257}{T}\right) \text{ (h}^{-1}\text{)} \quad (14)$$

Given that the wetting constant is a function of seed diffusivity and radius then,

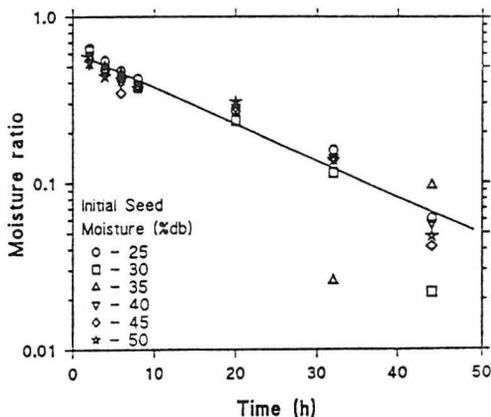


Fig. 3. Change in moisture ratio with time for seeds germinated at 12°C.

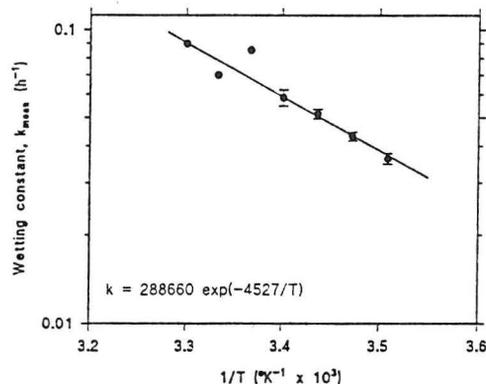


Fig. 4. Mean wetting constant (k_{mean}) for the group of water uptake curves at each hydration temperature.

Table 1. Wetting constant ($k \cdot 10^2$) for each initial seed moisture content and hydration temperature with mean wetting constant (k_{mean}) for each temperature

Initial moisture content (% d.b.)	Hydration temperature (°C)						
	12	15	18	21	24	27	30
25	4.30	5.97	4.09	8.49	9.98	7.08	9.64
30	7.00	6.18	4.87	5.69	8.23	9.14	26.40
35	3.60	4.65	5.85	8.94	11.60	-	8.93
40	3.75	6.43	6.38	4.77	9.74	7.11	13.29
45	3.56	3.90	2.82	11.12	7.06	6.36	12.81
50	3.29	5.14	6.04	10.34	10.81	7.54	8.44
k_{mean}	3.62	4.32	5.15	5.85	8.53	6.99	8.98
s.e.	0.15	0.15	0.19	0.37	0.17	0.07	0.20

taking the mean seed radius to be 0.2 cm [4,18], from Eq. (14):

$$D = 0.325 \exp\left(\frac{-9000}{RT}\right) (\text{cm}^2/\text{s}) \quad (15)$$

where R (cal/mol K) is the gas constant.

From Eq. (15), at 12 °C the value of D is $4.1 \cdot 10^{-8} \text{ cm}^2/\text{s}$ and at 30 °C, D is $10.5 \cdot 10^{-8} \text{ cm}^2/\text{s}$. These diffusivity values are of the same order of magnitude but are approximately twice those obtained in previous experiments with non-germinating wheat seed [1,4,11]. The activation energy of 9 kcal/mol is lower than the values (11.0 -12.3 kcal/mol) found in those studies. Factors such as the significant effect of seed protein content and associated hardness (a soft wheat variety was used in these experiments) may account for some of the difference [24]. Results from experiments with non-germinating wheat show no significant difference between the diffusivity of hard and soft wheats [1,11,4]. It is therefore possible that this difference may be due to changes in the diffusivity of the sub-aleurone layer and the endosperm around the embryo of a germinating seed.

CONCLUSIONS

The results of these experiments suggest that previous models of water uptake in non-germinating wheat seed are not adequate to describe water uptake by germinating seeds. It is shown to be a valid technique [20] to replace the equilibrium or saturation moisture content parameter used in diffusion models of water uptake by non-germinating seeds by the maximum moisture content obtained before germination. The value of this parameter was found to be 86 % db (s.e. 2.6%, $n=36$) for the variety Riband, a soft wheat. The value of the diffusion coefficient was double, while the activation energy was lower than, that determined previously for non-germinating wheat seed. If enzymatic activity is altering the structural integrity of the seed kernel prior to emergence of the radicle, then the diffusivity value calculated in the model presented

here may in fact be simply an average value. However, the model predicted the actual water uptake curves quite well and, if the diffusivity were a function of moisture content, then this should be reflected in the fit of the model [14].

While the quantitative model presented here is adequate to describe changes in whole seed moisture content it is not able to link the change in seed mass with mass transfer processes within the seed. These results indicate that a study of seed microstructural changes during germination in conjunction with gravimetric and other measurements will be necessary to better explain the underlying mass transfer mechanisms.

REFERENCES

1. **Becker H.A.**: On the absorption of liquid water by the wheat kernel. *Cereal Chem.*, 37, 309-323, 1960
2. **Bewley J.D., Black M.**: *Physiology and Biochemistry of Seeds in Relation to Germination*. vol. I, Springer-Verlag, Berlin, 1978.
3. **Brown A.J., Worley F.P.**: The influence of temperature on the absorption of water by seeds of *Hordeum vulgare* in relation to the temperature coefficient of chemical change. *Proc. Royal Soc., London*, B85, 546-533, 1912.
4. **Chung D.S., Fan L., Shellenberger J.A.**: Volume increase of wheat kernels accompanying absorption of liquid water. *J. Biochem Microbiol. Technol. Eng.*, 3, 377-393, 1961.
5. **Collis-George N., Melville M.D.**: Water absorption by swelling seeds. I. Constant boundary conditions. *Aust. J. Soil. Res.*, 13, 41-158, 1975.
6. **Collis-George N., Sands J.E.**: Comparison of the effect of the physical and chemical components of soil water energy on seed germination. *Aust. J. Agric. Res.*, 10, 628-636, 1962.
7. **Crank J.**: *The Mathematics of Diffusion*. Oxford University Press, Oxford, 1975.
8. **CRC Handbook of Chemistry and Physics**. CRC Press, Florida, 1978.
9. **Dasberg S.**: Soil water movement to germinating seeds. *J. Exp. Bot.*, 22, 999-1008, 1971.
10. **Engels C., Hendrickx M., De Samblanx S., De Gryze I., Tobback P.**: Modelling water diffusion during long-grain rice soaking. *J. Food Eng.*, 5, 55-73, 1986.
11. **Fan L., Chung D.S., Shellenberger J.A.**: Diffusion coefficients of water in wheat kernels. *Cereal Chem.*, 38, 540-548, 1961.

12. **Hadas A.**: Factors affecting seed germination under soil moisture stress. *Israel J. Agric. Res.*, 20, 3-14, 1970.
13. **Heydecker W., Orphanos P.I.**: The effect of excess moisture on the germination of *Spinacia oleracea* L. *Planta* (Berlin), 83, 237-247, 1968.
14. **Hsu K.H., Kim C.J., Wilson L.A.**: Factors affecting water uptake of soybeans during soaking. *Cereal Chem.*, 60, 208-211, 1983.
15. **Hsu K.H.**: A theoretical approach to the tempering of grains. *Cereal Chem.*, 61, 466-470, 1984.
16. **International Seed Testing Association.** International rules for seed testing, *Seed Sci. & Technol.*, 13, 299-355, 1985.
17. **Mayer A.M., Poljakoff-Mayber A.**: The Germination of Seeds. Pergamon Press, Oxford, 1989.
18. **Mohsenin N.N.**: Physical Properties of Plant and Animal Materials. Gordon and Breach, New York, 1970.
19. **Monahar M.S.**: Measurement of the water potential of intact plant tissues III. The water potentials of germinating peas. *J. Exp. Bot.*, 17, 231-235, 1966.
20. **Phillips R.E.**: Water diffusivity of germinating soybean, corn and cotton seeds. *Agron. J.*, 60, 568-571, 1968.
21. **Shaykewich C.F., Williams J.**: Resistance to water absorption in germinating rapeseed (*Brassica napus* L.). *J. Exp. Bot.*, 22, 19-24, 1971.
22. **Shull C.A.**: Temperature and rate of moisture intake by seeds. *Bot. Gaz.*, 69, 361-390, 1920.
23. **Shull C.A., Shull S.P.**: Temperature coefficient of absorption in seeds of corn. *Bot. Gaz.*, 77, 262-279, 1924.
24. **Stenvert N.L., Kingswood K.**: Factors influencing the rate of moisture penetration into wheat during tempering. *Cereal Chem.*, 54, 627-637, 1977.
25. **Taylor D.L.**: The influence of oxygen tension on respiration, fermentation and growth in wheat and rice. *Am. J. Bot.*, 29, 721-738, 1942.
26. **Woods J.L., Favier J.F.**: Apparatus for thin-layer drying and associated error analysis. *J. Agric. Eng. Res.*, 55, 113-127, 1993.