

# Unlocking basal and acquired thermotolerance potential in tropical sorghum

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## Abstract

Basal and acquired thermotolerance of 50 elite tropical sorghum genotypes was assessed in seedlings. Two sets of each assay were conducted following a split plot in a Completely Randomised Design replicated three times in two heat stress treatments in separate incubators. Coleoptile length was measured before and after heat treatments, and the differences were subjected to analysis of variance for heat treatments, genotypes and their interactions. Highly significant differences ( $p < 0.001$ ) were observed between heat treatments, genotypes, and their interactions for both basal and acquired thermotolerance assays, signifying adverse effects of heat stress and the existence of genetic diversity in the thermotolerance of the assessed genotypes. Popular varieties 'Macia' and 'SV4' did not feature among the top performers for both forms of tolerance, indicating the risk subsistence farmers relying on them are to heat stress. Two genotypes were consistently amongst the top ten performers in terms of basal thermotolerance in the two sets, these are genotypes NPGRC1704, and IS24426. Genotypes NPGRC3093, and IS24272 consistently demonstrated superiority in acquired thermotolerance. Genotypes NPGRC1704, IS9567, NPGRC1197, NPGRC1868, and NPGRC1782 exhibited potential in both basal and acquired thermotolerance. The identified genotypes may be used as potential donors in crop improvement programs that seek to improve thermotolerance in sorghum.

**Citation:** Ndlovu E, Maphosa M, Van Staden J. 2024. Unlocking basal and acquired thermotolerance potential in tropical sorghum. *Technology in Agronomy* 4: e026 <https://doi.org/10.48130/tia-0024-0023>

## Introduction

The recent drastic and unforeseen changes in climatic patterns, especially recurrent heat waves in sub-Saharan regions, calls for a revolutionized focus on crop improvement. Temperature and rainfall are one of the two most important cardinal environmental factors which affect the growth and development of plants<sup>[1,2]</sup>. All plant species have specific temperature thresholds for different phases of growth and development<sup>[3,4]</sup>. An increase in temperature beyond critical threshold levels stimulates the production of reactive oxygen species (ROS) in plant cells<sup>[3]</sup>. The resultant imbalance in the level of production and removal of the ROS in plant cells results in oxidative stress, thus the emanation of heat stress<sup>[4]</sup>. Heat stress destabilizes biological molecules, structural stability, and enzymatic reactions which are key for the normal functioning of most biochemical and physiological reactions in plant cells<sup>[1]</sup>. The accumulation of ROS induced by extreme temperatures is more detrimental to delicate stages of growth and development of plants, particularly germination and seedling establishment<sup>[5]</sup>.

In the wake of reports that soil temperatures can reach 50 °C at midday in semi-arid and arid regions<sup>[4]</sup>, it is becoming clear that crop establishment and growth in such areas are at risk. This will worsen the already dire situation for the resource poor farmers whose agricultural practices and means are climate dependent which of late has, however, proved variable and unreliable<sup>[6]</sup>. In field crops, the only way to reduce soil temperatures is through irrigation which is beyond reach for many smallholder farmers in marginal areas of semi-arid tropics of

Africa. This calls for increased efforts in the exploration of resilient genotypes of known robust graniferous crops like sorghum so that their production can continue under sub-optimal conditions to meet the ever-increasing food demand.

The widely accepted range of optimum temperatures for sorghum growth and development is between 20 and 32 °C<sup>[7]</sup>. In a study by Peacock<sup>[8]</sup>, seedling emergence in sorghum failed at 45 °C. Similarly, in maize, coleoptile growth came to a halt at 45 °C<sup>[9]</sup>, thus coleoptile elongation has been used as an indicator for heat stress tolerance<sup>[10–12]</sup>. Even pearl millet, a known hardy crop that is a good candidate to complement and/or substitute sorghum, is equally affected by heat stress at germination and seedling establishment<sup>[6,12]</sup>. However, genotypic differences in inherent tolerance and natural acclimation to temperature extremes and fluctuations exist in sorghum<sup>[11]</sup>, hence efforts can be directed to promising genotypes among the existing large populations. Thus the need for rapid and low-cost but effective techniques for evaluating large populations of genotypes for acquired and basal thermotolerance<sup>[12]</sup>.

Basal thermotolerance is the inherent ability of a plant to survive heat stress due to evolutionary adaptation<sup>[3]</sup>. While the ability to survive potentially lethal extreme temperatures through prior exposure to mild heat stress is termed acquired thermotolerance<sup>[13]</sup>. Acquired thermotolerance is measured in the laboratory by comparing the growth of germinants that have received prior exposure to supra-optimal temperatures to those that are directly exposed to high temperatures without acclimatization<sup>[14]</sup>. Controlled heat induction in the laboratory

can be used to mimic field shocks or gradual increase in soil temperature<sup>[12]</sup>. Some genotypes possess higher basal than acquired thermotolerance<sup>[15]</sup>. Acquired thermotolerance is controlled by genes that code for principal regulatory factors called heat shock proteins (HSPs)<sup>[10]</sup>. HSPs are molecular chaperones that are involved in the reduction of ROS, and repairing and reconfiguration of proteins which offers some level of protection to heat stress in plants<sup>[7,16,17]</sup>. Activation of such genes when plants are gradually exposed to heat stress results in increased synthesis of several metabolites, and proteins which confers some level of protection<sup>[3]</sup>. Accordingly, this study aimed at identifying sorghum genotypes with potential basal and acquired thermotolerance from a pool of genotypes that have never been tested obtained from the local and international gene banks with a view of using them as a tool to minimize sorghum losses due to heat stress.

## Materials and methods

### Plant material

Fifty diverse sorghum genotypes of sorghum were selected from a pool of 300 accessions obtained from the Genetic Resources and Biotechnology Institute and International Crop Research Institute of the Semi-Arid Tropics (ICRISAT) in Zimbabwe, multiplied and characterized through preliminary studies at Lupane State University experimental plots located in semi-arid part of Zimbabwe. The genotypes used in this study were selected based on yield potential and desirable morphological traits (Supplemental Table S1). Lupane State University plots are characterized by deep Kalahari sands with an annual rainfall average of 450–650 mm and temperature range of 10 to 35 °C. The temperatures at the study site ranged from 19.8 to 39.9 °C during the study period (Table 1).

### Germination procedure and experimental design

Twenty seeds for each genotype were surface sterilized for 5 min using 1% sodium hypochlorite, thoroughly rinsed three times in deionized water and germinated in Petri dishes lined with double Whatman No. 2 filter papers moistened with deionized water in a growth chamber at 30–35 °C. Petri dishes were placed in a completely randomized design with three replicates in an incubator and two sets of the experiment were done in tandem.

### In vitro basal thermotolerance of sorghum germplasm

Five healthy two-day-old seedlings were randomly selected and exposed to heat shock treatment at 50 °C for 10 min in an incubator and then allowed to recover at 30–35 °C for 36 h in a growth chamber. Control treatments were not exposed to the heat shock treatment. The experiment was arranged following a split plot in Completely Randomised Design (CRD 50 × 2 × 3);

**Table 1.** Rainfall (mm) and temperature (°C) data during the study period season (2022/23) at Lupane State University.

Season		Months			
		Oct	Nov	Dec	Jan
2022/23	Mean minimum temperature	26.6	26.1	24.4	19.8
	Mean maximum temperature	39.9	37.4	31.9	28.1
	Total rainfall	9.6	164	75	161

Source: Lupane State University weather station.

where 50 genotypes were replicated three times in two separated heat stress treatments. Changes in coleoptile length after 36 h for the seedlings that were exposed to heat shock treatments as well as those not exposed to heat shock were measured using a digital Vernier caliper and differences were determined.

### Acquired thermotolerance of sorghum germplasm

Five healthy two-day-old seedlings were exposed to heat stress treatment by gradually increasing the temperature in the growth chamber from 30 to 5 °C every hour until it reached 45 °C and was kept constant at that temperature for 1 h. Then, the seedlings were allowed to recover at 30–35 °C for up to four days. Seedlings were then exposed to a second heat shock at 50 °C for 10 min in a growth chamber and then allowed to recover again at 30–35 °C for up to four days. Control treatments were not acclimatized through gradual heat shock treatments but were exposed to a heat shock treatment at 50 °C. Similarly, the experiment was arranged following a split plot in Completely Randomised Design (CRD 50 × 2 × 3); where 50 genotypes were replicated three times in two separate heat stress treatments. Coleoptile length was measured before and after heat treatments using a digital Vernier caliper and the differences were determined.

### Statistical analysis

In the assessment of basal and acquired thermotolerance, quantitative data on coleoptile length changes was subjected to a two-way analysis of variance (ANOVA) following a CRD in Genstat statistical package 14<sup>th</sup> edition, to determine significant differences in means for the two heat treatments, 50 genotypes and their interactions. Means were compared at 95% level of significance and separated using Bonferroni's test where significant differences were observed. Data was subjected to the tests of assumptions of ANOVA before being subjected to the F-test.

## Results

### Response of seedlings for 50 sorghum genotypes to heat shock and acclimatization treatments

Assessment of 50 tropical sorghum accessions for basal and acquired thermotolerance using coleoptile elongation as an indicator revealed that heat shock of 50 °C, just for a short period of time suppressed coleoptile elongation in sorghum emergents while prior exposure of seedlings to gradually increasing temperatures up to 45 °C reduced the effects of heat shock as indicated by the extent of coleoptile elongation. Heat shocking of sorghum emergents significantly reduced coleoptile elongation ( $p < 0.001$ ) as demonstrated by the F-test results for both sets of basal and acquired thermotolerance (Table 2). Significant variability in sorghum genotypes that were tested for basal and acquired thermotolerance at germination was also observed in the two sets of experiments for each test. The differential response of the assessed genotypes to heat shock and acclimatization treatments was demonstrated by the highly significant interaction of genotypic factors and the heat stress treatments in both sets of basal and acquired thermotolerance tests (Table 2). In both basal and acquired thermotolerance tests, temperature had the greatest effect as indicated by large mean of square errors (Table 2).

## Thermotolerance in sorghum

**Table 2.** Analysis of Variance for basal and acquired thermotolerance in diverse tropical sorghum accessions done in two sets.

Source of variation	DF	Basal	Acquired
		Mean squares	Mean squares
Set 1			
Temperature (T)	1	3,987.4***	11,556.2***
Genotype (G)	49	586.7***	30.9***
G × T	49	282.2***	49.8***
Error	1,400	119.2	6.5
Set 2			
Temperature (T)	1	13,700.5***	5,441.1***
Genotype (G)	49	50.6***	139.9***
G × T	49	32.5***	95.0***
Error	1,400	6.7	16

DF = degrees of freedom, \*\*\* significant at < 0.001.

In both sets of the basal thermotolerance assay heat shocking of sorghum emergents significantly reduced coleoptile elongation by 13.7% and 31.9%, respectively (Table 3), when compared to their counterparts that were not exposed to heat shock. Acclimatization of sorghum emergents reduced the effects of heat shock, as demonstrated by significantly lower coleoptile elongation in non-acclimatized sorghum emergents in the two sets of the experiment by 62.1% and 52.5% respectively when compared to the acclimatized emergents (Table 3).

### Differential expression of basal thermotolerance in elite tropical sorghum genotypes

Following significant interactions of genotype and heat treatments for coleoptile elongation in sorghum emergents conferring differential expression of basal thermotolerance their means were separated using the Bonferroni's test. The top ten and five least performing genotypes in terms of coleoptile elongation were identified and are presented in Table 4 for the two sets of the experiment. Genotypes NPGRC1704 and IS24426 were consistently amongst the top ten performers in terms of basal thermotolerance in the two sets of the experiment (Table 4). 'Macia' a commercial check variety was amongst the top ten performers. In the first set only the two least performing genotypes namely IS30164 and NPGRC3127 were significantly different from the top two best performers in basal thermotolerance (Table 4).

In set two all the five least performers were significantly different from the top three performers (Table 4). Only one genotype NPGRC3127 consistently appeared in the least five performers in both sets of basal thermotolerance tests. 'SV4' a commercial check variety had the lowest mean change in coleoptile length in set 2, indicating a lack of basal thermotolerance when compared to the tropical sorghum genotypes that were assessed in the current study.

### Differential expression of acquired thermotolerance in tropical sorghum genotypes

Genotypes NPGRC3093, and IS24272 consistently demonstrated superiority in acquired thermotolerance in two sets of the test as confirmed by the separation of means using the Bonferroni's test (Table 5). No genotype showed consistency in the least performers for the two sets. Interestingly, several genotypes that were among the least performers in basal thermotolerance showed superiority in acquired thermotolerance. These genotypes are NPGRC1704, IS9567, NPGRC3093, IS12391,

**Table 3.** Mean comparison of coleoptile changes for heat treatments of sorghum emergents indicating basal and thermotolerance in two sets of each experiment.

Treatments	Basal thermotolerance		Acquired thermotolerance	
	Set 1	Set 2	Set 1	Set 2
Heat shocked	20.54 <sup>b</sup>	12.91 <sup>b</sup>	3.40 <sup>b</sup>	3.45 <sup>b</sup>
Non-heat shocked	23.80 <sup>a</sup>	18.96 <sup>a</sup>	8.96 <sup>a</sup>	7.26 <sup>a</sup>
LSD (5%)	1.11	0.26	0.26	0.41

Non heat shock for acquired thermotolerance means genotypes were acclimatized through incremental temperature increase. Means with similar superscripted letters in the same column were significantly different at ( $p < 0.05$ ) measured as coleoptile length in millimeters.

and IS9548 (Tables 2 & 3). Genotype NPGRC 3127 which was the only genotype that consistently showed a lack of basal thermotolerance (Table 4) and also showed a lack of thermotolerance in one of the sets for the acquired thermotolerance experiment (Table 5).

## Discussion

The study established the existence of basal and acquired thermotolerance in sorghum as previously observed in several other studies<sup>[1,11,12]</sup>. Coleoptile length was successfully evaluated as an indicator for both basal and acquired thermotolerance in heat-shocked and non-heat-shocked treatments, and between acclimatized and non-acclimatized treatments respectively. In a similar study by Arya et al.<sup>[18]</sup>, germination and coleoptile elongation was reduced at temperatures above 35 °C in pearl millet which is a hardy crop that can match or surpass sorghum. High temperatures that were used to heat shock seedlings at 50 °C in this study mimic the soil temperatures in agronomic habitats of crop plants in semi-arid and arid tropics which may exceed 50 °C as postulated by Yadav et al.<sup>[19]</sup>. It is noteworthy that the effects of heat stress are organ and stage of growth specific<sup>[20]</sup>. Temperatures that exceed the threshold lead to heat stress which is associated with the accumulation of Reactive Oxygen Species (ROS) that manifests itself to oxidative stress<sup>[6,21–23]</sup>. Reduced coleoptile elongation that was noted is a result of direct and indirect consequences of oxidative stress on cellular homeostasis which includes inhibition of protein synthesis, denaturation of proteins and other macromolecules, disintegration of membrane lipids, and loss of membrane integrity<sup>[24,25]</sup>. The prime indirect effect is obstruction of cell division and cell elongation which are critical physiological processes in the growth and development of all organisms<sup>[2,23,24]</sup>.

At the peak of the reported unfavorable effects of heat stress, sorghum has been proven to be among crops that tolerate and adapt to excessive temperatures above their threshold even at early stages of growth<sup>[1]</sup>. These observations in the present study, together with the existing assertions, cement the notion by Craufurd & Peacock<sup>[26]</sup>, that survival and crop establishment of these aforementioned thermophilic crops is mainly hinged on thermotolerance than drought stress tolerance and is associated with genetic variation. This study confirmed the existence of genetic variability within sorghum genotypes for basal and acquired thermotolerance, as previously shown in several studies on sorghum and other related hardy crops like pearl millet and finger millet<sup>[27–30]</sup>. Genotypes like NPGRC1704,

**Table 4.** Mean comparison of coleoptile changes for 50 sorghum genotypes indicating seedlings basal thermotolerance in two sets.

Genotype	Set 1		Genotype	Set 2	
	Heat shocked	Non-heat shocked		Heat shocked	Non heat shocked
<b>Top 10</b>			<b>Top 10</b>		
NPGRC1695	30.80 <sup>abcdef</sup>	36.06 <sup>ab</sup>	<b>NPGRC1704</b>	16.72 <sup>g-x</sup>	22.5 <sup>ab</sup>
<b>IS24426</b>	30.56 <sup>abcdefg</sup>	28.86 <sup>abcdefg</sup>	IS9567	16.57 <sup>h-z</sup>	22.13 <sup>abc</sup>
NPGRC1478	29.24 <sup>bcdefgh</sup>	33.28 <sup>abcd</sup>	<b>IS24426</b>	16.22 <sup>i&gt;-z</sup>	18.48 <sup>b-n</sup>
NPGRC1592	22.77 <sup>bcdefghi</sup>	27.67 <sup>bcdefghi</sup>	NPGRC1222	15.03 <sup>t-D</sup>	18.31 <sup>c-n</sup>
NPGRC3087	22.95 <sup>bcdefghi</sup>	26.33 <sup>bcdefghi</sup>	NPGRC175*9	14.86 <sup>m-D</sup>	18.22 <sup>c-o</sup>
"MACIA"	19.11 <sup>bcdefghi</sup>	26.20 <sup>bcdefghi</sup>	NPGRC1628	14.20 <sup>o-D</sup>	19.32 <sup>b-j</sup>
NPGRC1868	22.80 <sup>bcdefghi</sup>	24.91 <sup>bcdefghi</sup>	NPGRC1197	14.08 <sup>o-D</sup>	18.45 <sup>b-n</sup>
IS2867	20.81 <sup>bcdefghi</sup>	24.75 <sup>bcdefghi</sup>	NPGRC1868	14.07 <sup>o-D</sup>	21.0 <sup>a-f</sup>
IS26191	13.47 <sup>fg</sup>	24.67 <sup>bcdefghi</sup>	NPGRC1178	14.07 <sup>o-D</sup>	20.24 <sup>a-j</sup>
<b>NPGRC1704</b>	24.57 <sup>bcdefghi</sup>	25.31 <sup>bcdefghi</sup>	NPGRC1782	13.98 <sup>p-D</sup>	14.66 <sup>n-D</sup>
<b>Bottom 5</b>			<b>Bottom 5</b>		
IS9548	14.52 <sup>fg</sup>	18.34 <sup>cdefghi</sup>	IS12391	11.56 <sup>D</sup>	17.97 <sup>c-q</sup>
IS9303	14.11 <sup>fg</sup>	19.09 <sup>bcdefghi</sup>	NPGRC3087	11.33 <sup>D</sup>	18.63 <sup>b-n</sup>
IS6944	13.01 <sup>g</sup>	18.81 <sup>bcdefghi</sup>	NPGRC3127	11.20 <sup>D</sup>	15.94 <sup>i-c</sup>
IS30164	10.92 <sup>h</sup>	17.97 <sup>cdefghi</sup>	NPGRC3092	11.13 <sup>D</sup>	19.02 <sup>b-m</sup>
<b>NPGRC3127</b>	9.65 <sup>i</sup>	20.42 <sup>bcdefghi</sup>	SV4	11.0 <sup>D</sup>	18.66 <sup>b-m</sup>
<b>Overall mean</b>		22.17		15.94	
<b>LSD</b>		7.82		1.85	

Means with similar superscripted letter(s) in the same column were significantly different at  $p < 0.05$ . Genotypes appeared in the top performers or at least performers common in both sets and genotypes in bold maintained superiority in both sets.

**Table 5.** Mean comparison of seedlings coleoptile length changes for 50 sorghum genotypes acquired thermotolerance.

Genotype	Set 1		Genotype	Set 2	
	Acclimatized	Non- acclimatized		Acclimatized	Non -acclimatized
<b>Top 10</b>					
IS13837	13.56 <sup>a</sup>	1.88 <sup>B-D</sup>	NPGRC3124	22.32 <sup>a</sup>	4.64 <sup>d-j</sup>
NPGRC1704	12.5 <sup>ab</sup>	3.24 <sup>S-D</sup>	IS12391	18.2 <sup>ab</sup>	7.18 <sup>c-j</sup>
NPGRC1619	12.09 <sup>a-c</sup>	1.63 <sup>CD</sup>	IS29925	18.18 <sup>ab</sup>	2.98 <sup>g-j</sup>
IS9567	11.99 <sup>a-d</sup>	2.8 <sup>v-D</sup>	<b>IS24272</b>	13.30 <sup>bc</sup>	2.32 <sup>g-j</sup>
NPGRC1699	11.65 <sup>a-d</sup>	2.9 <sup>t-D</sup>	<b>NPGRC3093</b>	10.72 <sup>cd</sup>	4.12 <sup>e-j</sup>
NPGRC1476	11.48 <sup>a-d</sup>	2.75 <sup>w-D</sup>	NPGRC1197	10.11 <sup>c-f</sup>	2.25 <sup>g-j</sup>
<b>NPGRC3093</b>	11.24 <sup>a-e</sup>	1.94 <sup>B-D</sup>	NPGRC1868	10.02 <sup>c-f</sup>	3.31 <sup>g-j</sup>
<b>IS24272</b>	11.21 <sup>a-e</sup>	2.64 <sup>v-D</sup>	NPGRC1478	8.71 <sup>c-g</sup>	2.76 <sup>g-j</sup>
NPGRC3195	11.13 <sup>a-e</sup>	4.42 <sup>o-D</sup>	NPGRC1782	8.48 <sup>c-h</sup>	5.8 <sup>d-j</sup>
IS9548	11.12 <sup>a-e</sup>	3.40 <sup>S-D</sup>	IS30164	8.42 <sup>c-i</sup>	4.98 <sup>d-j</sup>
<b>Bottom five</b>					
NPGRC3105	6.69 <sup>9-y</sup>	1.74 <sup>CD</sup>	NPGRC3195	4.22 <sup>e-j</sup>	4.55 <sup>d-j</sup>
IS13813	6.43 <sup>i-z</sup>	5.07 <sup>m-C</sup>	NPGRC1862	3.78 <sup>e-j</sup>	2.86 <sup>g-j</sup>
NPGRC3127	5.94 <sup>k-B</sup>	3.51 <sup>S-D</sup>	NPGRC3105	3.6 <sup>f-j</sup>	1.55 <sup>j</sup>
NPGRC1593	5.08 <sup>m-C</sup>	2.89 <sup>t-D</sup>	IS9548	2.67 <sup>g-j</sup>	3.15 <sup>g-j</sup>
NPGRC1782	4.66 <sup>n-D</sup>	3.41 <sup>S-D</sup>	IS6944	2.45 <sup>g-j</sup>	3.8 <sup>e-j</sup>
<b>Overall mean</b>		6.18		5.35	
<b>LSD</b>		1.83		2.87	

Means with similar superscripted letters in the same column were significantly different at  $p < 0.05$  and genotypes in bold represent top performers in both sets.

and IS24426 consistently exhibited inherent superiority in the current study showing relatively less inhibition of coleoptile elongation. Confirming the existence of basal thermotolerance in sorghum. Demonstrating the profound claims that some genotypes can emerge and continue to grow at temperatures above optimal<sup>[6]</sup>.

Basal thermotolerance is conceivably dependent on the intrinsic expression of transcripts for heat shock proteins, ROS scavenging enzymes like catalase, osmoprotectants, secondary metabolites, and antioxidant factors that offer protection against oxidative stress without prior exposure to lethal temperatures<sup>[11,17,31,32]</sup>. It is associated with swift response and

protection against acute heat episodes that are becoming frequent in semi-arid tropics (SATs)<sup>[20]</sup>.

Some genotypes, i.e. NPGRC3093, and IS24272, consistently exhibited resilience to heat shock but after their prior exposure to gradual increases of temperatures up to suboptimal temperatures which is suggestive of the presence of acquired thermotolerance. Acquired thermotolerance is uniquely achieved through the stimulation of specific defense pathways in response to gradually increasing temperatures<sup>[17,33,34]</sup>. During the 'priming' period there is an accumulation of certain transcripts that code for molecular chaperones such as HSPs that offer protein folding, osmolytes like polyamines, proteins,



secondary metabolites, including ROS-quenching enzymes like catalase (CAT) and ascorbate peroxidase (APX) that offer protection against oxidative stress<sup>[17,24]</sup>. The heat-shock based protection mechanism is complemented by a highly conserved sensory and signaling network that triggers heat shock regulation (HSR) pathways thereby enhancing acquired thermotolerance<sup>[24,35]</sup>. If we are to go by the mechanisms that confer acquired thermotolerance in crop plants, adaptation, and evolution are also more likely possibilities that render this kind of thermotolerance<sup>[36]</sup>. Considering the well-documented claim that sorghum evolved in SATs characterized by high temperatures hence their resilience to extreme temperatures<sup>[31]</sup>.

Interestingly, two genotypes that were consistent in acquired thermotolerance in the current study, are research materials originating from Tanzania and Chiredzi in Zimbabwe, respectively. Though the exact location of origin of the Tanzanian genotypes is not known, most of the country is semi-arid<sup>[32]</sup>, and Chiredzi in Zimbabwe is in the Lowveld region characterized by high temperatures with an average maximum temperature ranging between 28 and 32 °C<sup>[34]</sup>. Chiredzi is a sugar cane area which is a typical C<sub>4</sub> plant like sorghum hence the convincing possibility of adaptation of these genotypes to high temperatures that rendered them the observed acquired thermotolerance. This could be a coevolutionary adaptation mechanism of germplasm to heat stress in these areas. In the current study, some genotypes displayed one type of resilience and not the other while some exhibited both. This all signifies that the differences in the type of thermotolerance displayed by crop plants is determined by the quality and quantity of the heat shock proteins that are produced prior to or during heat stress stimuli<sup>[6]</sup>. Whereas several genotypes in the present study exhibited traits of both basal and acquired thermotolerance, featuring in at least one of the sets of each assay. These were identified as NPGRC1704, IS9567, NPGRC1197, NPGRC1868, and NPGRC1782 (Tables 4 & 5). This is explained as thermotolerance diversity where certain subsets of HSR genes overlap rendering the genotype of both types of thermotolerance<sup>[34]</sup>. This is also shown in the expression of HSR genes across plant tissues, organs, and growth stages, thus hypocotyl, roots, and many more organs have been used as indicators of thermotolerance<sup>[3,17,33]</sup>. Significant positive correlation between acquired thermotolerance, expression of heat shock proteins and yield was established in wheat which is also a possibility in sorghum<sup>[36,37]</sup>.

The significance of G × E implies that genotypes can be specifically deployed to areas prone to heat stress. Popular varieties like 'Macia' and 'SV4' may not perform in the near future given the increased severity and recurrence of drought. This is of great concern given their large-scale production by subsistence farmers in Southern Eastern and Central Africa. According to IPCC<sup>[38]</sup>, global atmospheric temperature is likely to increase by 2.5 to 5.8 °C in the current century exacerbating the likelihood of heat stress. It was also interesting to note that differences in coleoptile elongation between the acclimatized and non-acclimatized sorghum emergents were greater than that observed between the heat-shocked and non-heat-shocked seedlings in the basal thermotolerance assay. This posits acclimation as a superior form of thermotolerance and an adaptive mechanism that enables crop plants to survive heat stress levels that would be otherwise lethal in their absence<sup>[20]</sup>.

## Conclusions and future perspectives

Sorghum genotypes showed a differential responses to heat shock in both basal and acquired thermotolerance indicating great diversity. Amongst the top ten performers for basal thermotolerance, genotypes NPGRC1704, and IS24426 emerged as the most consistent in the two sets of the assay while for acquired thermotolerance assay, genotypes NPGRC3093, and IS24272 consistently demonstrated superiority. Genotypes NPGRC1704, IS9567, NPGRC1197, NPGRC1868, and NPGRC1782 exhibited potential traits of both basal and acquired thermotolerance. Expression profiling will also be necessary in understanding the diversity of elicited proteins while phenotyping and genotyping of the identified potential genotypes may be extended to other growth stages to enhance selection efficiency. Identified genotypes are potential donors in crop improvement programs that seek to improve thermotolerance in sorghum.

## Author contributions

The authors confirm contribution to the paper as follows: conceptualization; data collection: Ndlovu E; acquisition of research materials, data analysis: Ndlovu E, Maphosa M; writing - original draft: Ndlovu E, Maphosa M; Van Staden J. All authors reviewed the results and approved the final version of the manuscript.

## Data availability

The data sets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Acknowledgements

The authors would like to thank the Genetic Resources and Biotechnology Institute in Zimbabwe for a generous donation of the landraces, International Crop Resources Institute for Semi-Arid Tropics, Bulawayo, Zimbabwe for a generous donation of germplasm.

## Conflict of interest

The authors declare that they have no conflict of interest.

**Supplementary Information** accompanies this paper at (<https://www.maxapress.com/article/doi/10.48130/tia-0024-0023>)

## Dates

Received 7 November 2023; Revised 16 July 2024; Accepted 18 July 2024; Published online 2 September 2024

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