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Time-Course Changes in High Temperature Stress and Water Deficit During the First Three Days After Sowing in Hydro-Primed Seed: Germinative Behaviour in Sorghum

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Abstract

Both drought and heat stresses substantially influence the germination pattern and subsequent establishment rates of sorghum. The timing of high temperature occuarrance, along with water deficit after seed sowing is investigated and methods for its alleviateion are evaluated. Two experiments were conducted on CSV 15 sorghum seeds after soaking treatments in 2, 4 or 6g $NaCl\ l^{-1}$ solutions. Several high temperature stress scenarios of 45°C were administered at various times during the second day after sowing, or at a fixed time during the first, second or third days after sowing. Results revealed that the 18^{th} hour of the second day after sowing is more sensitive, in terms of the final germination percentage and germination index attained, than the 6^{th}, 12^{th} or 24^{th} hour. Seed treatment with 2g $NaCl\ l^{-1}$ was superior to untreated seeds in its response to high temperature stress, attaning more positive germinative characteristics. Heat shock on the first day after sowing had more negative impacts on germination than on the second or third days. It also caused an increase in radicle growth at the expense of plumule growth, thus decreasing the plumule:radicle ratio.

Keywords: Heat, water-deficit, germination, seed treatments

1 Introduction

Rapid emergence is a trait under genetic control for all crops including sorghum, but its manifestation depends on the prevailing environmental factors (Madakade, I. *et al.*, 2001). Temperature extremes are known to have major detrimental effects on biological sytems (Lin, J. and Sung, J., 2001) and this is most clearly observed in germination (Al-Mudaris and Jutzi, 1998b,c,a). A seed sown to germinate may be exposed to varying environmental conditions in the seedbed before it emerges above the soil surface. These may include high temperatures within the supra-optimal range, limited moisture or both.The timing of environmental stresses, and not just their intensity, may play a major role in outlining the crop's subsequent emergence pattern (Ferrari, L. and Lopez, C., 2000; Castellani and Aguiar, 2001).

The effects of stress intensity have received considerable attention (Gallardo, K. *et al.*, 2001; Tesnier, K. *et al.*, 2002), whereas studies on the effect of timing of stress

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events after sowing are scarce (Galloway, L., 2001; Johnston, M. *et al.*, 2002). In this paper, the basic argument that timing of heat shock affects the germinative response of seeds was investigated. We also tested the hypothesis that hydro-priming alters the time-dependent response of seeds to both water deficit and high temperature stress. The first three days after sowing were chosen as the scenario-implementing period based on previous work in this laboratory (Kader, M., 2001; Kader, M. and Jutzi, S., 2001, 2002) and other studies (Demir, I. and Van de Venter, H., 1999; Chacalis and Smith, 2001).

2 Materials and Methods

2.1 Effect of Heat Shock During the Second Day After Sowing

Three osmotic hydro-priming seed treatments were applied to sorghum (*Sorghum bicolor* L. Moench) CSV 15 seeds. Certified seed lots were obtained from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and analysed following International Seed Testing Association regulations (ISTA, 1993). Lots used in this study had germination percenatges of 99.2%, moisture content of 13.8% and viability of 98.9% (tetrazolium). Seeds were soaked in solutions of 2, 4 or 6g $NaCl\ l^{-1}$ for 2 days (d) at 25°C in the dark. Dry, untreated seeds served as the control.

After treatment, seeds were surface dried (Voetsch Apparatus, Germany) at 25°C for 5 hours (h) and sown in batches of 100 seeds in 1 L polystyrene trays over creased filter paper (Schuess, Germany). Each tray received 40 ml of a polyethylene glycol 10,000 (Fluka Chemie, Germany) solution with an osmotic potential (Ψ_s) of -10 bar to simulate drought. Trays were then arranged in germination cabinets (Conviron Industries, Canada) and exposed to one of five scenarios representing variation in timing of heat shock as follows:

Scenario 1: No heat shock (Control: Seeds exposed to a continuos 30°C temperature during the whole 10 d test period, hereafter termed No Shock)

Scenario 2: Seeds exposed to a 45°C heat shock on the first 6 hours of the second day after sowing, and to a constant 30°C temperature thereafter (termed 6^{th} hour)

Scenario 3: Seeds exposed to a 45°C heat shock from the 6^{th} to the 12^{th} hour of the second day after sowing, and to a constant 30°C temperature thereafter (termed 12^{th} hour)

Scenario 4: Seeds exposed to a 45°C heat shock from the 12^{th} to the 18^{th} hour of the second day after sowing, and to a constant 30°C temperature thereafter (termed 18^{th} hour)

Scenario 5: Seeds exposed to a 45°C heat shock from the 18^{th} to the 24^{th} hour of the second day after sowing, and to a constant 30°C temperature thereafter (termed 24^{th} hour)

Seeds were scored daily for their germination for the whole 10 d period and from this data, the final germination percentage (FGP), mean germination time (MGT) and germination index (GI) calculated (Benech Arnold *et al.*, 1991). On the 10^{th} day after sowing, 10 germinated seeds were randomly removed from each tray and their plumules and radicles excised, dried at 80°C for 3 d, weighed and averaged. This gave the dry weight of plumule (DWP), dry weight of radicle (DWR) and, by dividing the DWP by the DWR, the plumule: radicle ratio (PRR). Data from the six replications of each treatment (scenario combination were subjected to an analysis of variance procedure (ANOVA) (WEBER, E. and ANTONIO, C., 1999) and mean separation, after arsine transformation of germination percentages (HOULE, G. *et al.*, 2001), was executed by Duncan's Multiple Range Test ($\alpha = 0.05$) (SAS, 1989).

2.2 Effect of Heat Shock During the First Twelve Hours of the First, Second or Third Day After Sowing

The same seed treatments (Dry Control, 2, 4 and 6g $NaCl\ l^{-1}$) mentioned above were applied to CSV 15 seeds. All conditions were similar to the previous experiment (including the -10 bar drought stress) except that seeds were exposed to one of four heat shock scenarios during the first three days after sowing as follows:

Scenario 1: No heat shock (as decsribed above)
Scenario 2: Seeds exposed to a 45°C heat shock on the first 12 hours of the first day after sowing, and 30°C otherwise (termed Day 1)
Scenario 3: Seeds exposed to a 45°C heat shock on the first 12 hours of the second day after sowing, and 30°C otherwise (termed Day 2)
Scenario 4: Seeds exposed to a 45°C heat shock on the first 12 hours of the third day after sowing, and 30°C thereafter (termed Day 3)

Here, also, 100 seeds/tray were replicated six times, observed daily for 10 d and the FGP, MGT, GI, DWP, DWR and PRR determined and analysed as above.

3 Results and Discussion

3.1 Effect of Heat Shock During the Second Day After Sowing

The results of Table 1, showing the pooled effects of seed treatments, indicate that the 2g $NaCl\ l^{-1}$ treatment yielded the highest FGP. Although the dry control germinated to a greater extent than the 4 or 6g $NaCl$ treatments, all three salt concentrations (2, 4 and 6g) significantly increased the speed of germination by reducing the MGT. The GI, relating the final germination percentage with germination speed, was greater in 2g $NaCl$-treated seeds than in all other treatments, which did not significantly differ from each other. All three salt treatments gave greater DWP and DWR values than their untreated counterparts, but the PRR, did not differ between treated and untreated seeds (Table 1).

Timing of the 45°C heat shock did not clearly affect germination in the way treatments did. Whether it was administered on the 6^{th}, 12^{th} or 24^{th} hour of the second day after sowing, heat shock did not modify the FGP, its speed or index (data not shown). The DWP and DWR were also unaffected. However, heat shock on the 18^{th} hour produced a lower FGP than that on the 6^{th} or 12^{th} hour, and a lower GI than all other timings (No Shock, 6^{th}, 12^{th} or 24^{th} hour) (data not shown). The DWP was not clearly affected by heat shock timing, but shock on the 12^{th} hour gave higher DWP values than the

Table 1: Effect of seed treatments on germination and seedling characteristics of sorghum CSV 15 under various heat shock scenarios and drought

Seed Treatment (g $NaCl$/l)	FGP (%)	MGT (day)	GI	DWP (mg)	DWR (mg)	PRR
0 (Dry Control)	89.0 b	3.4 a	670.0 b	2.9 c	1.3 c	2.2 a
2	94.3 a	2.4 c	805.6 a	4.4 a	2.3 a	1.9 a
4	80.6 c	2.9 b	650.1 b	4.2 ab	1.9 b	2.2 a
6	81.0 c	2.4 c	690.2 b	3.9 b	1.8 b	2.2 a

Means in columns followed by similar letters are not significantly different according to Duncan's Multiple Range Test ($p \leq 0.05$). FGP: Final Germination Percentage, MGT: Mean Germination Time, GI: Germination Index, DWP: Dry Weight of Plumule, DWR: Dry Weight of Radicle and PRR: Plumule: Radicle Ratio.

No Shock scenario. The No Shock and 6^{th} hour shock scenarios gave lower PRR values than the 12^{th}, 18^{th} or 24^{th} hour shock treatments.

Interactive analysis exhibited the same trend, with the 2g $NaCl\ l^{-1}$ treatment being superior to other seed treatments and the 18^{th} hour shock event timing exhibiting partial sensitivity (Figs. 1a-c and 2a-c).

3.2 Effect of Heat Shock During the First Twelve Hours of the First, Second or Third Day After Sowing

All three salt treatments increased the speed of germination, with the 2g $NaCl$ treatment yielding the highest GI, DWP and DWR (data not shown). Seeds treated with 2g $NaCl$ also exhibited a higher FGP than untreated or 6g $NaCl$-treated seeds, but the PRR was not affected by seed treatments. Analysis of the effects of heat shock scenarios (data not shown) revealed a lower FGP for non-shocked and Day 1-shocked seeds than Day 2 or 3-shocked ones. The MGT was not affected by shock treatment, but Day 1-shocked seeds gave the lowest GI and PRR. DWP did not differ among shock treatments, but the DWR values of non-shocked seeds were lower than those of Day 1 or Day 2-shocked counterparts.

The results of interactive analysis of seed treatment (heat shock revealed that the FGP (Fig. 3a), in the case of 6g $NaCl$, was lower when seeds were not exposed to heat shock than when a shock was imposed on the 1^{st}, 2^{nd} or 3^{rd} days after sowing. This trend, although also detected in the 4g $NaCl$ treatment, was not statistically significant in the latter. No significant differences were observed between the FGP of seeds at one particular treatment when combined with the four shock scenarios (Fig. 3a). The MGT was also not affected by treatment (shock combinations (Fig. 3b), but the GI of dry, untreated seeds dropped as heat shock was administered (Fig. 3c). The greatest drop in GI was observed when untreated seeds were shocked on the first day after sowing. Salt-treated seeds, on the other hand, were either unaffected by shock (in the case of 2g $NaCl$) or their GI increased as shock was applied (in the case of 6g $NaCl$) as observed in Figure 3c. Similar behaviour was noted in the DWP. Dry, untreated seeds not exposed to shock attained a DWP of 2.4 mg, whereas when shock was applied on the first day after sowing, this dropped to 0.7 mg (Fig. 4a). Seeds treated with 2g $NaCl$ gave 3.2 mg DWP values when non-shocked and 4.4 mg when shocked on the first day after sowing, whereas 6g $NaCl$ yielded 2.3 mg and 2.2 mg values, respectively (statistically insignificant differences) (Fig. 4a).

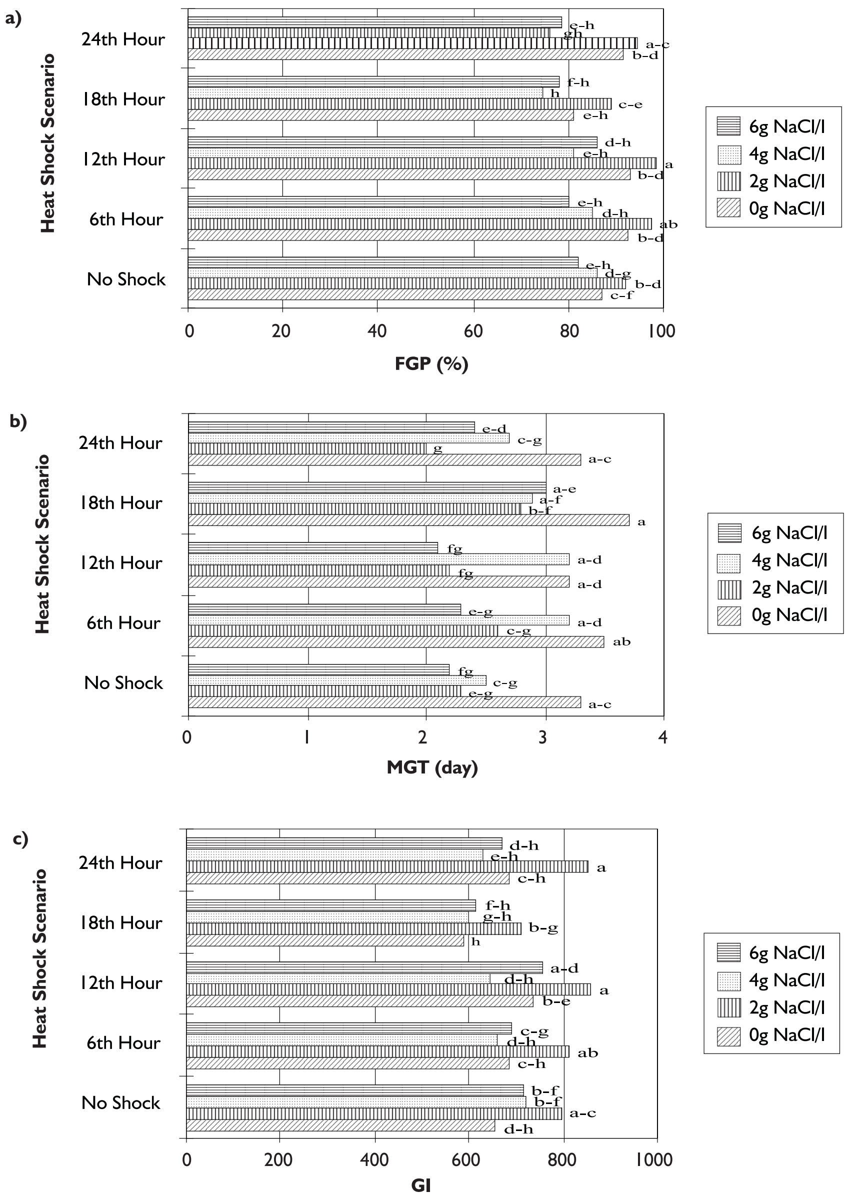
The DWR was modified by seed treatment and heat shock in another way. Here, dry, untreated seeds responded to shock by increasing growth (and thus the dry weight) of plumules. This increase as a response to heat shock was observed in all four seed treatments at all three heat shock timings (Day 1, 2 or 3) as illustrated in Figure 4b. There were, however, no significant differences in the DWP between heat shock timings themselves except in two cases. Seeds treated with 2g $NaCl$ exhibited their highest DWR when shocked on Day 1, whereas 6g $NaCl$-treated seeds gave the highest DWR when shocked on Day 2 (Fig. 4b). Though not always significantly, the greatest drop in the PRR was observed when seeds were shocked on the first day after sowing (Fig. 4c). This drop was statistically significant in untreated and 6g $NaCl$-treated seeds, and meant that heat shock caused a change in the balance of shoots and roots in favour of the latter.

In this investigation, $NaCl$-based seed treatments increased the speed of germination, the DWP and the DWR. The 2g $NaCl$ treatment gave the highest FGP and GI, but no differences were detected between seed treatments regarding the PRR.

In previous work (KADER, M., 2001; KADER, M. and JUTZI, S., 2001), the most sensitive period to heat stress was determined to be the second day after sowing. Thus, in this investigation, heat shock was applied at four different times within this second day in an attempt to pin-point the most susceptible period during this phase. Results revealed that the timing (between the 6^{th} and 24^{th} hour of the second day after sowing) of heat shock did not clearly affect germination or seedling growth in a stepwise manner. Rather, the 18^{th} hour of the second day yielded lower FGP and GI values than the 6^{th} or 12^{th} hour but not lower than the 24^{th} hour. In outlining the phases of germination in such a way, it is assumed that susecptibility to heat stress in sorghum seeds starts at or after the 18^{th} hour on the second day after sowing. However, "pure" heat stress applied without drought ($\Psi_s = 0$ bar) is different from a combined water deficit/ high temperature stress. Here, heat shock (45°C) was accompanied by a -10 bar drought stress. Water and temperature interact, such that a seed threshold water potential, for example, depends largely on temperature and *vice versa* (AL-MUDARIS and JUTZI, 1998b; KADER, M. and JUTZI, S., 2001).

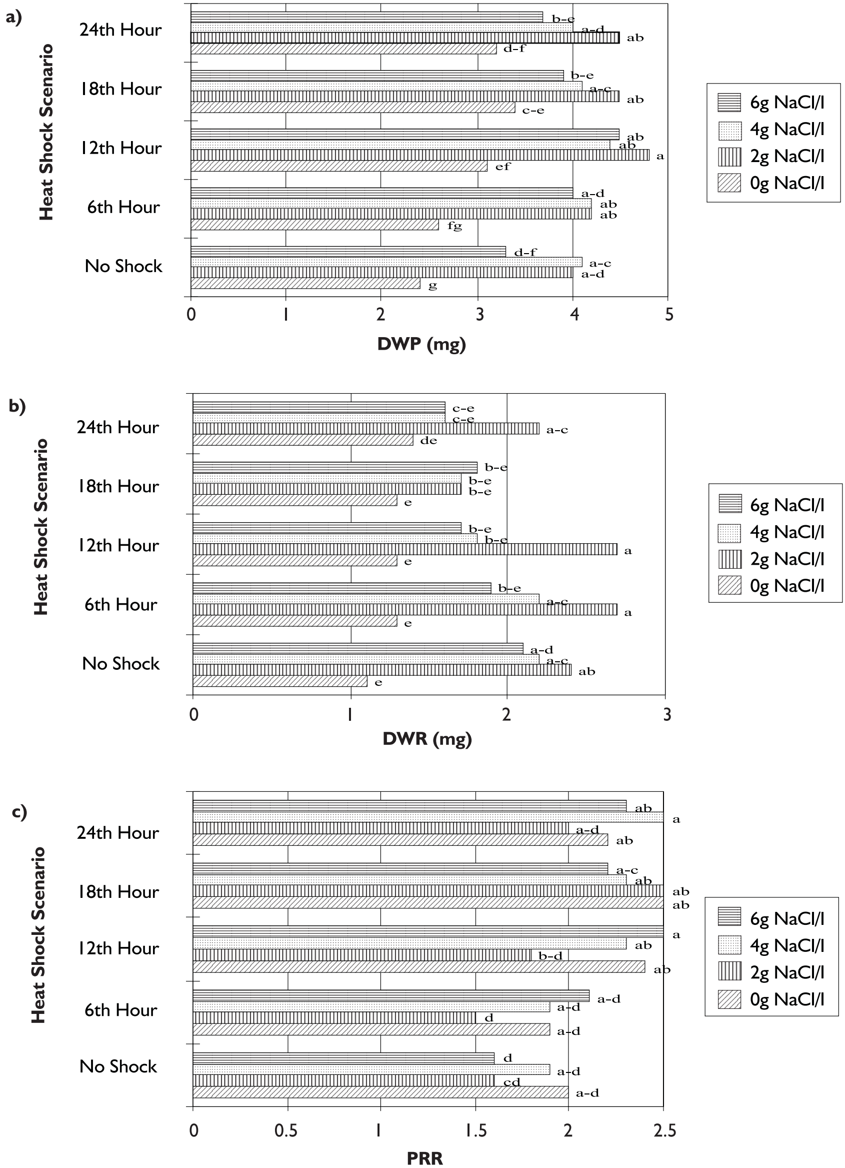
When heat shock was imposed on the first, second or third days after sowing (accompanied by -10 bar drought stress) the most sensitive phase, in terms of the GI, was not the second day (AL-MUDARIS and JUTZI, 1998c), but rather the first day. We suspect, then, that once exposed to combined stresses, the sensitivity of a seed to the environment is realised earlier in its seed-bed life cycle than when heat alone or drought alone are imposed upon it. This may be due to the fact that drought affects certain enzymes (e.g. glutamine synthetase essential for germination) in another way than heat stress (SUN, W. and LIANG, Y., 2001).

Figure 1: Interactive effects of seed treatment and heat shock scenarios on (a) the final germination percentage (FGP), (b) mean germination time (MGT) and (c) germination index (GI) of sorghum CSV 15 seeds



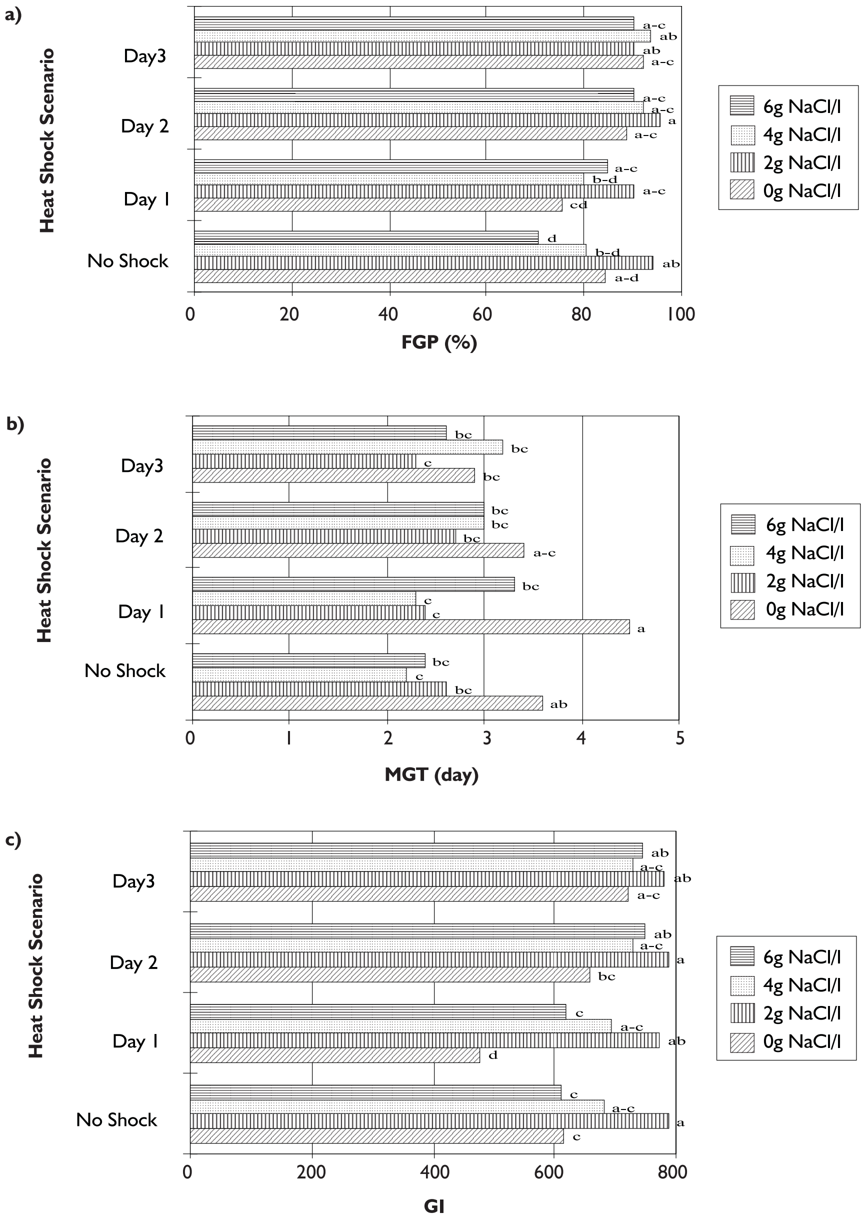
Bars having similar letters represent means that are not significantly different according to Duncan's Multiple Range Test ($p \leq 0.05$).

Figure 2: Interactive effects of seed treatment and heat shock scenarios on (a) the dry weight of plumule (DWP), (b) dry weight of radicle (DWR) and (c) plumule:radicle ratio (PRR) of sorghum CSV 15 seedlings



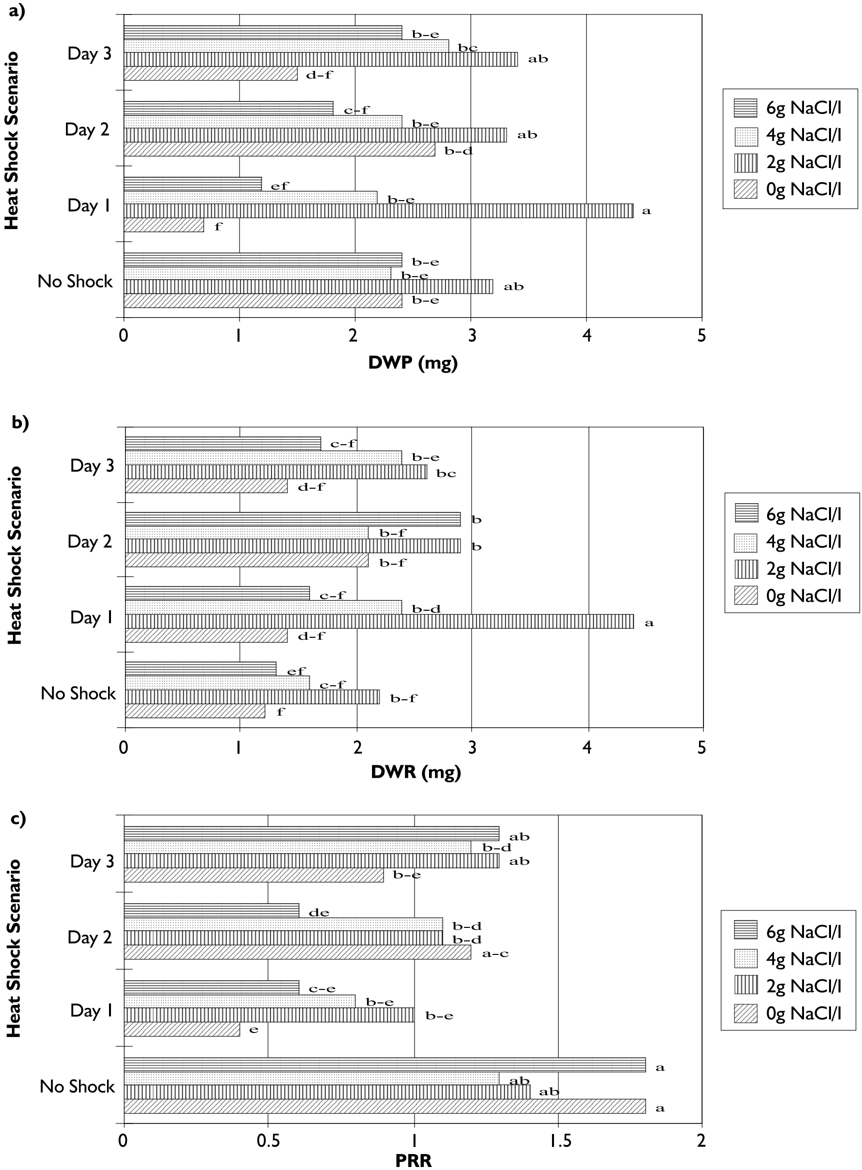
Bars having similar letters represent means that are not significantly different according to Duncan's Multiple Range Test ($p \leq 0.05$).

Figure 3: Interactive effects of seed treatment and heat shock scenarios during the first three days after sowing on (a) the final germination percentage (FGP), (b) mean germination time (MGT) and (c) germination index (GI) of sorghum CSV 15



Bars having similar letters represent means that are not significantly different according to Duncan's Multiple Range Test ($p \leq 0.05$).

Figure 4: Interactive effects of seed treatment and heat shock scenarios during the first three days after sowing on (a) the dry weight of plumule (DWP), (b) dry weight of radicle (DWR) and (C) plumule: radicle ratio (PRR) of sorghum CSV 15



Bars having similar letters represent means that are not significantly different according to Duncan's Multiple Range Test ($p \leq 0.05$).

Such an interaction, where germination differs at a fixed drought level with differing temperatures or *vice versa*, has been reported for other species (De Castro *et al.*, 2000; Tigabu, M. and Oden, P., 2001). The timing of susceptibility or tolerance to heat stress is, thus, apparently affected by such an interaction.

Genotypic differences in maximum percentage germination at high temperature have been proposed to be best detected after 24 h of sowing (Johnston, M. *et al.*, 2002). It is also suggested that seeds are more sensitive to high temperature during the first 12 h of the first day after sowing than the second 12 h. This timing is highly correlated with the formation of Heat Shock Proteins within the seed (Johnston, M. *et al.*, 2002). Howarth, C. (1989) documents that a characteristic set of heat shock proteins (HSPs) is synthesized as a result of sudden high temperature stress, whereas "normal" proteins are synthesized in decreased amounts or cease to be synthesized. He described two major categories of HSPs; high molecular weight (HMW) proteins, greater than 60 kDa in size, and low molecular weight (LMW) proteins, less than 30 kDa in size. Sorghum seeds (Howarth, C., 1989) are able to synthesize HSPs during the first 8 h of imbibition. The involvement of RNA (which is also heat-sensitive) in such a phenomenon has also been established (Howarth, C., 1990). As a result, we propose the whole 24-42 h phase of germination to be sensitive to heat, or heat + drought stress.

Although hydro priming (osmotic treatment) has been reported to increase tolerance of seeds to high temperature (Cheng and Bradford, 1999) and alleviate thermodormancy (Lima, W. *et al.*, 2001), its effectiveness under non-stress conditions depends on other factors. Part of the alleviating effect may come from the fact that seed priming involves biochemical or biophysical processes leading to a rejuvenated and enduring seed population (Warren, J. and Bennett, M., 1999). In sorghum, the response to $NaCl$ seed treatments under heat stress is such that the greater the stress (in this case heat), the lower the reduction in germination caused by $NaCl$ (Kader, M., 2001). Therefore, the reasons for lower FGP values under non-shock conditions can be understood.

The relationship between radicle growth, PRR and stress, yielded interesting observations in this investigation. The DWR values of non-shocked seeds were lower than those shocked on the first and second days after sowing, thus confirming our earlier speculation that one of the seed's responses to stress is manifested in producing larger radicles (later on larger root sytems).

Practical considerations in the field should take into account not just the timing of a "sensitive" phase to heat, but the level of drought in the soil, since, at a wide temperature range, germination, which is influenced by temperature, is retarded by rises in the osmotic potential (De Castro *et al.*, 2000). Also, increasing the supply of water in the field under heat conditions can restrict the supply of oxygen that is necessary for germination. Oxygen is sparingly soluble and its solubility decreases with increasing temperature, whereas the metabolic demand for this gas increases with temperature (Benjamin, 1990).

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