Journal & Proceedings of the Royal Society of New South Wales, Vol. 135, p. 73–83, 2003
ISSN 0035-9173/03/020073–11 $4.00/1

Ionic Combating Mechanisms and their Comparative Effects on Seed Hardening under Simulated Supra-Optimal Environmental Conditions

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Abstract

Heat extremes and limited moisture are two of the most dominant environmental factors impacting stand establishment of rainfed sorghum (*Sorghum bicolor* L. Moench). Hardening is the process of exposing plants to gradual levels of stress and acclimation to foster better response to post-treatment stress factors. Three experiments were carried out under phytotron and germination cabinet conditions to test the effects of osmotic soaking of sorghum seeds with sodium chloride (NaCl) on germination and growth under simulated heat stress. The hypothesis was that the NaCl treatment forms an acclimation to stress by inducing hormonal responses to ionic toxicity caused by salt. This acclimation would lead to a lowered degree of response when the seed is exposed to future stress; namely, heat and/or drought. Independent variables included NaCl concentration, treatment duration, storage and genotype, whereas germination and growth were dependent variables. Further experiments tested various methods of achieving the initial acclimation "signaling" whilst reducing ionic toxicity through combating ions. Longer soaking treatment durations (2–3 days) and higher NaCl concentrations (16 g NaCl l^{-1}) were detrimental to germination in comparison to lower concentrations (8 g NaCl l^{-1}) and shorter durations (1 day). An interaction between concentration and duration of treatment existed where high concentrations performed better at lower treatment durations and vice versa. Combining 10 g NaCl l^{-1} with 5 g calcium sulphate l^{-1} to combat ionic toxicity produced a greater advancement of germination than NaCl alone. Drying duration of seeds did not affect subsequent germination nor did storage for 10 days to 1 month. The effects of osmotic conditioning are discussed and could have potential for improving sorghum success rates in harsh arid environments.

Keywords: ions, acclimation, stress, sorghum, germination

INTRODUCTION

The fate of sorghum (*Sorghum bicolor* L. Moench) seeds sown into dry or gradually drying seedbeds that hamper emergence is not well known. Even though some seeds may germinate and give rise to seedlings, the majority will fail to emerge (Al-Mudaris and Jutzi 1998). This clearly sets back stand establishment and subsequent yield due to thermo and other forms of dormancy (Silvertown 1999). Treating seeds with osmotic solutions before sowing, also termed "osmoconditioning", has been shown to improve germination and seedling emergence in a range of species (Heydecker and Gibbins 1978, Brocklehurst and Dearman 1984). The use of sodium chloride (NaCl) as the osmotic agent in such treatments has also been investigated and shown to yield enhanced germination patterns in sorghum (Al-Mudaris 1998). Both the concentration of NaCl and treatment duration seem to play major roles in the response exhibited by seeds. However, little is known of the role of both factors or of the effect of various salt mixtures on germination and early seedling growth of treated seeds. This is especially the case when ionic toxicity is taken into account as this is the single most important factor affecting NaCl usage as a priming agent. Ionic combating by way of adding extra elements to the NaCl solution may aid in reducing the neg-

ative effects of Na^+ and Cl^- ions (Al-Mudaris and Jutzi 1999).

Conditioning whole plants to stress by gradual exposure to limited and increasing levels of the particular stress factor has been found to alleviate part of the stress at later stages due to an early peaking of abscisic acid (ABA) production and a better hormonal balance in favour of Kinetin (Al-Mudaris 1998a). The concept of conditioning seeds to heat stress by exposing them to pre-germination salinity stress may aid in "hardening" seeds and improving subsequent germination and seedling growth under heat stress.

This paper investigates the effects of NaCl concentration, treatment duration, salt mixtures and storage on germination and growth parameters in four sorghum genotypes. It also evaluates the effect of combining NaCl with other salts in advancing the "hardening" effect to improve germinative performance under drought and/or heat stress by way of ionic combating.

MATERIALS AND METHODS

Effect of Salt Concentration, Osmoconditioning Treatment Duration and Drying

Seed lots of the sorghum variety IRAT 204 were used in this set of experiments. Seed tests revealed a 1000 seed weight of 34 g, a moisture content of 15%, viability of 100% and germinability of 98.0% following International Seed Testing Association (ISTA) rules (ISTA 1993).

Previous work (Al-Mudaris and Jutzi 1998 and 1998a) showed the upper range of positive responses to NaCl to lie between 10 and 20 g NaCl l^{-1}. Therefore, two concentrations around this range were used. These were 8 and 16 g NaCl l^{-1}. A water-soaked (distilled water) wet control was also evaluated. Sodium chloride solutions were prepared at the concentrations mentioned, and seeds soaked in them at 10°C in the dark inside glass beakers for one of three durations; namely 1, 2 or 3 days (d). The wet control was also soaked in water for the same periods of time. The 10°C incubation temperature proved low enough to prevent premature germination (visible signs of radicle emergence after imbibition) during soaking in water.

After treatment, seeds were either sown fresh without drying or surface dried by exposing to an airflow of 25°C for 3 hours (h) inside an incubator and sown dry. Seeds were sown in batches of 100 in 1000 mL polystyrene trays filled with equal volumes of sieved sand (weight basis) and irrigated to weight with 200 mL of water, initially, and as they lost one third of their weight thereafter. Trays were weighed daily at 7:00am. Experiments were conducted in a 18 m^3 walk-in phytotron (Heraeus-Voetsch, Germany) set at the environmental conditions shown in Table 1. These conditions were an attempt to simulate likely heat stress during the course of a day (Al-Mudaris 1998a).

Time (hh.mm)	Temperature (°C)	Relative Humidity (%)	Light (33 klux)
24.00 – 05.00	15	65	Absent
06.00 – 08.00	17	62	Activated
09.00 – 12.00	29	50	Activated
13.00 – 19.00	43	38	Activated
20.00 – 21.00	25	55	Activated
22.00 – 23.00	23	58	Absent

Table 1. The course of temperature, relative humidity and light activation in the phytotron during a 24 hour cycle

Treatment combinations were replicated four times each at 100 seeds per replicate (3 treatments × 3 durations × 2 drying treatments × 4 replicates = 72 experimental units). Trays were arranged in a Randomized Complete Block Design (RCBD). Emergence counts were taken daily for 12 d and from them the final germination percentage (FGP), mean germination time (MGT) and germination index (GI) calculated. MGT and GI were calculated following Orchard (1977) and Benech Arnold et al. (1991), respectively. The MGT is a measure of the mean time taken for a seed lot to germinate, while the GI assigns maximum weight to a higher number of seeds germinating earlier (Al-Mudaris 1998). Data were arcsin transformed (Yang et al. 1999 and Houle et al. 2001) and analysed in ANOVA using the General Linear Model (GLM PROC) of the SAS® statistical package for Windows®.

At 12 days of age seedlings were collectively harvested from each tray, separated into shoots and roots, and, after washing roots under running tap water, dried at 80°C for 4 d in a reverse cycle oven (Conviron Industries, Canada). Average dry weights of shoots (DWS) and roots (DWR) and the shoot : root ratio (SRR) were obtained and averaged. Also, after harvest, the contents of each tray were emptied into a sieve with 2 mm openings, and germinated but unemerged seeds retrieved and counted (hereafter termed GUE). Those that had neither germinated nor emerged were classified as non-germinated seeds and represented the difference between emerged and germinated unemerged seeds (Munir et al. 2001). These were subjected to a tetrazolium test of viability following ISTA (ISTA 1993) to verify their viability status, but data was not analysed. Individual seeds were also studied under a dissecting microscope for further viability and anatomy notes following Hidayati et al. (2001). Germination and growth data were exposed to one-way and two-way analysis of variance (ANOVA) procedures for single factors and interactive factors of seed treatment × duration (Weber and D'Antonio 1999).

Effect of Salt Concentration, Osmoconditioning Treatment Duration and Storage

The same NaCl treatments mentioned above (0, 8 and 16 g NaCl l^{-1}) were used in combination with the same treatment durations (1, 2 or 3 d). After treatment, IRAT 204 seeds were dried back at 25°C for 24 h and stored at 22°C and 50 to 52% relative humidity for 30 d in the dark. Thereafter, seeds were retrieved from storage and sown in batches of 100 in 1000 mL polystyrene trays lined with creased filter paper. Each tray was moistened with 40 mL of a polyethylene glycol solution (PEG) (Fluka Chemie, Germany) and covered with a lid to minimise evaporation. The solution had an osmotic potential (ψ_s) of -10 bar (circa -1.0 MPa) simulating drought (Marschner 1995, Dodd and Donovan 1999). The PEG molecular weight (m.w.) was 10,000. Trays were placed in an incubator set at 42/25°C (day/night, 12 h/12 h). Germination counts were taken daily for 12 d and from them the FGP, MGT and GI calculated. Statistical arrangements were similar to the first experiment with experimental factors being treatment and soaking duration applied in RCBD (Dodd and Donovan, 1999).

Effect of Salt-Based Mixtures and Drying Duration

Three sorghum varieties were tested in this trial. These were ICSV 112, ICSV 745 and M35-1. Seed lot tests revealed germinability, moisture content and viability levels comparable to those of IRAT 204 sorghum used in the previous two experiments.

The hypothesis to be tested here was that mixing NaCl with other minerals might provide both the stress acclimation (hardening) effect and a mineral uptake effect, thus improving seed performance under stress. The "softening" effect of other elements in the mixture might, thus, lead to a balance and a combating of Na^+ and Cl^- ions. A basic 10 g NaCl l^{-1} (ψ_s of -7.7 bar) (Knauer Osmometer, Germany) treat-

ment was mixed with calcium sulphate or one of three fertilizers as follows:

T_1: Dry Control (dry, untreated seeds)
T_2: 10 g NaCl l^{-1} + 5 g $CaSO_4.2H_2O$ l^{-1} (calcium sulphate)
T_3: 10 g NaCl l^{-1} + 7.5 g Urea fertilizer l^{-1} (water-soluble nitrogen-source fertilizer)
T_4: 10 g NaCl l^{-1} + 10 g NPK fertilizer l^{-1} (slow release compound fertilizer with 6% N, 12% P_2O_5 and 18% K_2O)
T_5: 10 g NaCl l^{-1} + 15 g DAP fertilizer l^{-1} (di-ammonium phosphate, soluble phosphorous source)
T_6: 10 g NaCl l^{-1}

Seeds were soaked in the above mentioned solutions for 3 d at 18°C in the dark. The concentrations were based on earlier work with sorghum (Al-Mudaris 1998). After treatment, seeds were dried back at 25°C for 7, 14 or 21 h and stored for 1 month at 24°C in the dark. Subsequently, seeds were sown in batches of 100 in polystyrene trays at 40/20°C (day/night temperatures, 12 h/12 h) under a PEG-induced (m.w. 10,000) drought of -3.3 bar (0.3 MPa). The change in temperature down to 40/20°C was based on observation of partial fungal infection at the 42/25°C level in the previous trial. Again, the FGP and MGT were calculated in addition to the coefficient of velocity of germination (CVG) (Jones and Sanders 1987). The CVG increases when the number of germinated seed increases and the time required for germination decreases. Theoretically, the highest CVG possible is 100 and would occur if all seeds germinated on the first day (Jones and Sanders 1987). Statistical procedures were the same as those for the second experiment.

RESULTS AND DISCUSSION

Effect of Salt Concentration, Osmoconditioning Treatment Duration and Drying

The 16 g NaCl l^{-1} treatment reduced the FGP and GI in comparison to the wet control and the 8 g NaCl l^{-1} treatment. Both salt soaks reduced the time needed to germinate as seen from lower MGT values (Table 2). Neither growth parameters (DWS, DWR, and SRR) nor the number of GUE seeds differed between treatments. The longer the duration of soaking in NaCl solutions, the lower the final germination percentage and germination speed, and the higher the number of GUE seeds (Table 3). Drying seeds, on the other hand, did not affect germination characteristics (FGP, MGT and GI) but reduced the DWR and, thus, increased the SRR (Table 4).

The interactive effects of NaCl concentration, soaking duration and drying on germination and growth characteristics of IRAT 204 revealed no significant interactions between treatment combinations regarding the parameters studied (data not shown)

Seed Treatment	FGP (%)	MGT (day)	GI	DWS (mg)	DWR (mg)	SRR	GUE (seeds)
Wet Control	78.8 a	4.3 a	278.6 a	6.6 a	9.4 a	0.75 a	4.7 a
8g NaCl l^{-1}	73.2 a	3.5 b	262.2 a	6.6 a	9.1 a	0.75 a	4.2 a
16g NaCl l^{-1}	62.1 a	3.5 b	228.0 b	6.3 a	8.6 a	0.84 a	6.0 a

Table 2. Effect of NaCl treatments on germination and growth characteristics of sorghum IRAT 204 under phytotron conditions.
Means in columns followed by similar letters are not significantly different ($\alpha \leq 0.05$). FGP: Final Germination Percentage, MGT: Mean Germination Time, GI: Germination Index, DWS: Dry Weight of Shoot, DWR: Dry Weight of Root, SRR: Shoot : Root Ratio and GUE: Germinated Unemerged Seeds.

Treatment Duration (days)	FGP (%)	MGT (day)	GI	DWS (mg)	DWR (mg)	SRR	GUE (seeds)
1	79.4 a	3.5 b	296.8 a	6.7 a	8.6 a	0.84 a	3.3 b
2	70.0 b	4.0 a	242.5 b	6.3 a	9.8 a	0.69 a	5.6 a
3	64.7 b	3.7 ab	229.5 b	6.5 a	8.7 a	0.80 a	5.9 a

Table 3. Effect of duration of soaking in NaCl solutions on germination and growth characteristics of sorghum IRAT 204 under phytotron conditions.
Means in columns followed by similar letters are not significantly different ($\alpha \leq 0.05$). FGP: Final Germination Percentage, MGT: Mean Germination Time, GI: Germination Index, DWS: Dry Weight of Shoot, DWR: Dry Weight of Root, SRR: Shoot : Root Ratio and GUE: Germinated Unemerged Seeds.

Drying Treatment	FGP (%)	MGT (day)	GI	DWS (mg)	DWR (mg)	SRR	GUE (seeds)
No Drying (Fresh Sown)	72.7 a	3.6 a	263.0 a	6.5 a	10.0 a	0.69 b	4.6 a
Drying (25°C, 3 h)	70.1 a	3.9 a	249.5 a	6.5 a	8.1 b	0.86 a	5.2 a

Table 4. Effect of drying after seed treatment on germination and growth characteristics of sorghum IRAT 204 under phytotron conditions.
Means in columns followed by similar letters are not significantly different ($\alpha \leq 0.05$). FGP: Final Germination Percentage, MGT: Mean Germination Time, GI: Germination Index, DWS: Dry Weight of Shoot, DWR: Dry Weight of Root, SRR: Shoot : Root Ratio and GUE: Germinated Unemerged Seeds.

Effect of Salt Concentration, Osmoconditioning Treatment Duration and Storage

The germination pattern of treated seeds after storage revealed that in both the Wet Control and 8 g NaCl l^{-1} treatment, a soaking duration of 2 days yielded better FGP values than 3 or 1 day soaking treatments, respectively. At the apparently high 16 g NaCl l^{-1} level, soaking seeds for 1 day only was superior to soaking for 2 or 3 days (Table 5). Neither the MGT nor the GI were clearly affected by treatment and duration interactions. However, the highest GI value (best germination percentage and germination speed relationship) was observed in seeds treated with 8 g NaCl l^{-1} for 2 days.

Effect of Salt-Based Mixtures and Drying Duration

The interactive analysis of seed treatment, genotype and drying duration did not reveal significantly different germination percentages. From Table 6 it can be seen that the lowest FGP was observed in the NaCl + DAP fertilizer treatment. All seed osmoconditioning treatments reduced the MGT (seeds germinated faster) and increased the CVG (better germination percentage and rate) over untreated seeds. This means that seed osmoconditioning increased overall germination speed. Genotypes differed in their response to osmoconditioning with M35-1 performing in an in-

ferior manner in comparison to ICSV 112 and ICSV 745 as far as the FGP, MGT and CVG were concerned (Table 7). The duration of drying, on the other hand, did not affect any of the germination parameters studied (data not shown) pointing to the possibility of drying seeds after treatment in order to improve storage life.

Seed Treatment	Duration (days)	FGP (%)	MGT (day)	GI
Wet Control	1	78.6 bc	4.2 ab	255.0 b-d
	2	86.6 ab	5.2 a	219.3 cd
	3	72.6 c	4.7 ab	223.6 cd
8 g NaCl l^{-1}	1	53.3 d	3.4 b	201.0 cd
	2	94.6 a	3.6 b	348.0 a
	3	86.6 ab	4.0 ab	298.3 ab
16 g NaCl l^{-1}	1	84.0 bc	4.4 ab	275.3 bc
	2	58.0 d	4.1 ab	200.0 cd
	3	54.0 d	4.1 ab	185.3 d

Table 5. Interactive effects of NaCl concentration and soaking duration on the germination of sorghum IRAT 204 seeds after storage for 10 d under ambient conditions.
Means in columns followed by similar letters are not significantly different ($\alpha \leq 0.05$). FGP: Final Germination Percentage, MGT: Mean Germination Time and GI: Germination Index.

Seed Treatment	FGP (%)	MGT (day)	CVG
Dry Control	74.2 b	3.7 a	27.7 c
NaCl (10 g/l) + Calcium Sulphate (5 g/l)	81.2 a	2.9 c	36.1 ab
NaCl (10 g/l) + Urea Fertilizer (7.5 g/l)	66.4 c	2.9 bc	33.9 ab
NaCl (10 g/l) + NPK Fertilizer (10 g/l)	71.0 bc	2.7 c	36.8 a
NaCl (10 g/l) + DAP Fertilizer (15 g/l)	56.8 d	3.1 b	32.7 b
NaCl (10 g/l)	68.7 bc	2.7 c	36.4 ab

Table 6. Effect of NaCl and NaCl-based seed osmoconditioning treatments on germination characteristics of sorghum varieties ICSV 112, ICSV 745 and M35-1 after storage for 1 month at 30°C.
Means in columns followed by similar letters are not significantly different ($\alpha \leq 0.05$). FGP: Final Germination Percentage, MGT: Mean Germination Time and CVG: Coefficient of Velocity of Germination.

Genotype	FGP (%)	MGT (day)	CVG
ICSV 112	71.2 b	2.9 b	35.7 a
ICSV 745	84.4 a	2.9 b	34.9 a
M35-1	53.6 c	3.2 a	31.1 b

Table 7. Effect of genotype on germination characteristics of sorghum after storage for 1 month at 30°C.
Means in columns followed by similar letters are not significantly different ($\alpha \leq 0.05$). FGP: Final Germination Percentage, MGT: Mean Germination Time and CVG: Coefficient of Velocity of Germination.

From the results of the first experiment, which was carried out under simulated conditions in the phytotron, it is clear that NaCl concentration is decisive in the post-treatment germinative response seeds exhibit. While 8 g NaCl l^{-1} improved germination, 16 g NaCl l^{-1} retarded it in terms of FGP and GI. Both concentrations of salt, however, increased germination speed over water-soaked controls, but neither affected seedling growth or the fate of seeds which did not germinate. The longer the duration of soaking, the less positive effects were observed. Additionally, longer soaking durations (2 or 3 d in comparison to 1 d) almost doubled the number of germinated but unemerged seeds (Table 3). This response observed in fresh sown seeds was also observed in the second experiment where seeds were dried back and stored. The 8 g NaCl l^{-1} and water-soaking treatments were better than 16 g NaCl l^{-1} except that a 2-day treatment duration was observed to be better than 1 d for water and 8 g treatments, whereas 1 d was more suited for 16 g treatments. Again, 8 g NaCl l^{-1} combined with a 2 d treatment duration advanced germination as seen from higher GI values. This shows that storage of treated seeds at ambient temperatures for a duration of 30 d does not negatively affect performance of pre-storage-hardened seed.

The fact that longer treatment durations increased the number of germinated unemerged seeds (first experiment) and reduced overall germination (16 g NaCl for 2 or 3 d in the second experiment) may be a direct effect of NaCl toxicity to seeds. That seeds germinate but do not emerge reflects a reduced vigor and/or abnormality (microscopic evidence, data not shown) since all seeds were planted at the same depth of 2 cm. Moisture supply was also regulated by weight and so the effect of external factors seems unlikely. A replication of the same treatments was conducted in a separate experiment and seeds/seedlings retrieved at 1, 3, 5 and 7 days after sowing. These were analysed for Na^+ and Cl^- content and showed levels up to five times as high as non-treated seeds/seedlings. The results of this experiment will be reported in a subsequent paper, but would indicate that ionic toxicity occurred. An analysis of hormonal levels would point to a sharp increase in ABA levels during soaking treatments and a mild increase during and after heat shock (Kader, unpublished data). This is where the hardening effect is likely to have taken effect, but at excessive NaCl levels a germination block would have occurred due to the shortage in Kinetin and GA_3 as a direct result of this physiological shock (Al-Mudaris 1998, Kader and Jutzi 2002). This points to the possibility that hardening can only provide alleviation from stress at moderate stress levels and becomes a stress itself at higher degrees of heat, drought or salinity (Noe and Zedler 2000).

The observation that 1 d was better for 16 g NaCl l^{-1} treatments tends to confirm the toxicity hypothesis, since 1 d would not be enough to inflict such stress due to the uptake of water by the seed at high rates during the first day of treatment (Al-Mudaris and Jutzi 1998ab). Bussell and Gray (1976), in their work on osmoconditioning tomato seeds at -5 to -15 bars, observed that the length of soaking period had little effect at low osmotic potentials but not at high potentials. The 8 and 16 g NaCl l^{-1} treatments measured -6.02 and -11.1 bar on the osmometer, respectively. This means that longer durations would expose the seeds to more osmotic stress.

Soaking sorghum in water alone, on the other hand, has been reported to increase germination speed as soaking period increased (Harris 1996). This has also been reported for pepper seed treated with the non toxic, inert manitol (Georghiou et al. 1987). The problem, then, lies within the nature of the osmoticum used. Seeds coming into contact with NaCl solutions have been found to have higher Cl^- concentrations in their different components, the accumulation of which, in the embryo (Esechie 1995) and endosperm (Al-Mudaris, 1998), was associated with germination failure. Fulbright (1988) observed reduced germination in Indiangrass (*Sorghastrum nutans* cv. Cheyenne, Lometa) at 0.12 mol NaCl l^{-1} (6.9 g NaCl l^{-1}),

whereas Shanmugasundaram and Kannaiyan (1989) found 1.0% NaCl (10 g NaCl l^{-1}) to give the highest germination percentage in pearl millet (*Pennisetum glaucum* L. R. Br.) in comparison to 2.5% (25 g NaCl l^{-1}).

Increasing the salt concentration of a solution in contact with sorghum seeds reduces α-amylase and protease activity, reducing and non-reducing sugar contents and the rate of reserve protein mobilization (Khan et al. 1989). Additionally, if a seed takes up solutes or mobilizes its reserves in an osmotically active form, its own water potential will be reduced although physiological processes may be inhibited both by the low water potential and the toxicity of ions (Bannister 1978). Ells (1963) reported that the priming effect of seed treatment with nutrient solutions (including 2% NaCl) is not due to the salts, nor to the amount of water retained by the seed from the treatment, but rather to certain enzymatic activities which take place within the seed while it is being held in a moist condition.

Reduced emergence, after seed germination (germination in the seedbed, but lack of emergence above the soil surface) was observed in the phytotron trial. If the radicle emerges from the testa and the soil water content is reduced below the initial soil water content due to drying, emergence is reduced (Helms et al. 1996). This could have been the case where trays were re-irrigated by weight only when they lost one third of their initial moisture content. This would have been more deleterious to seeds osmoconditioned for longer periods due to their higher initial moisture contents and would have led to a loss of the capacity to emerge (Peske 1983).

Combining NaCl with calcium sulphate improved seed response as seen from the third experiment, whereas other mixtures did not raise the final germination percentage but improved germination speed over controls. This may be due to the fact that the fertilizers used were, in themselves, salts and as such contributed to the ionic stress discussed above. A notable point is that of solubility. Calcium sulphate was not totally soluble at the rates used, whereas sodium chloride was. The NPK fertilizer was also only partly soluble, whereas urea and DAP were more soluble.

Mixing sodium chloride with calcium probably increased Ca^{+2} content of seeds (Bharati and Vaidehi 1989, Al-Mudaris 1998, Kader, unpublished data). Calcium has been found to play a major role in tolerance to NaCl where tolerant genotypes of vegetables contained higher Ca^{+2} reserves in their seeds (Guerrier 1983). It has also been noted as modifying seed response to heat shock in maize (Gong et al. 1997) due, probably, to increasing membrane stability (Marschner 1995). Amzallag et al. (1997) also reported that leaf malformations in plants exposed to high NaCl concentrations were prevented by the addition of Ca^{+2} to the nutrient solution.

Drying duration did not affect seed response to osmoconditioning. This agrees with the results of Emmerich and Hardegree (1996) who found that the germination of four warm-season grasses was not affected by length of the dehydration period. It is also in line with the work of Brocklehurst and Dearman (1984) who found that drying vegetable seeds after treatment did not interact with either the priming chemical used or the species tested and those of Al-Mudaris and Jutzi (1998ab) and Al-Mudaris (1998a). Drying the seed slowly by controlling humidity may impact germination rates achieved through conditioning (Mueller 1996). The loss of cell membrane integrity during drying is repaired when seeds are allowed to imbibe water, albeit after a certain period (Knypl and Khan 1981). It follows that the rate of drying (Dell Aquila and Trito 1990) and its timing after initial imbibition (Kutschera 1995) play the major roles (Al-Mudaris and Jutzi 1999 and 1999a). Both the degree of drying and its timing used here seem to fall within the range which does not alter osmoconditioning effects. This ranged between 14 and 19.5% moisture content following treatment and after drying prior to storage.

CONCLUSIONS

The three experiments were carried out under varying temperature and drought stress situations and after storage at ambient temperatures. The response of sorghum seeds to osmoconditioning in all three cases was generally more affected by the priming agent itself, its concentration and the duration of treatment than by drying or storage. This drying and storage is of great practical significance in the field, for if hardening is to be practiced, convenience in handling seeds must be fostered. This is difficult to achieve in moist batches of seed, which would be prey to fungal infection and render sowing a difficult task.

In conclusion, it would appear that seed hardening of sorghum via an NaCl-based soak has some potential to improve performance under post-treatment supra-optimal environmental conditions like drought or heat stress. The decisive factor in this is the thin line between this hardening actually inducing germination and it being an additional plant stress factor itself.

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(Manuscript received 5.11.2002)
(Manuscript received in final form 04.02.2003)