Journal & Proceedings of the Royal Society of New South Wales, Vol. 134, p. 79–88, 2001
ISSN 0035-9173/01/020079–10 $4.00/1

Heat Shock Events, Inhibition of Seed Germination and the Role of Growth Regulators in Stress Alleviation

MOHAMAD A. KADER

Abstract: The timing of heat stress after sowing is crucial in the success of pearl millet crops. Several heat shock events were evaluated and the impact of seed treatments on germination was investigated. Segmenting seed treatments into phases and sequencing growth regulators with water was also evaluated. Seven growth regulator-based seed treatments were applied to pearl millet seeds with the goal of improving the germination and early seedling growth under these heat shock events. Both gibberellic acid (GA_3) and kinetin were sequenced with water in one or two cycles (growth regulator/water) for 4 hours. Otherwise, seeds were soaked in water alone for 4 hours. Heat shock (46°C) was administered on the first three days after sowing seeds, the fourth, the fifth or sixth day and in alternating form (shock/no shock). Results revealed that sequencing growth regulators with water advanced germination to a greater extent than growth regulators alone. Seed treatments increased the speed of germination over controls and the first three days after sowing were more sensitive to heat shock than days 4, 5 and 6. The physiology of seed response to heat shock is discussed.

Keywords: heat, germination, growth, stress

INTRODUCTION

Pearl millet (*Pennisetum gluacum* L. R. Br.) is a staple grain source in the arid tropics and subtropics. It is similar to maize in its varying uses and acts as both a food and fodder source. Environmental stresses, primarily limited moisture content and supra-optimal temperature, restrict successful seed germination and plant establishment of pearl millet in arid and semi-arid regions of the world. Soil temperature is an important physical property that affects evaporation from the soil surface, soil moisture, seed imbibition (McCarty, 1992; Hardegree, 1994; Horne and Kahn, 2000), plant development and water movement (Mathan and Natesan, 1989). The temperature of the first two to three centimeters of the soil, which constitutes the seedbed of pearl millet, periodically reaches levels considerably higher than air temperature (Laude et al., 1952; Noe and Zedler, 2000) thus affecting seed performance. Studies on the effect of temperature on germination in the field are somewhat difficult to implement and so investigations are usually done in water baths or sand tables set at different temperatures (Clegg and Eastin, 1978). A seed is, however, usually exposed to varying temperatures (Cornett et al., 2000) during the course of the day ranging anywhere between minimum, optimum or maximum temperatures for germination, changing as time goes by (Flower et al., 1990). The faster germination and emergence occur, the less the time a seed will be exposed to such fluctuations and the more likely it is to succeed in emergence and plant establishment.

Previous studies on the germination of pearl millet and sorghum have shown seed priming treatments to improve germination under drought stress, but not under heat stress (Al-Mudaris and Jutzi, 1997). The objective of this investigation was to test the influence of timing of heat shock on germination of three pretreated and stored pearl millet genotypes and to test the impact of various heat shock timings/events on treated and untreated seeds.

MATERIALS AND METHODS

Heat Shock During the First Three Days After Sowing

The seeds of pearl millet variety Nokha, a local landrace grown by farmers near Nokha, Bikaner, in the Indian state of Rajasthan, were treated in one of seven ways as shown in Table 1. Nokha is a photosensitive pearl millet hybrid that is used for food and fodder (International Crops Research Institute for the Semi Arid Tropics ICRISAT, personal communication). Seed lots were obtained from ICRISAT and tested following International Seed Testing Association (ISTA) guidelines (ISTA, 1993) and showed germination percentages of 98%, 1000 seed weight of 7.4 g, moisture content of 14% and viability (tetrazolium) of 99.3%.

Seed treatments were administered by wrapping seeds in cheese cloth, tieing the end with a string and lowering them into the treatment solution/s. Growth regulators GA_3 and kinetin (Sigma Chemical, USA) were dissolved in 5% acetone and mixed with distilled water to achieve 200 ppm (200 mg/l) of GA_3 and kinetin, respectively. Water-soaking involved distilled water with 5% acetone added to it to account for any possible acetone effect. In sequential treatments of growth regulators and water, pouches were lowered in one solution, taken out and rinsed in distilled water and lowered in the next solution. All treatments took place at ambient temperatures of 22–25°C under daylight conditions. Relative humidity (RH) in the laboratory was 51% (Schulter Thermohygrograph, Germany) and all treatments were conducted in 3-litre glass beakers.

After treatment, seeds were blotted on Whatman No. 1 filter paper and dried back in a reverse cycle cabinet (Conviron Industries, Canada) at 25°C for 16 hours (h). Thereafter, they were stored in paper bags at 20°C and 50–55% RH for 4 months in a dark seed store. At termination of the storage period, seeds were retrieved and sown in 1-litre polystyrene trays between two layers of creased, moistened filter paper (Schuess, Germany). Two hundred seeds were sown per tray and each treatment combination replicated 4 times (7 seed treatments × 4 heat shock scenarios × 4 replicates). Trays were arranged in a Randomized Complete Block Design (RCBD) inside growth chambers (Hereaus Voetsch, Germany). Germination was then undertaken at one of four heat shock regimes (Table 2). These were designed to expose the seeds to a heat shock of 46°C either on the first, first and second, or first, second and third days after sowing (DAS) to test post-shock responses.

Treatment	Description
W	Wet Control: Seeds soaked for 4 hours (h) in distilled water.
W-K-1	Seeds soaked for 1 h in water, 1 h in kinetin (200 mg/l), 1 h in water and, finally, 1 h in kinetin.
W-K-2	Seeds soaked for 2 h in water then for 2 h in kinetin.
K	Seeds soaked for 4 h in kinetin.
W-G-1	Seeds soaked for 1 h in water, 1 h in GA_3 (200 mg/l), 1 h in water and, finally, 1 h in GA_3.
W-G-2	Seeds soaked for 2 h in water then for 2 h in GA_3.
G	Seeds soaked for 4 h in GA_3.

Table 1. Soaks with growth regulators used to treat Nokha pearl millet seeds.

Regime	Details
HS 0	No heat shock (Control): Seeds germinated at a constant 30°C temperature for the whole 10 day period.
HS 1	Heat shock administered on the day of sowing with a temperature of 46°C for 24 h (total = 24 h). Thereafter, a constant 30°C was used till 10 DAS.
HS 12	Heat shock (46°C) administered on the first and second days after sowing (total = 48 h). Thereafter, a constant 30°C was used till 10 DAS.
HS 123	Heat shock (46°C) administered on the first, second and third days after sowing (total = 72 h). Thereafter, a constant 30°C was used till 10 DAS.

Table 2. Heat shock regimes applied to Nokha pearl millet seeds on the first 3 days after sowing (DAS).

Germination counts were taken daily for 10 days and from them the final germination percentage (FGP), mean germination time (MGT) and coefficient of velocity of germination (CVG) calculated. The CVG gives an indication of the rapidity of germination (Jones and Sanders, 1987). It increases when the number of germinated seeds 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. The fresh weight of plumule + radicle after separation from the seed (hereafter termed FWSD) was averaged for 20 seeds and recorded. All data were exposed to an analysis of variance (Weber and Antonio, 1999) after arcsine transformation of germination percentages (Yang et al., 1999; Houle et al., 2001), and mean separation conducted using the General Linear Model (PROC GLM) of the SAS® statistical package (SAS, 1989) at 5% probability.

Heat Shock on the Fourth, Fifth and Sixth Days After Sowing

Due to the fact that the first five to six days after sowing are the most sensitive to temperature fluctuations, in as far as the success or failure of germination is concerned, this test was designed to impose heat shock in the second half of this phase, namely days 4, 5 and 6 after sowing. The pearl millet hybrid ICMH 356 obtained from ICRISAT was treated in the same manner as Nokha in the previous experiment and exposed to four heat shock regimes (Table 3). ICMH 356 had germination, moisture and viability percentages corresponding to those of Nokha and a 1000 seed weight of 10 g. It is a short, grey coloured hybrid that is resistant to downey mildew and used as a source of grain. The same germination and growth parameters as above were employed. Statistical arrangements were similar to those of the first experiment.

Regime	Details
HS 0	No heat shock (Control): Seeds germinated at a constant 30°C temperature for the whole 10 day period.
HS 6	Heat shock (46°C) administered on the sixth day after sowing (total = 24 h). Thereafter, a constant 30°C was used till 10 DAS.
HS 56	Heat shock (46°C) administered on the fifth and sixth days after sowing (total = 48 h). Thereafter, a constant 30°C was used till 10 DAS.
HS 456	Heat shock (46°C) administered on the fourth, fifth and sixth days after sowing (total = 72 h). Thereafter, a constant 30°C was used till 10 DAS.

Table 3. Heat shock regimes applied to ICMH 356 pearl millet seeds on the fourth, fifth and sixth day/s after sowing (DAS).

RESULTS AND DISCUSSION

Heat Shock During the First Three Days After Sowing

When treatments were pooled over heat shock regimes, all six growth regulator seed treatments improved germination characteristics over controls. Seeds soaked in growth regulators germinated to a higher extent and at faster rates than untreated seeds. This was evident in the FGP, MGT and CVG values observed (Table 4). Sequencing growth regulators with water did not seem to affect the final germination percentage since hormonal treatments were similar to each other in this regard. Generally, GA_3 treatments gave earlier germination patterns that ended sooner. They also gave higher CVG values than controls, and, in some cases, than kinetin soaks. The fresh weight of seedlings was significantly affected by seed treatment. Growth regulator treatments induced larger and, thus, heavier plumules and radicles to form. The best enhancement of seedling growth was observed in seeds treated with W-G-2. Second best was W-G-1 followed by W-K-1 and W-K-2. Sequencing improved the performance of growth regulators in inducing growth (Table 4).

Heat shock regimes pooled over treatments affected the FGP and FWSD, but had no apparent effect on the speed of germination (Table 4). Heat shock in all three forms gave lower FGP values than the 30°C no-shock treatment. The longer the duration of this shock, the weaker and, thus, lighter in weight, were the seedlings produced (Table 4). Interactive analysis of seed treatments and heat shock regimes confirmed this (data not shown for brevity). Heat shock reduced germination and seedling growth, seed treatments improved performance, and sequencing was superior to continuous treatments.

Heat Shock on the Fourth, Fifth and Sixth Days After Sowing

Again, all six growth regulator treatments gave better germination characteristics, in terms of percentage and speed, than the water-soaked seeds (Table 5). Sequenced GA_3 increased the FGP and CVG and reduced the MGT greater than kinetin or unsequenced GA_3. Kinetin, on the other hand, was not affected by sequencing with all three kinetin treatment forms advancing germination over controls. The FWSD was not affected by seed treatment. An exception to this was lower FWSD values for seeds treated with GA_3 for 4 h (Table 5). Heat shock at all three timings significantly reduced the germination percentage but did not affect germination speed.

When heat shock was administered on the sixth day after sowing, it significantly reduced the fresh weight of seedlings to 140.3 mg from the 145.1 mg control (Table 5). However, as the timing of heat shock approached 4 DAS, and as its duration increased (HS 456), the FWSD dropped to 71.8% of that of the control (calculated from Table 5). The earlier the heat shock and the longer its duration, the less developed were the seedlings.

The two experiments reported above indicate that the heat sensitive phase of pearl millet germination is mainly in day 1 rather than days 3–5. The earlier the heat shock after sowing, the more its negative effects. Seed treatment with growth regulators helps in the advancement of seed germination. That GA_3 treatments induced earlier and more synchronous germination patterns is consistent with previous knowledge about the action of growth regulators (Eastwood et al., 1969; Hof and Saha, 1999; Rock and Ng, 1999; Christianson, 2000). It also confirms the results of Al-Mudaris and Jutzi (1997) where GA_3 was superior to kinetin in this advancement. This reveals that the storage of growth regulator-treated seeds seems not to adversely affect their performance.

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	FGP (%)	MGT (day)	CVG	FWSD (mg)
Seed Treatment				
W	62.8 b	2.9 a	34.3 c	103.3 f
W-K-1	80.9 a	2.3 b	43.7 c	115.3 c
W-K-2	76.2 a	2.1 bc	46.8 b	110.3 d
K	80.3 a	2.0 c	50.0 a	108.6 de
W-G-1	77.8 a	2.0 c	48.6 a	119.5 b
W-G-2	80.3 a	2.1 c	47.9 a	130.8 a
G	77.8 a	2.0 c	50.0 a	104.9 ef
Heat Shock Regime				
HS 0	85.5 a	2.1 a	46.8 a	132.0 a
HS 1	70.1 c	2.3 a	44.0 a	121.0 b
HS 12	77.6 b	2.2 a	46.4 a	109.0 c
HS 123	73.0 bc	2.2 a	46.4 a	91.5 d

Table 4. Effect of growth regulator seed soaks and heat shock regimes on germination and growth parameters of Nokha pearl millet. Seed treatment regimes are as shown in Table 1. Heat shock regimes are as shown in Table 2.

Means of treatment effects in columns followed by similar letters are not significantly different (alpha=0.05). The same applies to the means of heat shock regimes.

FGP: Final Germination Percentage, MGT: Mean Germination Time, CVG: Coefficient of Velocity of Germination and FWSD: Fresh Weight of Seedling (plumule + radicle).

	FGP (%)	MGT (day)	CVG	FWSD (mg)
Seed Treatment				
W	68.7 d	3.8 a	26.5 c	129.0 a
W-K-1	90.0 b	3.0 bc	33.3 b	131.6 a
W-K-2	87.5 b	3.0 bc	33.3 b	129.4 a
K	90.0 b	2.8 c	34.3 b	129.5 a
W-G-1	93.4 a	2.0 d	48.9 a	129.5 a
W-G-2	92.8 a	2.0 d	50.0 a	130.9 a
G	78.7 c	3.1 b	32.2 b	115.8 b
Heat Shock Regime				
HS 0	88.0 a	2.7 a	37.1 a	145.1 a
HS 6	85.5 b	2.8 a	37.1 a	140.3 b
HS 56	85.0 b	2.8 a	36.8 a	122.2 c
HS 456	85.0 b	2.8 a	36.5 a	104.3 d

Table 5. Effect of growth regulator seed soaks and heat shock regimes on germination and growth parameters of ICMH 356 pearl millet. Seed treatment regimes are as shown in Table 1. Heat shock regimes are as shown in Table 3.

Means of treatment effects in columns followed by similar letters are not significantly different (alpha=0.05). The same applies to the means of heat shock regimes.

FGP: Final Germination Percentage, MGT: Mean Germination Time, CVG: Coefficient of Velocity of Germination and FWSD: Fresh Weight of Seedling (plumule + radicle).

It is known that sufficiently high temperatures can inhibit germination or mitosis in non germinated seeds (Haber and Luippold, 1960) and induce stress and heat shock protein production (Hamilton and Coleman, 2001). Also known is that various forms of stress induce the production of abscicic acid (ABA) (Sebanek, 1992; Jacobs, 1998). Accordingly, studies on the interaction between growth regulators and seed germination have shown that cytokinins overcome the inhibitory action of abscisic acid (Thomas et al., 1975) and that ABA reduction leads to a changed hormonal balance (Farnsworth and Farrant, 1998). The application of exogenous GA_3 has also been proven to reverse physiological inhibition of seed germination (Kepczynski and Knypl, 1988) albeit on a species-specific basis (Arnold et al., 1996). The inhibition of seed germination in response to heat stress may have been the result of high ABA levels, low GA_3 and cytokinin levels or both. That growth regulator applications advanced germination over controls may be seen as a re-balancing of this hormonal shift in favour of germination promoters.

Sequencing growth regulators with water proved superior to constant growth regulator soaks in advancing germination. It may have evoked this effect through a late activation phase (Kepczynski and Knypl, 1988) where a lag phase is witnessed upon transformation from the growth regulator to water.

Bush (1996), studying the effect of GA_3 on wheat aleurone cells, found that GA_3 induced a steady-state increase in cytosolic calcium which is important for the primary response to GA (the production and secretion of hydrolytic enzymes) and subsequent germination. This increase was initiated within a few minutes of treatment with GA and was fully developed after 30–90 minutes. If this were the case in pearl millet, it would probably mean that the peak action of GA_3 existed in the first one to one and a half hours after initial soaking, and that the remaining treatment period (total treatment period was 4 h) acted in a purely physical form through loosening of the seed coat.

The effects of heat shock on germination of sorghum and millet seeds were clearly negative. Not surprisingly, 46°C given at any one of the first six days after seed sowing reduced germinative performance in the genotypes studied. The first day after sowing seems to be the most sensitive phase to heat shock, and consequently, when stressed at this particular time, seeds respond with a drastically reduced germination. Coincident with this reduction was the oozing of brown exudates from the seed and eventual deterioration. This was particularly clear in earlier stages of heat shock application. Similar exudate oozing has been reported in maize, rice, sorghum, soybean, sunflower, wheat and groundnut (Sweet and Bolton, 1979). This would mean that once reaching a particular hydration level - as happens after 25 h of imbibition - heat shock may prove deleterious to germination not only by affecting its physiological mechanism, but by inducing microbial deterioration. An earlier observation by Hunter and Erickson (1952) is the covering of seeds with mycelia of fungi and eventual decay in the soil environment under moisture stress conditions. Clearly, then, the earlier the heat shock, the more negative are the carry-over and side effects. This also agrees with the moisture stress scenarios reported by Al-Mudaris and Jutzi (1997) where drought on the first day after sowing carried effects over to post-stress stages and those of drought, and salinity stress studies (Olsson et al., 1996; Howard and Mendelssohn, 1999). Growth regulator treatments helped in alleviating heat shock, probably, as mentioned, by altering the hormonal balance between inhibitors and promoters of germination. However, even though other reports (Haber and Luippold, 1960) have confirmed this, they also state the possibility of loss of GA_3 activity at high temperatures.

Garcia-Huidoboro et al. (1982) reported failure of *Pennisetum typhoides* seeds to germinate at 47/16°C, and so the range of hormonal action seems to be limited. The speed of germination decreased as heat shock duration increased or its application shifted to earlier days after sowing. Although the response of seeds to temperature, with respect to germination speed, is linear up to the optimal germination temperature (Mc Ginnies, 1960; Hsu et al., 1984), it appears to drop as soon as the supra-optimal temperature range is entered. The base temperature for *Pennisetum americanum* seed germination has been reported to be around 8 to 11.5°C (Mohamed et al., 1988). Lines and hybrids of sorghum and pearl millet that are tropically adapted have been reported to have different base temperatures than temperately adapted ones (Maiti, 1996).

Our results are in line with those of Martin et al. (1935) and Macchia and Dinelli (1989) where temperatures higher than 40°C reduced sorghum germination due to a reversible strain which results from a reduction in the rate of chemical reactions and physical processes at extreme temperatures (El-kholy et al., 1997) and an altered moisture uptake by the seed (Seong, 1989). An interesting result in our work is that day 1 after sowing is more sensitive than subsequent days. Also, when seeds experience alternating temperatures in which the mean temperature exceeds the optimum, germination decreases with increase of mean temperature (Murdoch et al., 1989).

That optimal temperatures for germination and seedling growth differ is also important. Whereas germination may respond more favorably to 35°C, seedling growth is optimal at 25°C (Kader, unpublished data). This may be due to the fact that temperature is likely to affect seedling establishment by influencing the balance between photosynthesis and respiration (Bannister, 1978) in addition to coleoptile elongation (Carberry and Campbell, 1989) in a different way than that of its effect on the physiological induction to initiate germination. This supports the hypothesis of Ross and Hegarty (1979) that the process of the initiation of cell elongation during germination is under a separate metabolic control from elongation itself. The fact that heat shock reduced seedling growth may be due to the direct effects of temperature or to indirect side effects showing up later, even when seedlings are transported to more neutral temperatures as reported for *Phaseolus acutifolius* and *Phaseolus vulgaris* seedlings (Udomprasert et al., 1995).

CONCLUSIONS

In conclusion, it appears that growth regulator seed treatments may aid in mitigating the effects of heat shock on pearl millet seeds. The 46°C shock applied in this investigation lies close to the maximum temperature reported for other pearl millet cultivars (42.1 to 45.6°C) (Mohamed et al., 1988). In the field, the soil derives its heat from two main sources: direct radiation from the sun and by conduction from the interior of the earth. The soil surface temperature is lowest in the early morning and highest in the early afternoon (Maiti, 1996). If the seed escapes the first phase of its life in the seedbed (post day 1) without major injuries through oozing and deterioration, a better stand of plants may be expected.

ACKNOWLEDGEMENTS

The expert input of Professor Samuel Jutzi, Director, United Nations Food and Agriculture Organisation (FAO) - Animal Health Division, Rome is greatly appreciated. The advice of Profs. P. Harris, University of Wales and F. Ratunde, International Crops Research Institute is acknowledged as is the financial support from SUET Seed, Germany. The Plant Physiology Facility was kindly provided by the University of Kassel, Witzenhausen, Germany.

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Mohamad A. Kader
Director, Consultica Worldwide
PO Box 3089 Tamarama NSW 2026
Australia
m.kader@mbox.com.au

(Manuscript received 16.10.2001)
(Manuscript received in final form 11.01.2002)