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Original article

Variability of maize seed imbibition rates as influenced by seed size distribution and coating application

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Abstract – Irregular coating application levels may modify the variability of seed imbibitions and thus lengthen germination and emergence. In order to characterise this effect, imbibitions of non-coated and coated maize (*Zea mays* L.) seeds were performed in air saturated with water vapour. Three coatings were used at five application levels and water content variability was characterised. Data were modelled to estimate the coatings' water diffusion coefficients. Stochastic simulations were then performed on theoretical seed sets. The effects of coatings on this variability were either absent, positive or negative. For non-coated seeds and two coatings, the imbibition model simulated water content variabilities very close to the experimental ones by accounting only for the distribution of the 'surface/volume' ratios. For the third coating, it was necessary to account also for the correlation between seed size and coating weight. (© Inra/Elsevier, Paris.)

seed / coating / imbibition / variability / model

Résumé – Influence de la taille des semences de maïs et du pelliculage sur la variabilité des vitesses d'imbibition. Le pelliculage peut modifier l'imbibition des semences et une application irrégulière des pellicules peut modifier la variabilité des vitesses d'imbibition, entraînant un étalement des germinations et des levées. Pour caractériser cet effet, les imbibitions de semences de maïs (*Zea mays* L.) non-traitées et pelliculées ont été réalisées dans une atmosphère saturée en vapeur d'eau. Trois pellicules ont été appliquées à cinq doses chacune. La variabilité des humidités a été caractérisée sur toute la durée d'imbibition pour les semences non-traitées et au moins pour une date et à une dose pour chaque pellicule. L'utilisation d'un modèle a permis de calculer les coefficients de diffusion des pellicules et de simuler l'imbibition stochastique de lots de semences virtuelles. L'effet des pellicules sur la variabilité des vitesses d'imbibition est nul, positif ou négatif. Quand le modèle d'imbibition ne tient compte que de la distribution des rapports « surface/volume » des semences, les variabilités simulées sont très proches des variabilités expérimentales pour les semences non-traitées et deux pellicules. L'augmentation de la variabilité des vitesses d'imbibition par la troisième pellicule est reproduite par le modèle en tenant compte de la corrélation entre taille de semences et quantité de pellicule appliquée. (© Inra/Elsevier, Paris.)

semence / pelliculage / imbibition / variabilité / modélisation

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1. INTRODUCTION

Rapid emergence is an important prerequisite for obtaining satisfactory stands and optimum crop yield potentials. The rate of germination seems as important as the initial time to germination and emergence, since slow germination rates can lead to heterogeneous maturity stages at harvest [11]. With slow germination rates, there is also a risk for some seeds to be attacked by soil fauna and fungi or to be reached by soil drying coming down from the surface. Germination rate is also believed to be reduced by some seed coatings, which are applied to protect seeds and young seedlings from diseases and pests [12].

Under field conditions, germination rate is influenced by various factors, including soil moisture, temperature and aeration, and these parameters, which depend partially on agricultural practices, vary across space and time. Under favourable controlled and homogeneous conditions, variable germination times are also recorded. They may be inferred to variable imbibition rates, which may in turn be related to heterogeneous seed sizes.

Thus, imbibition models should account for variations in seed sizes. Several authors have shown that small soybean seed types imbibed water faster than large seed types ([7], [14] cited in [5]). The same correlation was reported for maize seeds germinated under stress conditions [10], and for split peas which took up water more quickly than unsplit peas [16]. Qualitative and quasi-quantitative hypotheses were developed to explain this correlation. Muchena and Grogan [10] explained that smaller seeds needed to imbibe smaller quantities of water for germination. Waggoner and Parlange [16] showed that the ratio of the water uptake rates by split and unsplit peas (1.55) was essentially equal to the 1.5 ratio of the area in contact with free water. Calero et al. [5] showed that indirect effects of seed size are also involved in water absorption of soybean seeds. Electron microscopic studies indicated that pores in the seed coat of small seeds were open and, therefore, functional, whereas pores were often distorted and plugged in larger seeds where the seed coat had been stretched over a large surface. Thus, for various species, the permeability of seed coats to water is correlated with the seed size. These various reports indicate a need to account for the seed size distribution in any study on the imbibition and germination of seeds. In this regard, a modelling approach could provide a better understanding of seed size effects on imbibition.

Changes in the variability of seed water uptake rate as the consequences of seed coating applications have not yet been investigated although seed coating processes sometimes lead to variable coating thicknesses between the seeds.

In this paper, we show how a simple imbibition model, i.e. the porous layer model proposed by Bruckler [3] and presented by Schneider and Renault [12, 13] can quantify the effects of each mechanism by which seed size affects water uptake. For non-coated seeds, it enabled us to identify the seed-size effect as a 'surface/volume' effect, and to reject the idea of a permeability effect. For coated seeds, the porous layer model showed that coating effect on water uptake variability could be explained by correlations between seed-size and coating thickness.

Seeds were either non-coated or coated with three different coatings applied at five levels. They were imbibed individually in air at 100 % relative humidity, in order to maximise coating effects on water uptake [13].

2. MATERIALS AND METHODS

2.1. Seeds

Maize seeds were supplied by Pioneer Semences (Aussone, France). Seeds were stored either at 5 °C and 50 % relative humidity at the factory in Aussone or at 20 °C without any control of air humidity at the Research Station in Avignon during the last months preceding the experiments. In order to minimise the variability of the initial water contents, seeds were equilibrated at a relative humidity of 55 % over a saturated solution of $Mg(NO_3)_2$ for 15 days before experiment initiation.

To analyse the imbibition data with the porous layer model [3], estimates of the seed dry weights, surfaces and volumes were required. Moreover, since seeds swelled during imbibition, we had to estimate the volumes of the seeds as a function of the water content. The surface was estimated for one water content only and we assumed that the seed did not change shape.

Average water contents of 17 samples of 20 seeds each were obtained for vapour-phase water uptake durations between 3 and 120 h. Seeds were weighed at each stage. Their volume was measured by immersion in kerosene [9]. Seeds were then dried for 24 h at 105 °C and weighed again. Their water content and volume were deduced from these measurements.

For seeds stored in the laboratory with no control of the relative humidity, similar volume measurements were taken on 25 seeds, whose surfaces had been previously measured. The seeds were initially covered with a black plastic coating. This plastic coating was then peeled off from the seed surface and laid down on a white planar surface. Its surface was measured with an image analyser.

2.2. Coatings

Three coatings A, B and C were used in this study. Coating A is a commercial acrylic polymer formulation, B a polyvinyl acetate polymer applied as a water based emulsion and C a commercial cellulosic polymer formulation. Five levels of each coating were applied to the maize seeds. These levels were noted as multiples of a standard n level, which corresponded to theoretical applications of 0.1, 0.06 and 0.06 $kg{\cdot}kg^{-1}$ seeds for coatings A, B and C, respectively. The application levels were 0.5-, 0.75-, 1.0-, 1.5- and 2.0n for coating A, 0.5-, 1.0-, 2.0-, 3.0 and 4.0n for B, and 0.5-, 1.0-, 1.5-, 2.0- and 2.5n for coating C.

2.3. Morphological characterisation of the coatings

Seed coating weight and thickness were measured. Coating weights for B and C seed lots were measured according to the following procedure. Coated seeds were dried and weighed. Coatings were then removed with a wet cloth and seeds were redried and weighed. Coating dry weight was inferred from the difference in seed weight. These measurements were made on 20 or more seeds for each coating application level.

Coating A weights could not be measured with the same procedure since oven-drying melted coating A which could no longer be removed from the seed surface. Instead, coating A was peeled off the seed surface without any preliminary heating and its fresh weight was calculated on the basis of the difference in seed weight before and after peeling.

Coating thicknesses were measured via electron microscopy. Measurements were taken on 2–4 seeds from each treatment. The number of electron micrographs ranged from 10 to 40 per seed, depending on the quality of the cross and longitudinal sections. We focused on different locations (on the embryo, the sides opposite and perpendicular to the embryo, and ridges).

2.4. Imbibition in air saturated with water

Imbibition measurements were performed both globally and individually on batches of 20 seeds. For global measurements, seeds imbibed at 100 % relative humidity in closed containers (plastic boxes or glass jars) on a wire mesh placed 2 cm above 100 mL free water. Each container was used for a specific imbibition time. For each treatment, there were 15 sampling times. Experiment durations were comprised between 96 and 144 h. At each sampling time, the seeds were weighed with the coatings. The average water content was calculated on a dry weight basis, the dry weights being inferred from the initial storage weights and the average storage water content. The average storage water content was determined on 15 seeds.

For individual seed imbibition measurements, the procedure was similar to the previous one, but the containers were smaller and held only one seed. Thus, 20 containers were used per treatment and per sampling time. Water contents of non-coated seeds were measured over the whole imbibition period, but measurements were made for only a few application levels and imbibition times for coated seeds.

All experiments were performed at a constant temperature of 20 °C.

3. THEORY AND NUMERICAL PROCEDURES

3.1. The porous layer model

Bruckler [3] assumed that the resistance of seeds to water uptake may be related to a porous layer

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(PL) having a thickness ΔR_{PL} (m) and the same average water content as the seed. For imbibition in humid air, water transport is described by Fick's law [3]:

$$q_v = D_{PL}(\varpi_s)\left[\frac{M_w}{\rho_w RT}\right]\frac{P_{v_s} - P_{v_e}}{\Delta R_{PL}} \quad (1)$$

where q_v is the flux of water (m·s^{-1}), D_{PL} is the vapour diffusion coefficient of the porous layer (m^2 s^{-1}) expressed as a function of the seed average water content ϖ_s (g·g^{-1}), M_w the molar mass of water (kg·mol^{-1}), ρ_w the bulk density of liquid water (kg·m^{-3}), R the gas constant (8.315 J mol^{-1}·K^{-1}), T the temperature (K), and P_{v_s} and P_{v_e} the water vapour pressures in the seed and external medium, respectively (Pa).

Since ΔR_{PL} is unknown and has no real significance, Bruckler [3] defined the following quantity:

$$D_{PL}' = \frac{D_{PL}}{\Delta R_{PL}} \quad (2)$$

in which D_{PL}' may be regarded as the conductance and $1/D_{PL}' = R_{PL}'$ the resistance of the seed to water transport.

The general mass balance equation may then be written as follows:

$$\frac{\partial \varpi_s}{\partial_t} = -\gamma_v S_t D_{PL}'(P_{v_s} - P_{v_e}) \quad \text{with } \gamma_s = \frac{M_w}{m_s RT} \quad (3)$$

where S_t is the seed surface area (m^2) and m_s is seed dry mass (kg).

Since it is easier to describe the relationship between seed water potential ψ (Pa) and water content ω (g·g^{-1}), Kelvin's equation was used to convert vapour pressure into water potential:

$$\psi = \frac{\rho_w RT}{M_w}\ln\left(\frac{P_v}{P_{v-sat}}\right) \quad (4)$$

where $P_{v\text{-}sat}$ is the water saturation vapour pressure (Pa).

3.2. Parameter estimation and numerical simulations

The relationship between ψ_s and ϖ_s was described by an exponential function as previously [3, 4, 12, 13]:

$$\psi_s = -377 \times \exp(-15.5 \times \varpi_s) \quad (5)$$

where ψ_s is the water potential (MPa), ϖ_s the average water content (g·g^{-1}) of the seed.

The relationships between D_{PL}' and ϖ for non-coated and coated seeds were also described by exponential functions:

$$D_{PL}'(\varpi_s) = a_v \exp(b_v \varpi) \quad (6)$$

where a_v (m·s^{-1}) and b_v are two constants relative to the 'seed-coating' system.

As reported by Schneider and Renault [13] for coating B, a_v and b_v were first estimated simultaneously with a non-linear procedure [2] by fitting simulated imbibition data to corresponding experimental data for coatings A and C. Since a_v and b_v were highly correlated and since b_v estimates did not vary greatly with the coating application level, (results not shown), a mean b_v estimate was assigned to each coating and a_v was estimated a second time. For the stochastic simulations of seed imbibitions, the second set of data, with b_v characterising the 'seed-coating' system and a_v varying with the application level was used.

A classical finite difference method was used to solve the differential equation (5). A fully implicit scheme was used to advance the solution in time. The program was written in standard Fortran 77.

3.3. Stochastic approach of seed imbibition

For non-coated seeds, 1.0n A-, 1.5n A- and 3.0n B-seeds, the behaviour of each seed within a set of 20 seeds was simulated according to the following procedure.

1) Generation of a set of seed weights according to the experimental mean, standard deviation and statistical density function.

2) Generation of the volume and surface area according to the regression lines fitted on the experimental relationships between weight and volume and between volume and surface, after appropriate unit changes. At the initial water content (0.08 $g \cdot g^{-1}$), the volume of each seed was estimated according to *figure 1*. The imbibed volume increase was then calculated with equation (1). For coated seeds, a correction was introduced to account for the average coating thickness:

$$V_{cs} = V_s + S_s \cdot \overline{\Delta R_c} \qquad (7)$$

where V_{cs} is the coated seed volume (mm^3) and $\overline{\Delta R_c}$ the average coating thickness (mm).

Possible swelling of the coating itself was not included in the model. The seed surface was calculated with equation (9).

3) Generation of coating weights correlated to seed surface area according to experimental relationships (case 1) or assignment of the average measured coating weight for every seed (case 2).

4) Generation of values that depended upon coating levels inferred from previously simulated coating weights (case 1) or assignment of a single value for the resistance R_{PL}' for the 'seed-coating' systems (case 2).

5) Simulation of water imbibition for every seed generated.

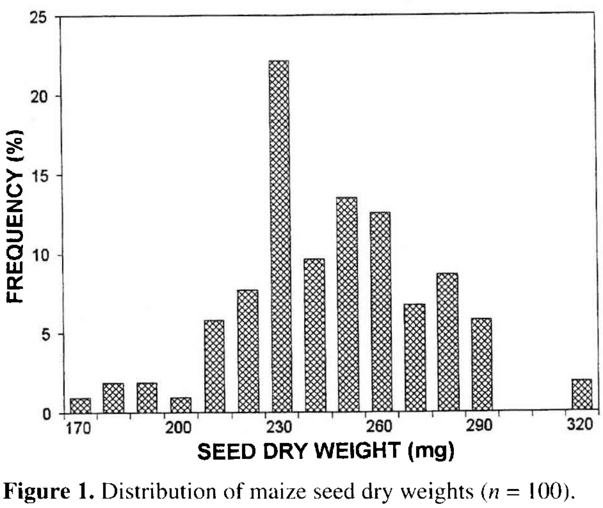

Figure 1. Distribution of maize seed dry weights (n = 100).

6) Comparison of the relationships between seed weight and water content at some specific imbibition time and analysis of coating effects on the variability of water uptake rate.

4. RESULTS

4.1. Morphological characteristics of the seeds

The mean seed dry weight is equal to 241 mg with a standard deviation of 26 mg (*figure 1*). Minimum and maximum values are equal to 170 and 320 mg, respectively.

At the storage water content (0.08 $g \cdot g^{-1}$), the relationship between seed volume V_s (mm^3) and seed dry weight m_s (mg) is linear with an intercept of the ordinate axis nearly equal to zero (*figure 2*).

The mean volume of seeds increases linearly with the mean water content:

$$\overline{V_s} = 242\overline{\omega}_s + 188 \quad R^2 = 0.95 \qquad (8)$$

where V_s is the mean seed volume (mm^3) and $\overline{\omega}_s$ the mean water content ($g \cdot g^{-1}$) of sets of 20 seeds for various imbibition durations.

The relationship between surface area and volume may be described by the following relationship:

$$S_s = 5.4 \times V_s^{\ 2/3} \qquad (9)$$

where S_s is the seed surface area (mm^2), V_s is the seed volume (mm^3).

The relationships between seed water potential and seed water content were measured using water solutions saturated with various salts producing relative humidities from 22 to 93 % [13].

4.2. Morphological characteristics of the coatings

The relationships between coating weights and nominal coating application level are presented in *figure 3*. For coating A, the actual coating rate increases linearly with the nominal level, except for 1.5n where the coating weight deviates significantly from the expected value. The intercept of the regression line with the ordinate axis is negative, possibly a result of coating being lost on the machine surfaces during the coating process. For coating B, coating weights were very similar for 0.5n and 1.0n. At higher levels, coating weight increased linearly with the nominal level, but, as for coating A the intercept with the ordinate axis was negative. For coating C, the coating weight was directly proportional to the application level. The slopes of the regression lines were 18.2, 13.2 and 19.4 mg per nominal application n for coatings A, B and C, respectively.

The thickness of the coating varied according to the position on the seed surface. Due to the irregular shape of the seeds, the thickness of the coating varied by a factor of more than 2 in some places. The relationships between average coating thickness and the nominal coating rate are very similar to those previously described and shown in *figure 3*. Through linear fits and exclusion of outlier values such as 1.5n for A and 0.5n for B, mean coating thicknesses of about 62, 45 and 95 µm per n application level for coatings A, B and C, respectively, were obtained.

The variations of coating weights among seeds were also investigated for the coatings that significantly influenced the water uptake by seeds, i.e. coatings A and B. Since the amount of coating applied was expected to be related to the seed surface, we focused on the relationship between the coating weight and the quantity $m_s^{2/3}$, which is proportional to the seed surface (*figure 4*). We found no correlation between these parameters for coating A at 1.5n, and although there was a statistical significant linear increase of the coating weight with increasing seed surface area for the same coating at 1.0n, the slope of the regression line was quite low and the amount of coating per surface area unit (the 'coating weight/$m_s^{2/3}$' ratio) did not vary significantly. For coating B at 3.0n, coating weight increased significantly with seed surface and the amount of coating per surface area unit varied between –50 and + 30 % of the mean value for the smallest and largest seeds, respectively. Coating thickness is therefore related to seed surface, and since coating resistance to water transfer depends on coating thickness, we can suspect a relationship between seed surface and coating effect on imbibition.

4.3. Imbibition in air saturated with water vapour

Non-coated and coated seeds were allowed to imbibe in humid air. Comparison between the imbibition curves showed that coatings had various

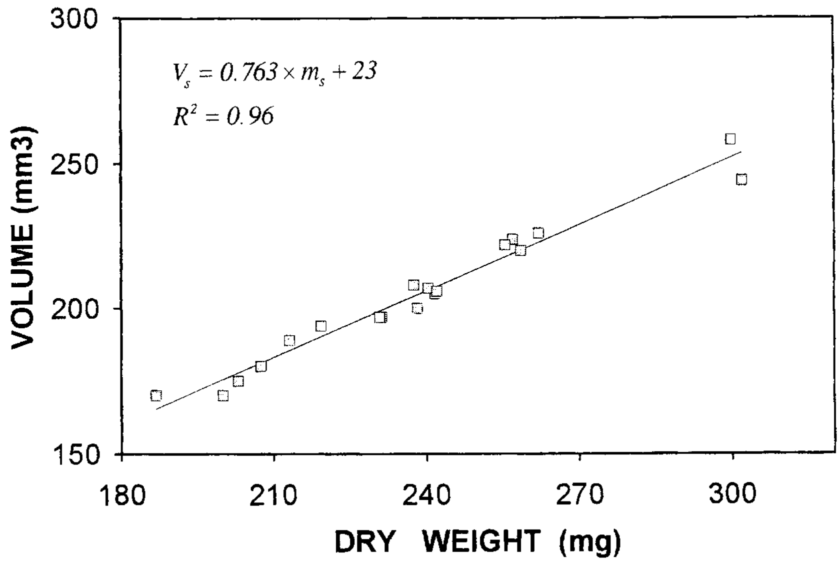

Figure 2. Volumes of corn seeds compared to seed dry weights at an average water content of 0.08 g·g^{-1} (n = 20).

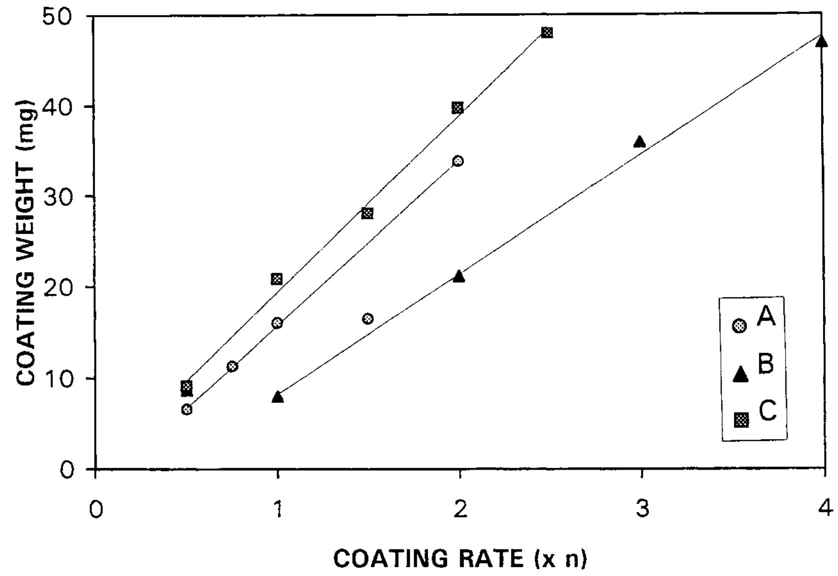

Figure 3. Actual average coating weights as a function of the nominal coating rate for coatings A, B and C.

effects related to the application level. Coating C did not affect the water uptake rate regardless of the application level (*figure 5c*). This lack of effect probably results from the early splitting of the coating which gradually breaks loose from the seed surface. Coating A slowed the imbibition but this effect could not be easily correlated with the coating level (*figure 5a*). This retardation of imbibition is probably related to the good adhesion and stability over time of coating A, which is very elastic and did not visibly crack during imbibition. The effects of the third coating (B) are more complex (*figure 5b*). Indeed coating B slightly enhanced water uptake at levels 0.5n and 1.0n (data not shown), and slowed imbibition at higher levels. The negative coating effect increased with increasing application rates. A wetting reaction which predominates at low application levels and a barrier effect to water uptake at higher levels were inferred [13].

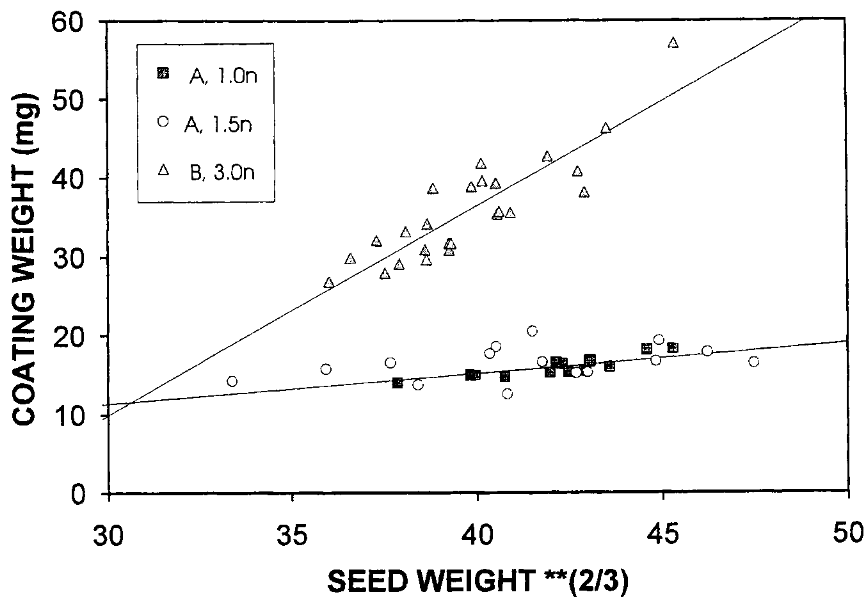

Figure 4. Coating weights as a function of the (seed weight)$^{2/3}$ which is proportional to the seed surface for coating A at 1.0- and 1.5n and B at 3.0n. The continuous lines are the regression lines fitted on 1.0n coating A- and coating B-data.

Whatever the treatment, water uptake rates varied greatly among seeds. For non-coated seeds, water uptake variability increased with the average seed water content (*figure 6*) and was significantly correlated with the seed dry weight (*figure 7*). As previously reported, this correlation may result only from the effect of the 'surface/volume' ratio on the water uptake rate but may also be a consequence of differences in the seed coat structure between small and large seeds [5].

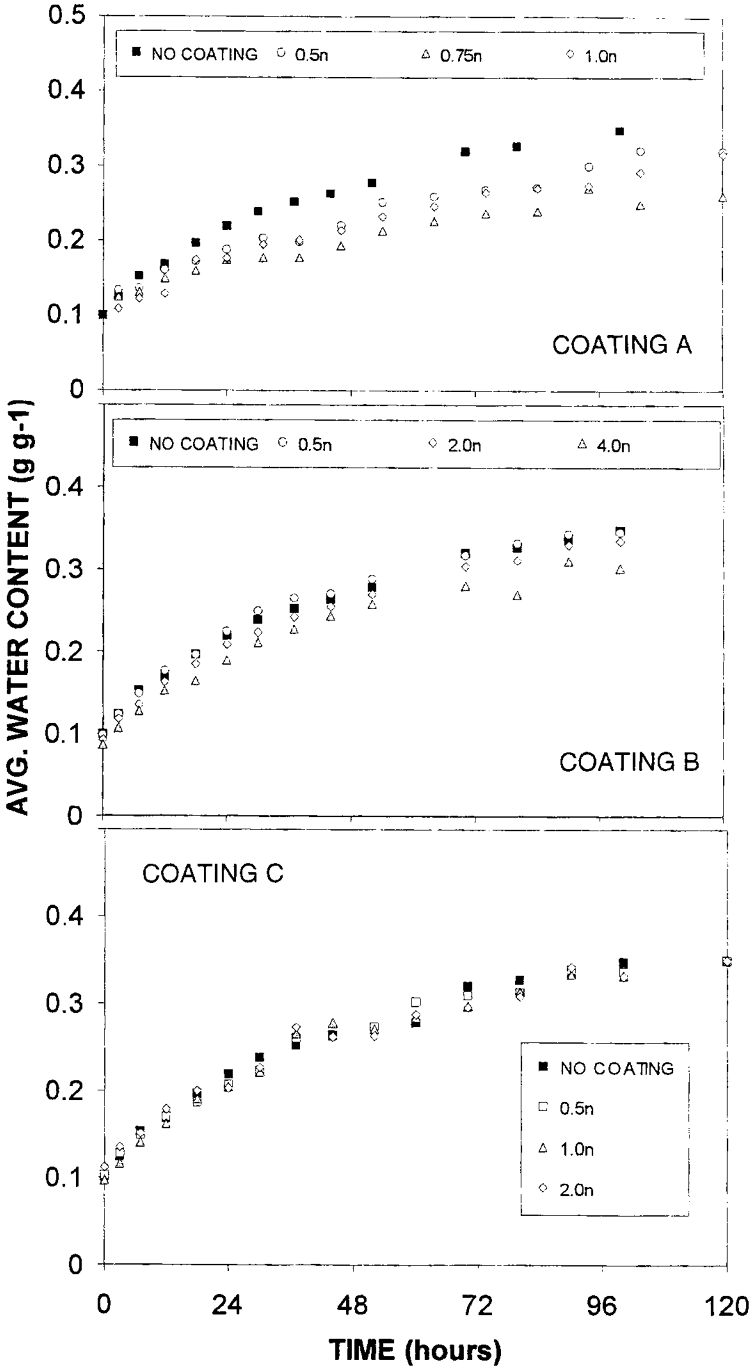

Figure 5. Experimental imbibitions of coated-seeds compared to the imbibition of non-coated seeds: a) coating A; b) coating B; c) coating C.

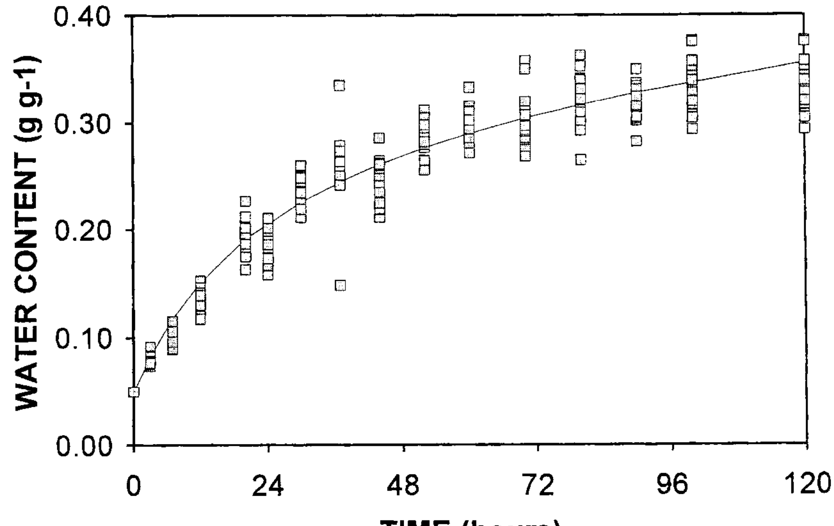

Figure 6. Imbibition of non-coated seeds in air saturated with water vapour. Each point is for one individual seed. The continuous line stands for the imbibition simulated by the the PL-model, which parameters have been fitted on the average experimental data.

For coated seeds, there were also significant correlations between seed weights and water contents at various imbibition durations (*table I*). For similar water contents, the slopes of the regression lines and their standard deviation error were slightly smaller for A-coated seeds, compared to non-coated seeds (*table I*). Thus, coating A reduces water uptake variability. On the contrary, slopes (mean value and std. dev.) for B-coated seeds were greater than for non-coated seeds of similar water contents, coating B therefore increases water uptake variability. Effect of coating B on water uptake variability may result from differences in coating thickness between smaller and larger coated seeds.

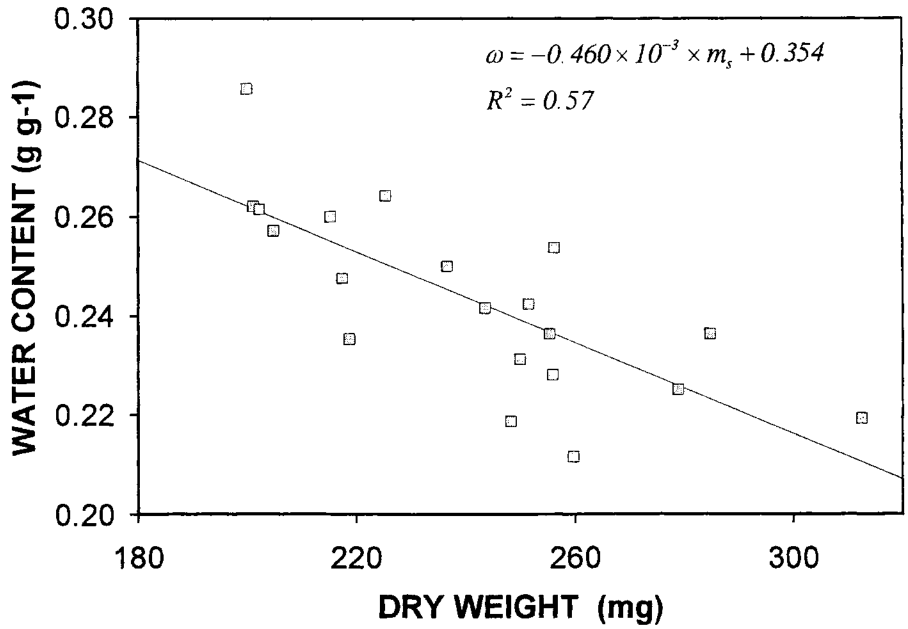

Figure 7. Experimental relationships between seed water contents and dry weights for non-coated seeds at an average water content of 0.249 $g \cdot g^{-1}$ (after 44 h imbibition in air saturated with water vapour). The continuous line stands for the regression line fitted on these data.

Table I. Comparison between the experimental and the simulated slope ($g \cdot g^{-2}$) of the linear relationship between the water content and the seed dry weight.

Coating	Level application	Water content	Measured slope Mean	Measured slope Std. dev.	Simulated slope Case 1	Simulated slope Case 2
		$g \cdot g^{-1}$	$g \cdot g^{-2}$			
No. coating		0.152	–0.291	0.068	–0.277	
		0.224	–0.373	0.078	–0.361	
	1.0 n	0.182	–0.270	0.067	–0.280	–0.278
A	1.5 n	0.158	–0.174	0.059	–0.163	–
	1.5 n	0.224	–0.273	0.051	–0.301	–
B	3.0 n	0.280	–0.557	0.119	–0.466	–0.320
	3.0 n	0.331	–0.609	0.127	–0.529	–0.366

Case 1 is for the actual relationship between coating thickness and seed weight, and case 2 is for an hypothetical constant coating thickness.

4.4. Stochastic simulation of seed imbibition

Simulations were in good agreement with experimental data regardless of coating, application level and number of parameters being estimated (*figure 6* and other data not shown). Nevertheless, for both coatings A and B, the $1/a_v$ ratio, which is proportional to the resistance R_{PL}', did not vary monotonously with the application levels. For coating A, the relationship between the $1/a_v$ ratio and the application level was very irregular (*figure 8*). The unexpectedly high values for 0.75 and 1.5n may have been caused by degradative changes in the structure of the coatings which were applied to seeds 4 months after the seeds had been coated at the other three application levels. Such changes may have been induced by variations in the temperature and relative humidity of the laboratory where the applications were performed. For coating B, the $1/a_v$ ratio was smaller than for non-coated seeds at low application levels (0.5n and 1.0n) and increased at higher application levels [13]. At low application levels, a coating wettability effect probably prevails over resisting effects.

In simulation case 2, coating weights were estimated according to the linear relationships fitted on experimental data (*figure 4*):

for coating A at 1.0n $m_c = 0.56 \times m_s - 7.37$ $(R^2 = 0.78)$ (10)

for coating B at 3.0n $m_c = 2.66 \times m_s - 69.78$ $(R^2 = 0.77)$ (11)

where m_s and m_c (mg) are seed and coating fresh weights for coating A, and seed and coating dry weights for coating B.

The corresponding coating application levels were calculated by the following equation:

$$L = \bar{L} \frac{[m_c / m_s^{2/3}]}{\bar{m}_c / \bar{m}_s^{2/3}} \quad (12)$$

where L and $\bar{L}$ are the actual and nominal application levels (× n), $\bar{m}_c$ and $\bar{m}_s$ (mg) are the average coating and seed fresh weights for coating A, and the average coating and seed dry weights (mg) for coating B, respectively. For each seed, the resistance R_{PL}' was then inferred from the relationship between the ratio $1/a_v$ and the application level L (*figure 8* for coating A). When coating A was applied at 1.5n, coating weights were not significantly correlated with seed surface areas, and L was equal to $\bar{L}$. In contrast, at application level 1.0n, L varied with the seed surface area. Since the

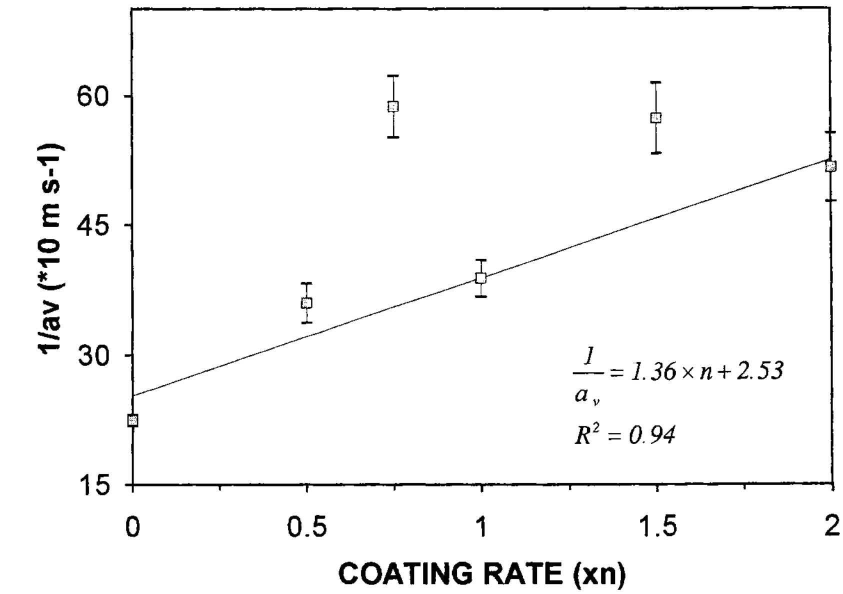

Figure 8. Relationship between the $1/a_v$ ratio and the application level of coating A. The continuous line stands for the regression line fitted on the experimental data after 0.75n and 1.5n values had been omitted.

relationship between R_{PL}' and the coating level was very irregular (*figure 8*), the resisting effect of the coating could not be properly estimated. Therefore, 0.75n and 1.5n values were omitted and a linear relationship was fitted to the remaining experimental data. Thus, a resistance R_{PL}' could be assigned to every calculated application level L. For coating B, the relationship between R_{PL}' and the application level was inferred from the regression line fitted on the 1.0n to 4.0n data:

$$\frac{1}{a_v} = 0.248 \times n + 1.53 \tag{13}$$

Imbibition was simulated for every generated seed. For the non-coated seeds, the porous layer model enabled us to obtain theoretical relationships

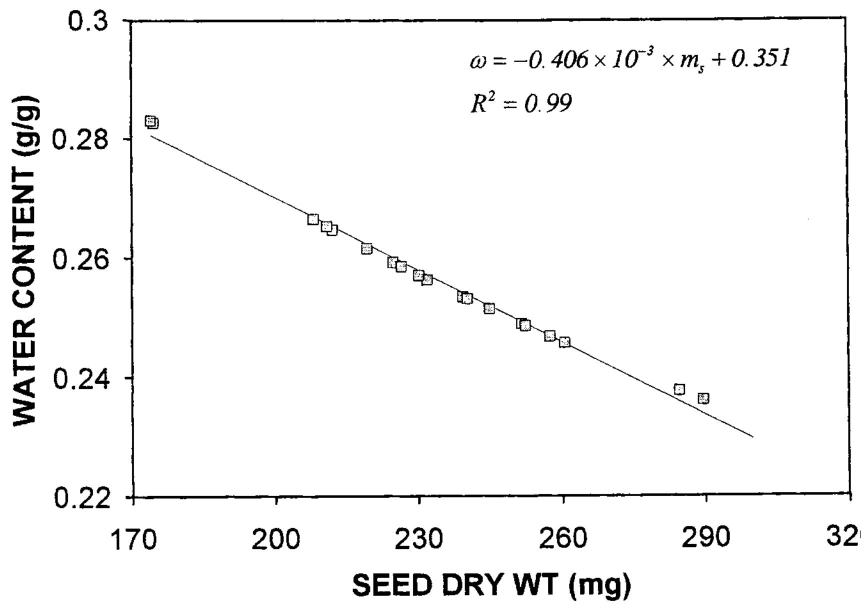

Figure 9. Simulated relationship between the seed water contents and dry weights for non-coated seeds at an average water content of 0.257 $g \cdot g^{-1}$ (after 44 h imbibition in air saturated with water vapour). The continuous line stands for the regression line fitted on these simulated data.

between seed weight and water content (*figures 9* and *10*). The slopes of the regression lines fitted on the simulated data were very similar to the experimental ones (*table I*), but residual variability was significantly reduced with the PL-model. Coating A reduced water uptake variability among 1.0 and 1.5n coated seeds in PL-simulations, which were in good agreement with the experimental data.

For coating B at 3.0n which increased water uptake variability, the PL-simulations were also in good agreement with experimental data (*table I*), but it was necessary to account for the relationship between seed surface areas and coating weights (*table I*, differences between case 1 and 2), which had not been necessary for coating A at 1.0n. Differences in coating effects on the variability of water uptake probably result from differences in the slopes of the regression line between coating weight and seed surface, which were probably too small for coating A at 1.0n (*figure 4*).

5. DISCUSSION AND CONCLUSION

In this study, we analysed the effects of three coatings on the variability of the water uptake rate by maize seeds. For non-coated seeds allowed to imbibe in air saturated with water vapour, the differences in water contents between small and large seeds may be as large as 0.08 g g^{-1} at a mean water content of 0.25 g g^{-1}. The porous layer model proposed by Bruckler [4] made it possible to simulate variations of the water content. As far as the slope of the regression line between water content and seed weight is concerned, the simulated variations were similar to the experimental ones by accounting for the distribution of seed dry weights only, i.e. for the 'surface area to volume' ratio. It therefore did not seem necessary to account for other seed characteristics which may also vary with the seed weight. Unlike soybean [5], the seed coat structure of corn seeds is probably not correlated with the seed size. Nevertheless, about ± 0.03 g.g^{-1} of the water content variability were not explained by the seed size distribution. This residual variability may result from heterogeneous initial water contents (± 0.02 g.g^{-1}), imprecision in measurements and variability in other characteristics, including seed shape and relations between $\psi_s(\omega_s)$ and $D_{PL}'(\omega_s)$.

Coating C had no effect on water uptake variability, whereas coatings A and B reduced and increased it, respectively. It can be inferred that the variability in water contents remains unchanged, when

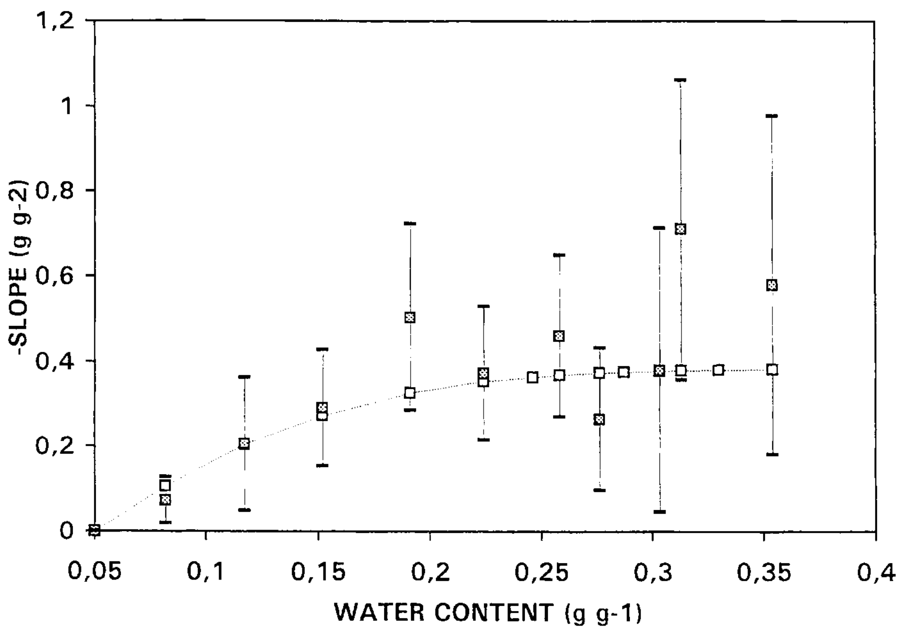

Figure 10. Experimental (closed squares) and simulated (open squares) slopes of the relationships between the water contents and dry weights as a function of the imbibition time for non-coated maize seeds. Experimental slopes are given with their confidence interval (95 %).

seeds are coated with a material which has no effect on the water uptake rate (coating C). Moreover, water uptake variability of coated seeds is reduced when the coating is highly resistant to water penetration, but only if coating thickness does not depend on seed weight (coating A). On the contrary, when the coating is highly resistant to water penetration and when coating thickness depends strongly on seed weight (coating B at 3.0n), water uptake variability of coated seeds is increased. In such a situation, it is necessary to account for the correlation between coating weight and seed surface area to estimate the variability of water uptake.

Germination of corn requires a minimum average water content threshold of about 0.35 $g \cdot g^{-1}$ on a dry weight basis (i.e. 0.25 $g \cdot g^{-1}$ on a fresh weight basis) [3]. When imbibition occurs exclusively in humid air, this threshold is reached after 3 and 5.5 days for the non-coated seeds, whose weights are equal to 170 and 320 mg, respectively. For B-coated seeds at 3.0n, the time to reach the hydration threshold was increased to 3.3 and 8 days. However seeds are normally placed in soils where water uptake patterns are quite different from those observed during imbibition in humid air. Imbibition rates in soil may be estimated by accounting simultaneously for the seed surface fractions in contact with humid air and in free water, respectively [4] and imbibition in free water, which leads to hydration threshold in less than 0.5 days [13], is very rapid in comparison to imbibition in humid air. Therefore, the effects of coatings on the variability of water uptake rates under field conditions are probably smaller than those described in this paper.

Although small seed sizes seem to provide an imbibition advantage through high 'surface/volume' ratios and, sometimes, smaller coating thicknesses, the consequences of the variability in water contents on germination and later on homogeneous crop stands is uncertain.

Indeed, large seed sizes seem to provide other advantages, such as larger seedlings and larger metabolic reserves [1, 8]. For sugar beet, larger seeds show greater hypocotyl vigour [15] but there is no difference in the hypocotyl elongation rate between smaller or larger seeds [6].

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