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The Influence of Genotyne. Priming Material. **Temperature and Osmotic Potential of Priming Solution on Imbibition and Subsequent Germination** of Sorghum and Pearl Millet Seeds During and After Treatment

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\mathbf{I} Introduction

Seed priming or osmoconditioning is a pre-sowing, controlled hydration treatment in which seeds are exposed to a water potential sufficiently low to permit pre-germinative metabolic activity without protrusion of the radicle through the seed coat (Heypecker and GIBBINS, 1978), whilst seed hardening involves water-soaking and drying back of seeds (Austin et al., 1969). Although primed batches of seed generally germinate more rapidly and uniformly than untreated ones, a major constraint of the technique's application is occasional germination of seeds during the prolonged treatment period (hereafter termed *premature germination*). Reports have indicated such germination at osmotic potentials of -0.5 bar (FRETT and Pu). 1989) and as promptly as 96 hours after initial treatment (JONES and SANDERS, 1987). Jett et al. (1996) established that the optimum enhancement of primed seeds would occur just below the osmotic potential threshold for their germination or else premature radicle protrusion occurs, while Mauromicale and Cavallaro (1995) suggested a cultivar-dependent response. Brockleburst and Dearman (1984) emphasized the role of the priming solution's osmotic potential in the prevention or acceleration of such a phenomenon. The osmotic potential of the priming solution influences premature germination through its effect on water uptake by the seed (PRAKASH and PRATHAPASENAN, 1988) as does the priming temperature (CHUNG SEONG et al., 1986).

Many researchers have taken this as evidence that the germination of seeds during priming depends not only on imbibition rate (BEWLEY and BLACK, 1978; SEBANEK, 1992) but also on genotype (MAITI and MORENO, 1995).

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The exact relationship between genotype, priming treatment and other inputs, and imbibition or germination during conditioning is, thus. worthy of further investigation. As part of a wider scheme to study seed priming effects on *Sorghum bicolor L. (Moench)* and *Pennisetum glaucum* L. R.Br., this paper addresses a preliminary screening of ten genotypes for their potential tolerance to priming treatments. A further set of experiments investigated the imbibitional pattern of sorghum seeds as affected by various priming and post-priming inputs.

$\overline{2}$ Materials and Methods

2 . .1 Premature germination during soaking

The four sorghum and six pearl millet genotypes tested included four sorghum varieties (ICSV 1, ICSV 112, ICSV 745 and M35-1), in addition to four millet varieties (BK 560, Harmer, CZ-IC 923, and Pusa 322) and two millet hybrids (ICMH 456 and HHD 67). Seeds werc received from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India, and stored at 5°C and 50% relative humidity until used. Germination, viability and quality tests were conducted on all seed lots (data not shown).

Sixty seeds of each genotype were counted into glass beakers and soaked in a specific volume of either distilled water (osmotic potential Ψ =0 bar) or a 10g NaCl/l water solution (Ψ = -7.7 bar) to achieve a seed: solution ratio of 1:10 based on the 1000 seed weight of the genotype. Beakers were sealed with parafilm, wrapped in aluminum foil and placed in incubators at 23, 29 or 35°C in 3 replicates. The beakers were monitored twice a day for germinating seeds. A seed was considered germinated (prematurely germinated) when approximately 3mm of the radicle had protruded from the seed coat. The day on which the first germination event for a given genotype or treatment occurred was considered the first day of germination (FDG). The final germination percentage (FGP) was that attained after 7 days in priming. Data were analyzed after arsine transformation of FGPs using the General Linear Model of the SAS, statistical package. Mean separation was executed through Duncan's Multiple Range Test (5%).

2.2 Imbibition in salt solutions

To quantify the imbibition rate during the first 54 hours (h) of priming, sorghum SPV 462 (a variety from ICRISAT, India) seeds were treated in one of five ways, i.e. watersoaked at 25° C or soaked in 10, 20, 30 or 40g NaCl $/$ water solutions at 25° C in the dark. Nine seeds were treated individually in petri dishes wrapped in parafilm to reduce water loss. Each individual seed was weighed prior to treatment, placed in the petri dish mentioned with the priming solution in an incubator at 25°C and re-weighed (after blotting dry) after 2, 4, 6, 8, 10, 24, 28, 48, and 54 h . After weighing, the seed was returned to its petri dish and re-wrapped in parafilm. Imbibition percentage was calculated as the difference bctween seed wet and dry weights in reference to the dry weight multiplied

by 100. Each treatment was replicated nine times and an analysis of variance conducted on the data at each time period separately. Again, Duncan's Multiple Range Test was used for mean scparation (5%).

2.3 Effect of soaking duration on imbibition

Four sorghum SPV 462 seeds were soaked in water, an 8g NaCUL solution or a 16g NaCl/l solution at 10°C for 1, 2 or 3 days. After treatment, seeds were dried back at 25° C for 36 h in a constant air-flow cabinet and subjected to imbibition trials in distilled water. Again, every single seed was weighed and treated as in the previous test and the imbibition percentages calculated at 1, 2, 3, 6 and 24 h after immersion. Replications and statistical procedures were similar to those mentioned above.

1.4 Imbibition after storage of treated seeds

The sorghum variety CSV-15 (ICRISAT, India) was used in this test. Nine seeds were either left untreated (dry control) or soaked in 2, 4, or 6g NaCl/L solutions for 3 days (d) at 25°C. They were dried-back as previously mentioned and stored at 25°C and 60 % relative humidity (RH) for 3 weeks. After retrieval from storage, imbibition percentages in distilled water were calculated at 2, 6, 16 and 24 h.

1.5 1mbibition under osmotic pressure

The dry control and 6g NaCl/L treatments from the above experiment were retrieved from storage after 3 weeks and placed in sucrose solutions having a measured osmotic potential of either -0.5 or -1.5 bar. Calculations of imbibition percentage were conducted on nine seeds for each treatment for the periods 6, 20 and 28 h after immersion in the solutions.

2.6 Effect of soaking temperature on imbibition

Nine seeds from the two treatments in the previous experiment were, after the 3 week storage mentioned, allowed to imbibe in distilled water at 10 or 40°C. Imbibition was recorded after 2, 6 and 20 h.

Results and Discussion $\overline{\mathbf{z}}$

3. 1 Premature germination during soaking

The FGP of seeds soaked in distilled water was over 3 times that of salt-soaked (primed) seeds with large varietal differences in this regard. The same applied to the FDG where water-soaked seeds tended to germinate earlier than those undergoing priming. The interactive effects of priming treatment, genotype and priming temperature on the FGP

and FDG of sorghum and pearl millet seeds are shown in Table 1. The highest overall FGP was found in the pearl millet variety CZ-IC 923 water-soaked at 35°C, whereas Pusa 322 showed a remarkably low FGP and high FDG both under water soaking and priming conditions. In other words, it prematurely germinated to a lower extent and at a slower rate meaning that it withstood priming we!!; this under all three priming temperatures. Sorghum generally tolerated the priming conditions better than pearl millet as exhibited by lower FGP values.

Interactive effects of temperature and genotype were not clear-cut; some sorghum genotypes responded to higher temperatures by increasing FGP, others by reducing it. A rise in temperature from 23°C upwards reduced the FDG for bolh water-soaked and primed seeds meaning that seeds prematurely germinated faster as priming temperature rose. Again, the pearl millet variety Pusa 322 out-performed all other genotypes, taking the longest time to initiate premature germination (10 d, primed at 29°C) although a less systematic pattern existed in other genotypes in regard to differences between sorghum and pearl millet in FDG (Table 1).

3.2 Imbibition in salt solutions

During the first two hours of priming, SPV 462 seeds imbibed significantly more water in the water-soak treatment than in the 10 or 30g NaCl/L solutions (Table 2) whilst attaining insignificant imbibitional differences with the 20 and 40g NaO-treated seeds. The same trend continued at the 4-hour phase but levelled-off after 6 h where a difference existed only between the water-soaked seeds and 10g NaCl-treated seeds, the former imbibing significantly more water. After 8 h, the 10 and 40g salt treatments yielded significantly lower imbibitional percentages than the water-soak. This persisted, more or less, to the IO'h hour with only a slight change in the 30g NaCl treatment which fell in its imbibition percentage in comparison to the water-soaked seeds. A change in this pattern became evident after 24 h where all NaCI-treated seeds had imbibed significantly less water than their water-soaked counterparts and continued to do so up to 54 h (2.2 days) afier initial contact with the salt solution.

3.3 Effect of soaking duration on imbibition

No significant differences were detected in imbibition rate between untreated and primed seeds at the 3 tested durations of priming between 1 and 24 h after initial soaking (data not shown).

3.4 Imbibition after storage of treated seeds

The dry control (untreated seeds), 2, 4 and 6g NaCl/l seed treatments did not exhibit significant differences in imbibition rate at 2, 6, 16 or 24 h after initial contact with water. The imbibition percentages after 24 h were 42.7, 42.2, 42.0 and 39.9 % for these treatments, respectively.

Table 1: Interactive effects of priming treatment, genotype and priming temperature on the FGP and FDG? of sorgburn and pearl millet seeds

Means followed by similar letters are not significantly different according to Duncan's Multiple Range Test (Ca-D.O5). Final germination percentage (%) Finst day of
germination (day)

Table 2: Effect of priming solution on imbibition of sorghum SPV 462 seeds at various times

Means in columns followed by similar letters are not significantly different according to Duncan's Multiple Range Test (Ct=0.05).

3.5 Imbibition IInder osmotic pressure

Interactive analysis showed that dry controls and 6g NaCI/l-treated seeds imbibed similar quantities of water after retrieval from storage. This held true for the 6, 20 and 28 h phases. Sucrose-induced osmotic pressure (-0.5 and -1.5 bar) did not affect this pattern of water uptake but simple effect analysis showed that, 28 h after exposure to the sucrose solutions, dry controls had imbibed significantly more water than NaCl-treated seeds (40.2 vs. 37.2 %, respectively) (data not shown).

3.6 Effect of soaking temperature on imbibition

At 2, 6 and 20 h after initial soaking, incubation temperature affected the imbibitional rate of seeds regardless of priming treatment (Table 3). A rise in temperature from 10 to 40°C significantly increased the imbibitional rate. Two hours after initial soaking, dry controls did not differ from NaCI-treated seeds in their response to temperature with both imbibing more water at 40 than at 10° C. However, after 6 h, the effect of temperature manifested itself more clearly in untreated than in primed seeds (a 19.3 % difference in imbibition between 10 and 40° C for untreated vs. 9.6 % for primed seeds. Table 3). This difference between untreated and primed seeds in response to temperature persisted up to 20 h after initial soaking. Dry controls responded to the 30°C rise in temperature by imbibing 15.4 % more water, whereas salt-primed seeds reacted through a mere 5.6 % increase in imbibition

Table 3. Interactive effects of priming treatment and incubation temperature on imbibition percentage of sorghum CSV-15 at various times

Means in columns followed by similar letters are not significantly different according to Duncan's Multiple Range Test $(\alpha=0.05)$.

Hardegree and Emmerich (1992) reported a plateau in seed water uptake for priming treatments (-1.5 MPa, i.e. -15 bar) in less than 24 h. whereas Chilembwe et al.(1992) ming similar up<:rimenlal procedures to these illustraled that water uptake by primed seeds (-0.6 to -1.2 MPa) was substantially greater during the first 18 h than the followe.g 240 h. They suggested that rates of water uptake were directly related to the priming solution's osmotic potential where distilled water allowed for higher imbibition rates than a -1.2 MPa solution of polyethylene glycol 6000. The reduction in FGP in saltstraked seeds may be due to the osmotic potential of the surrounding solution. The 10g NaCl/l solution had an electrical conductivity (EC) value of 16.8 mS cm⁻¹ and an osmotic potential of -7.7 bar (aprox. -0.77 MPa), a substantially harder solution for water uptake by the seed than distilled water ($\Psi_x = 0$ bar). However, it apparently was still low enough to cause premature germination after at least 2 d (Table 1). It may also be inferred that water may not feasibly be used alone for treating sorghum or pearl millet seeds without a proper osmoticum because premature germination started after 24 h of spaking, a result that agrees reasonably well with those of Hegarty (1978) and Hardegree and Emmerich (1992). ELLS (1963) arrived at similar conclusions for tomato seed where \approx 2 d treatment at 75°F (23.6°C) was enough to cause premature germination in water. Studies on barley (Hong and ELLs, 1992), however, have shown no germination at 15°C *After* 24 h in water. This is clearly lower than the base temperature used in this investigation (23°C). Thus, reduced water uptake (see soaking temperature experiment) and probably metabolic activity (BEWLEY and BLACK, 1978) at 15° C in the case of Hong and Ells (1992) may have kept the seeds quiescent for a longer period than in the solutions employed here. Shorter priming durations are generally required at higher priming temperatures and vice versa (HAIGH, et al., 1986) and so an eventual premature germination will occur sooner or later. The relationship in both cases, then, is such that premature permination may best be controlled by lowering the osmotic potential of the surround- $\frac{1}{2}$ solution, allowing for germination-free priming up to a 7 d period (SIVITREPE and Downano, 1995). Even the water soaking treatments may have vielded lower FGPs and

higher FDGs, had the water used been of lower quality (higher EC) than that actually applied (distilled water). Tap and irrigation water may vary considerably according to arca and even season and SO lower EC values (and thus higher osmotic potentials) may be expected under farm-household and field conditions.

The fact that sorghum germinated to a lower extent than pearl millet (a clear exception heing Pusa 322, Table 1) is not well understood. The key may reside not in a genotypic feature but rather in a phenotypic one. Pearl millet seeds are smaller and , thus, have a larger surface area for water uptake relative to their weight than sorghum. Therefore, the likelihood of reaching the critical threshold for germination (JETT et al., 1996) faster under priming conditions seems possible. Marcellos (1987) reported a relationship between the testa fraction of the seed and seed weight in faba beans where the fraction increased as seed weight decreased. Studies on alfalfa (RUMBAUGH, 1961) show that the seed coat is the primary governing factor in the varietal reaction to osmotically induced stresses during germination. Sorghum and pearl millet, as members of the *Gramineae*, may differ in this sense although a seed-coat-dependent response may not be ruled out. Certain cultivars of sorghum have also been shown to contain high levels of condensed tannins in their seed coats (BLAKELY et aI., 1979) which may interfere with water uptake. As the osmotic potential of the priming solution increased (from 0 to -7.7 bar), the difference between sorghum and pearl millet faded away. At 23°C the difference in FGP between sorghum and pearl millet genotypes soaked in water was 31.3 % in favor of the latter (calculated from Table 1), whereas in the salt-soak this difference dropped to 21.2 % meaning that the relationship between seed surface and water uptake is governed by the osmotic potential. It is speculated that at higher potentials of, e.g. -15 bar this difference in water uptake between sorghum and millet seeds would diminish.

Genotype-dependent characteristics seem not to fully provide a basis for explaining premature germination in the varieties used. Sorghum variety ICSV 1 is a medium duration photoinscnsitive variety with a 1000 seed weight of about 26 g and no testa. The seeds are hard and have a very good water absorption capacity (ICRISAT, 1995), whereas ICSV 112 seeds possess a thin pericarp. They have a similar water absorption capacity with 1000 seed weights of around 19g (ICRISAT, 1995). The variety ICSV 112 is considered as drought tolerant (ERDE) and TALEISNIK, 1993). ICSV 745 seeds are without a subcoat and have a pericarp and a beak. M35-1 has the largest and heaviest seeds of the four sorghum varieties tested and the cultivar has been reported as drought tolerant (NIRALE, 1995). The millet hybrid HHB 67 is relatively thermotolerant (PEACOCK et al., 1993) whilst Pusa 322 which gave the lowest premature germination percentage had ICMA 841 as a female parent with intermediate endosperm texture and an average 1000 seed weight of 6-8g (ICRISAT, 1994). It is known to be highly sensitive to environmental conditions such as moisture and nitrogen, responding well to their presence and performing very poorly in their absence (RATTUNDE, personal communication). In as much as these characters are concerned, differences in premature germination are hard to confidently relate to any particular one of the above traits.

Results of the imbibition experiments amply confirm that the first phase of imbibition is a rapid and purely physical process (MAYER and POLJAKOFF-MAYBER, 1975). The passage of water into the seed during this phase is centripetal so that the outer layers become more hydrated than the central tissue (Spaon and Wiran, 1975), hence the insignificant differences in imbibition between primed and untreated seeds up to 24 h. Seeds, regardless of pre-treatment, seem to have had the same suction force for water uptake during this period, and it is this suction force which determines the rate of imbibition over time [KUTSCHERA, 1995), dropping as the seed takes up more water (MANOHAR, 1966). Previnus studies (Ausrin et al., 1969), however, have shown that water-soaked and subsemently dried carrot seeds imbibed water at a higher rate than untreated seeds up to 3 h when imbibition rates became similar. Prakash and Prathanasenan (1988) reported reduced water uptake by NaCl-treated rice seeds, whilst Idris and Aslam (1975) found no efferences in the imbibition of wheat seeds by an increase in the concentration of NaCl in the imbibition medium MARSHALL and NAVLOR (1985), working with Italian ryegrass. showed that seeds in -11.5 bar solutions took up similar amounts of water as seeds in -4.5 and -7.3 bar solutions. They suggested that the water potential that allows imbibition is lower (more negative) than that permitting germination. It may well be that the suction force of untreated and primed seeds was not at all similar but still low enough (sufficiently negative matric potential of the seed) in both cases to take up water at the same rate. Priming duration did not play a major role in determining the pattern of imbibition because it seems not to have affected this suction force in any way. The same applies to storage of primed seeds for 3 weeks where even this wetting (priming) and devine cycle apparently did not change the physical behavior of the seed or did so in an undetectable manner. The results of Austin et al. (1969, see above) may have resulted from a physical rupturing of the seed coat due to a wetting-drying cycle leading to higher water untake rates. Although visible changes in sorghum seeds after priming. drying and storage were detected in the current investigation, microscopic studies were not conducted to validate this. Even a reduction in the Ψ , of the imbibition medium did not produce significant differences in the rate sorghum seeds imbibed water. However, -0.5 and -1.5 bar sucrose solutions were used and even -1.5 bar still seems safely within the range of accessible water uptake by the seed. Differences might have been detected, had the osmotic notential of the solution been brought to lower and, thus, more critical levels, since other reports have shown large reductions in water untake at -10 bar (Babu. et al., 1985). Although primed seeds did not differ from controls in their water uptake up to 24 h, they nonetheless imbibed significantly less water after 28 h. This arrest of imbibition after the first 24 h has no apparent reason and tends to lead to the assumption that seed sensitivity to primine is different at the various phases of imbibition and germination. Whereas primed seeds did not differ from controls in the first 24 h of imbibition. it may be that they are able to reach a "second, lowered" threshold leading to germination faster than unprimed controls. This will be the theme of another investigation.

An increase in incubation temperature from 10 to 40°C substantially increased imbibition rate regardless of treatment (Table 3). Pollock and Toole (1966), studying Phaseolus lumetus seeds, reported an immediate imbibitional uptake of water at 25°C for about 2 h, a lag period for the 2nd to the 6th h, and, finally, a rapid, linear uptake to about the 25th h. Both the duration of the lag phase and the second rapid uptake phase were dependent on imbibition temperature. Imbibition at lower temperatures (5 or 15° C vs. 25° C) lengthened the lag phase. In the soaking temperature experiment this may have meant that after 20 h, when tests were terminated, seeds exposed to the 10°C regime, regardless of treatment, had not yet completed the second rapid uptake phase due to a prolonged lagphase which may have extended beyond the 6° h. A further reading at 25 or 30 h may have shown differences in imbibition not so large as the currently available ones. Also, Lima bean seeds have a very strong suction force due to the nature of seed constituents which may differ from the sorghum seeds used in our study. Additionally, the 40°C. regime may have reduced water viscosity surrounding the seed and, thus, increased its diffusion (Woopsrock, 1988). Vertucci and Leopold (1983) suggested two components of early imbibition: An initial wetting reaction which is innuenced by the surface tension of the water and a subsequent flow of water through seed tissue which is influenced hy water viscosity. Consequently, the higher imbibition rate at 40°C may also be explained on the basis of lower water viscosity and, thus, higher water diffusion into the seed. The reason for a higher increase in imbibition of controls over primed seeds in response to this rise in incubation temperature remains a speculative issue and will be addressed in a subsequent paper.

Finally, it is recognized that the use of distilled water, as mentioned earlier, for determining the rate of imbibition in seeds falls short of simulating natural field situations where the soil solution (KRIEG and BARTEE, 1975) and seed-soil contact (BROWN et al., 1996) are different. This may manifest itself not only on the suction force a seed will require to take up soil water, but on the physical and thermal barriers it faces in this highly sensitive and important phase of germination and subsequent emergence of a crop.

Summary

A setback in the physiological hardening or osmoconditioning of seeds (priming) is seed germination doring treatment (premature germination). Ten genotypes of sorghum and nearl millet were screened for their tolerance to priming solution conditions and their subsequent premature germination at 23, 29 or 35°C. Priming in salt-based solutions gave lower premature germination percentages than in water (hardening) with the speed of germination increasing as priming temperature rose. Pusa 322, a pearl millet variety, was the most tolerant genotype. Generally, sorghum seeds were better adapted to treatments than those of pearl millet. Further experiments on imbibition of sorghum seeds showed that imbibition rates were higher in untreated than in primed seeds after periods greater than 24 hours of soaking and that a rise in priming temperature increased imbibition to a greater extent in the former.

Einflüsse von Genotyp, Saatgutbehandlung, Temperatur und osmotischem Wert der Behandlungslösung auf Wasseraufnahme-Fähigkeit und anschliessende Keimung von Sorghum und Perlhirse während und nach der Behandlung

Zusammenfassung

Ein Nachteil der physiologischen Behandlung von Saatgut mit Lösungen hohen osmotischen Wertes (Primino) ist dessen Keimung waehrend der Behandlung. Zehn Genotypen von Sorghum und Perlhirse wurden getestet, um ihre Toleranz gegen die Bedinguneen der Saateutbehandlung und die anschliessende Keimung bei 23. 29 und 35°C zur überprüfen. Priming in Salzlösungen gab niedrigere Keimraten als in Wasser, und die Geschwindigkeit der Keimung erhöhte sich mit steigenden Temperaturen, Pusa 322. eine Perlhirse-Sorte, war der toleranteste Genotyn. Weitere Versuche zeigten, daß die Wasseraufnahmeraten höher waren in unbehandeltem Saatout als in behandeltem Saatest nach mehr als 24 Stunden Behandlung, und daß eine Erhöhung der Behandlungstemperatur zu einer grösseren Zunahme der Wasseraufnahmeraten in unbehandeltem Saateut führte im Vereleich zu behandeltem Saateut.

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