



RESEARCH ARTICLE

Unravelling the combined abiotic stress responses of wheat under heat and drought conditions

T Muni Sai Kumar^{1†*}, Shailesh Kumar^{1†}, Swati Gaikwad^{1*} & Sweta Mishra²

¹Department of Plant Physiology and Biochemistry, College of Basic Sciences and Humanities, Dr. Rajendra Prasad Central Agricultural University, Pusa, Samastipur 848 125, Bihar, India

²Department of Genetics and Plant Breeding, PG College of Agriculture, Dr. Rajendra Prasad Central Agricultural University, Pusa, Samastipur 848 125, Bihar, India

[†]Both authors contributed equally

*Correspondence email - swati.gaikwad@rpcau.ac.in; shaileshk@rpcau.ac.in

Received: 21 April 2026; Accepted: 27 July 2026; Available online: Version 1.0: 02 September 2026

Cite this article: Muni SKT, Shailesh K, Swati G, Sweta M. Unravelling the combined abiotic stress responses of wheat under heat and drought conditions. Plant Science Today. 2026; 13(sp5): 1-8. <https://doi.org/10.14719/pst.15136>

Abstract

Most of the wheat (*Triticum aestivum* L.) growing areas of the world experience environmental stresses including drought (moisture stress) and high temperature (heat stress) that adversely affect crop growth, development and yield. Water-deficit often combined with high temperature stress is the main abiotic factor limiting crop growth and development. The present investigation was performed to study the effect on yield and physiological and biochemical traits of different wheat genotypes under individual heat stress (HS) and drought stress (DS) and combined stress (HS + DS) conditions. Distinct from prior studies which predominantly utilised pot experiments, this investigation offers valuable insights derived from field conditions, thereby providing a more accurate assessment of crop performance under HS + DS. The field experiment conducted in plant phenotyping facility, a total of 60 experimental plots was maintained, comprising 5 genotypes, 4 treatments and 3 replications. Grain yield declined by 31.9 % under HS, 61.6 % under DS and 66.6 % under HS + DS relative to the control. Both individual and (HS + DS) stresses also impaired physiological functioning. The HS + DS treatment induced more pronounced damaging effects on root architecture as well than either stress alone, with reductions of 42.8 % in root volume, 27.8 % in root surface area and 32 % in total root length compared with the control. Overall, HS + DS was more damaging than the individual stress, however, the interaction effect might be due to cross adaptation effect. The genotype DBW-14 exhibited a high grain yield (270 g plot⁻¹) under HS, DS and HS + DS conditions, indicating robust cross-adaptation mechanisms. Although genotype 11 HPYT433 demonstrated superior tolerance based on root parameters and relative water content (RWC), DBW-14 significantly outperformed all other evaluated genotypes in grain yield and overall physiological stability under the HS + DS treatment. Consequently, DBW-14 serves as a promising donor line for breeding climate-resilient cultivars.

Keywords: combined stress; drought stress; grain yield; heat stress; root traits

Introduction

Wheat (*Triticum aestivum* L.) is a major global staple, primarily cultivated in cool and dry winter climates with an optimal temperature range of 15–25 °C. In 2024–25, global wheat production exceeded 798.4 million tonnes (1), with China and India contributing 140 million and 117.95 million tonnes, respectively (2). In India, wheat is grown on 31.8–32.8 Mha, producing 117.95 million t, with Uttar Pradesh, Punjab, Madhya Pradesh, Haryana, Rajasthan and Bihar contributing significantly to total production (3). In approximately 40 countries, wheat provides nearly 85 % of calories and 82 % of protein intake (4). Wheat is highly sensitive during reproductive stages, with 15–20 °C being optimum for normal growth. Elevated temperature during the reproductive stage disturbs reproductive physiology and reduces yield.

Wheat productivity is increasingly threatened by climate-induced heat stress (HS) and drought stress (DS). These stresses severely affect critical growth stages, particularly vegetative development, anthesis and grain filling, leading to reductions in

photosynthesis, assimilate translocation, chlorophyll content and accelerated leaf senescence (5–7). Drought stress further results in decreased leaf area, kernel abortion and restricted mobilisation of reserves (8). Root traits play a central role in stress tolerance. Deeper and thicker roots enhance access to soil moisture and nutrient uptake, while fine roots with higher permeability improve absorption efficiency under water-limited conditions. Under mild drought, carbon allocation shifts toward primary root growth, aiding water acquisition (9). Root architecture thus serves as a key determinant of plant resilience and productivity under stressful environments.

Plants often face multiple stresses simultaneously and activate various adaptive mechanisms to tolerate adverse environments. Most wheat-growing regions experience drought (moisture stress) and high temperature (heat stress), which adversely affect crop growth, development and yield. Water-deficit stress combined with high temperature is the major abiotic constraint limiting wheat productivity. The present investigation was conducted to assess the effects of individual and combined heat and

drought stress (HS + DS) on yield, physiological and biochemical traits of different wheat genotypes under field conditions. While most previous studies on (HS + DS) have been conducted under pot conditions, this field-based study provides more realistic insights into stress responses and identifies traits associated with improved stress tolerance.

Materials and Methods

The experiment was carried out at the experimental field of Dr. Rajendra Prasad Central Agricultural University, Pusa. A total of five wheat genotypes that is HD 2967, 41 ESWYT, 38 SAWSN 3102, 38 SAWSN 3174, 11 HPWSN 433, genotypes collected from CASSC, RPCAU Pusa. Seeds were surface-sterilised in 0.1 % Bavistin for 10 min, rinsed thoroughly with distilled water (3–4 times). The experiment was conducted under field conditions using a randomised block design (RBD) with three replications at Plant Phenotyping Facility, Dr. Rajendra Prasad Central Agricultural University. Sowing was carried out when adequate soil moisture was available. A total of 60 experimental plots were maintained, comprising five genotypes, four treatments and three replications, with plot measuring 128 m². All treatments were sown on 28 November 2022 with a normal planting density, maintaining 20 cm row spacing. The treatments were as follows: Control (C) (normal conditions): Normal sowing with normal planting density and recommended agronomic practices throughout the crop growth period. Heat stress (HS): Normal sowing and planting density, with HS of + 4.5 °C imposed using a ceramic heater during the reproductive and grain-filling stages (approximately 45 days after sowing (DAS)). Drought stress (DS): Normal sowing and planting density, with drought stress induced by withholding irrigation after 30 DAS. Combined heat and drought stress (HS + DS): Normal sowing and planting density, where DS was imposed by withholding irrigation after 30 DAS, followed by the application of HS (+ 4.5 °C using a ceramic heater) during the reproductive and grain-filling stages. The stress condition maintained in field with upholding irrigation before 15 days of sowing. The data related to weather parameters supported this experimentation are plotted in Table 1.

Physiological and biochemical traits

Soil plant analysis development (SPAD) value

Soil plant analysis development (SPAD) readings were recorded using a SPAD-502 meter (Konica Minolta, Japan) from the topmost fully expanded leaf at vegetative and reproductive stages. Measurements were taken between 09:00–11:30 AM on three plants per replication.

Relative water content (RWC)

Fresh leaf samples were collected in sealed zip bags and immediately weighed (fresh weight). Samples were floated on water for 4 hr to obtain turgid weight, then oven-dried at 70 °C for 72 hr to record dry weight. Relative water content was determined by the formula given below.

$$\text{RWC} = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Turgid weight} - \text{Dry weight}} \times 100$$

Spike and tissue temperature

Spike temperature was recorded using an infrared thermometer

(Apogee, USA; Model MI-210) during the reproductive stage on sunny days (11:30 AM–2:30 PM). Three readings per replication were averaged.

Leaf temperature

Leaf temperature was recorded using the IRGA (CI-340). Measurements were taken from the youngest fully expanded leaves of stressed and control plants.

Photosynthetic rate, transpiration rate and water use efficiency

Net photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), transpiration rate ($\text{m mol m}^{-2} \text{s}^{-1}$) and water use efficiency (kg/m^3) was measured with the infrared gas analyser (CI-340) during 09:00–11:00 AM (10).

Root trait measurements

Root traits (length, volume and surface area) were quantified using an Epson Perfection V700 Photo Scanner and WinRHIZO V2009c (32-bit) image analysis software. Roots were carefully removed from pots without damaging the root system, then roots were washed gently and stored in labelled zip bags, washed roots were placed in a transparent water-filled tray for scanning, only fresh roots were scanned.

Yield

Crop is harvested after it reached physiological maturity in order to calculate grain yield per plot, from which yield per square metre was determined. Using an electronic digital weighing balance, grain yield sample weights were measured.

Statistical analysis

Data from three replications per treatment were analysed using two-way analysis of variance (ANOVA) (genotypes (G) $\times$ treatments (T)) in OPSTAT. Significance was determined using Fisher's LSD at $p \leq 0.05$. Levels of significance were denoted as $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ for corresponding response differences.

Results

Root volume

A significant genotype (0.025***) and G $\times$ T (0.036***) effect was observed for root volume whereas treatment interaction was found to be non-significant. The values varied from 0.218–0.628 cm³ across the genotypes and treatments. Maximum average values of root volume were observed in control (0.628 cm³) followed by HS + DS (0.397 cm³). Under control conditions genotypes, HD2967 (0.628 cm³) and 11HPYT433 (0.452 cm³) shows maximum and minimum root volume respectively while genotypes, 38SAWSN3174 (0.397 cm³) and HD 2967 (0.218 cm³) revealed maximum and minimum values of root volume under HS + DS conditions.

Root area

A significant genotype (17.087***), treatment (10.807***) and G $\times$ T (24.164***) effect was exhibited for root area. The values vary from 205.4–385.9 cm² across the genotypes and treatments. Maximum average values of root area were observed in control (385.9 cm²) followed by HS + DS (280.6 cm²). Under control conditions genotypes, HD2967 (385.9 cm²) and 38SAWSN3174 (286.1 cm²) shows maximum and minimum root area respectively while genotypes, 11HPYT433 (280.6 cm²) and 41ESWYT (205.4 cm²) shows maximum and minimum root area respectively under HS + DS conditions.

Table 1. Weekly weather data collected from Agrometeorology Division Centre for Advance Studies on Climate Change, Dr. Rajendra Prasad Central Agricultural University Pusa Samastipur, Bihar

SMW	Temperature (°C)		Relative humidity (%)		Wind speed	Rainfall (mm)	Evaporation (mm)	Bright sunshine (hr.)
	Max	Min	Morning	Evening				
1	14.3	9.3	96	84	4.1	0.0	0.8	0.0
2	16.7	6.7	98	73	4.2	0.0	1.2	2.1
3	20.5	6.3	99	62	2.3	0.0	1.3	2.8
4	23.9	11.3	99	68	2.6	0.0	1.3	2.3
5	23.3	10.8	98	65	4.1	0.0	2.1	4.4
6	26.0	10.0	98	54	2.3	0.0	2.1	6.4
7	26.2	10.0	96	44	3.0	0.0	2.5	6.9
8	29.6	12.8	97	48	2.1	0.0	3.2	5.9
9	30.6	13.6	97	47	1.9	0.0	3.2	6.8
10	30.2	13.9	90	47	3.5	1.8	4.1	7.5
11	31.3	16.7	94	57	2.9	0.0	3.6	4.8
12	28.3	16.5	95	57	4.0	18.0	3.4	5.5
13	32.4	16.6	83	39	4.6	0.0	5.6	7.6
14	34.5	15.7	77	29	4.6	0.0	6.7	9.1
15	37.6	16.7	74	22	4.1	0.0	6.4	9.2
16	38.8	20.8	62	24	4.1	0.0	6.5	8.3
17	33.6	19.2	78	41	4.7	1.4	4.6	5.8
18	32.5	20.3	83	48	2.7	4.4	4.4	5.7
19	38.1	19.4	70	27	4.4	0.0	6.9	9.7
20	35.2	22.1	81	50	6.1	12.4	6.4	8.6
21	33.8	21.6	84	59	5.3	20.6	4.6	7.0
22	39.0	23.4	72	35	4.1	0.0	6.7	11.1
23	41.0	23.4	67	30	3.7	0.0	7.3	10.5
24	40.1	25.9	80	40	7.6	0.0	8.1	7.8
25	37.3	25.2	87	55	7.2	1.2	6.2	5.0
26	32.6	24.7	91	71	9.2	118.2	5.2	3.0
27	32.4	24.8	93	75	5.8	1.4	4.0	3.2
28	33.5	25.3	93	80	4.4	35.4	2.6	1.7
29	34.8	25.8	87	63	6.6	0.0	5.5	8.6
30	35.6	26.0	86	60	6.1	0.0	5.1	7.2
31	33.9	25.3	90	71	6.2	101.4	4.4	5.0
32	30.0	24.2	97	88	4.1	369.7	2.0	0.4
33	33.8	24.9	94	71	2.2	43.2	3.7	5.5
34	30.8	24.3	95	84	1.8	101.2	3.3	1.6
35	34.4	25.6	89	68	3.1	28.2	4.0	3.5
36	33.3	24.0	93	80	2.0	70.8	3.5	2.7
37	33.5	25.3	93	70	2.8	0.0	4.1	7.0
38	32.2	23.9	94	80	3.2	293.2	3.2	4.5
39	31.0	24.0	96	78	1.1	42.4	2.4	3.6
40	31.1	24.8	94	78	2.5	38.4	2.7	4.0
41	33.7	24.4	94	62	0.8	0.0	3.2	7.6
42	31.6	21.0	95	65	1.6	1.2	3.1	7.9
43	31.5	18.9	94	55	1.1	0.0	3.1	9.1
44	32.0	19.0	95	52	0.9	0.0	2.5	7.9
45	29.6	17.3	96	56	1.3	0.0	1.6	1.6
46	29.9	16.3	95	53	0.4	0.0	2.3	8.0
47	29.0	14.5	93	49	1.7	0.0	2.1	4.9
48	28.4	15.8	95	55	3.9	0.0	1.5	4.0
49	26.6	16.1	97	67	-	4.6	1.4	2.9
50	24.2	9.3	97	49	-	0.0	1.8	5.4
51	24.2	9.1	97	52	-	0.0	1.6	6.0
52	23.9	11.7	97	70	-	0.0	1.3	3.0
Average/Total*	31.0	18.7	90	58	3.6	1309.1*	3.7	5.6

SMW: standard meteorological week.

Root length

A significant genotype (10.095***), treatment (6.385***) and G x T (14.277*** effect was observed for root length. The values vary from 121.15–251.89 cm across the genotypes and treatments. Maximum average values of root length were observed in control (251.89 cm) followed by HS + DS (163.38 cm). Under control conditions genotypes, 11 HPYT433 (251.89 cm) and 38SAWSN3102 (195.84 cm) shows maximum and minimum root length respectively while genotypes, 38SAWSN3174 (163.38 cm) and 11HPYT433 (121.15 cm) exhibited maximum and minimum root length under HS + DS condition respectively (Table 2).

Soil plant analysis development (SPAD) value

A significant genotype (1.565***), treatment (1.400***) and G x T (3.130*** effect was observed for greenness index. The values varied from 27.2–55.2 across the genotypes and treatments. Maximum average values of SPAD were observed in control (55.2) followed by HS (46.8), DS (38.6) and HS + DS (33.5). Under control conditions genotypes, 3SAWSN 3174 (55.2) and HD2967 (48.1) shows maximum and minimum SPAD values respectively. Similarly, under HS condition genotypes, 11HPYT433 (46.8) and DBW14 (40.4) shows maximum and minimum SPAD values respectively. Under DS condition genotypes, 11HPYT 433 (38.6) and NEST20-39 (32.8) shows maximum and minimum SPAD values respectively while genotypes, 11HPYT433 (33.5) and HD2967 (27.2) shows maximum and minimum SPAD values under HS + DS condition respectively.

Relative water content (RWC)

A significant genotype (2.342*** and G x T (4.685*** effect was observed for RWC whereas treatment interaction was found to be non-significant. The values varied from 52.2–80.5 % across the genotypes and treatments. Maximum average values of RWC were observed in control (80.5 %) followed by HS (69.2 %), DS (65.8 %) and HS + DS (56.9 %). Under control conditions genotypes, HD2967 (80.5 %) and 38SAWSN3174 (70.8 %) shows maximum and minimum RWC respectively. Similarly, under HS condition genotypes, 11HPYT433 (69.2 %) and NEST20-39 (60.5 %) shows maximum and minimum RWC respectively. Under DS condition genotypes, DBW14 (65.8 %) and NEST20-39 (58.2 %) shows maximum and minimum RWC respectively while genotypes, 11HPYT433 (56.9 %) and NEST20-39 (52.2 %) recorded maximum and minimum RWC under HS + DS condition respectively.

Water use efficiency (WUE)

A significant genotype (0.056***), treatment (0.050*** and G x T (0.112*** effect was observed for water use efficiency. The values varied from 0.92–2.26 kg/m³ across the genotypes and treatments. Maximum average values of water use efficiency were observed in

control (2.26 kg/m³) followed by DS (1.62 kg/m³), HS (1.43 kg/m³) and HS + DS (1.07 kg/m³). Under control conditions genotypes, 38SAWSN3174 (2.26 kg/m³) and 11HPYT433 (1.64 kg/m³) shows maximum and minimum water use efficiency respectively. Under HS condition genotypes, DBW14 (1.43 kg/m³) and HD2967 (0.98 kg/m³) shows maximum and minimum water use efficiency respectively. Under DS condition genotypes, DBW14 (1.62 kg/m³) and 11HPYT433 (0.95 kg/m³) shows maximum and minimum water use efficiency respectively while genotypes, DBW14 (1.07 kg/m³) and NEST20-39 (0.92 kg/m³) recorded maximum and minimum water use efficiency respectively under HS + DS condition.

Photosynthesis

A significant genotype (0.575***), treatment (0.514*** and G x T (1.150*** effect was observed for photosynthesis. The values varied from 7.4–21.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ across the genotypes and treatments. Maximum average values of photosynthesis were observed in control (21.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$) followed by HS (17.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$), DS (16.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and HS + DS (11.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Under control conditions genotypes, HD 2967 (21.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and DBW 14 (17.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$) exhibited maximum and minimum photosynthesis respectively. Similarly, under HS condition genotypes, 11HPYT433 (17.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and 38SAWSN3174 (12.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$) shows maximum and minimum photosynthesis respectively. Under DS conditions genotypes, DBW14 (16.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and 38SAWSN3174 (10.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$) recorded maximum and minimum photosynthesis respectively while genotypes, 11HPYT433 (11.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and 38SAWSN3174 (6.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$) recorded maximum and minimum photosynthesis under HS + DS condition respectively.

Transpiration rate

A significant genotype (0.170***), treatment (1.010*** and G x T (2.259*** effect was observed for transpiration rate. The values varied from 2.6–5.8 m mol m²s⁻¹ across the genotypes and treatments. Maximum average values of transpiration rate were observed in control (5.8 m mol m²s⁻¹) followed by HS (5.1 m mol m²s⁻¹), DS (4.7 m mol m²s⁻¹) and HS + DS (3.8 m mol m²s⁻¹). Under control conditions genotypes, HD2967 (5.8 m mol m²s⁻¹) and NEST20-39 (4.9 m mol m²s⁻¹) observed maximum and minimum transpiration rate respectively. Similarly, under HS condition genotypes, HD2967 (5.1 m mol m²s⁻¹) and NEST 20-39 (4.2 m mol m²s⁻¹) shows maximum and minimum transpiration rate respectively. Under DS condition genotypes, DBW14 (4.7 m mol m²s⁻¹) and NEST20-39 (3.9 m mol m²s⁻¹) shows maximum and minimum transpiration rate respectively while genotypes, DBW14 (3.8 m mol m²s⁻¹) and 38SAWSN3174 (2.6 m mol m²s⁻¹)

Table 2. Effect of root volume, root area and root length under heat and drought stress combination

Genotypes	Volume (cm ³)		Area(cm ³)		Length(cm)	
	C	HS + DS	C	HS + DS	C	HS + DS
11 HPYT 433	0.452 ± 0.01	0.362 ± 0.02	364.8 ± 7.6	280.6 ± 7.4	251.89 ± 5.2	121.15 ± 3.2
HD 2967	0.628 ± 0.02	0.218 ± 0.00	385.9 ± 11.8	271.3 ± 4.1	217.53 ± 6.6	129.28 ± 2.0
38 SAWSN 3102	0.587 ± 0.01	0.254 ± 0.01	343.2 ± 8.6	243.8 ± 7.4	195.84 ± 4.9	154.36 ± 4.7
38 SAWSN 3174	0.563 ± 0.01	0.397 ± 0.01	286.1 ± 7.6	269.1 ± 7.1	208.64 ± 5.5	163.38 ± 4.3
41 ESWYT 114	0.547 ± 0.01	0.314 ± 0.01	422.7 ± 11.2	205.4 ± 5.4	212.52 ± 5.6	159.61 ± 4.2
G	0.025***		17.087***		10.095***	
T	NS		10.807***		6.385***	
G x T	0.036		24.164***		14.277***	

Analysis of variance (ANOVA) was done with genotypes and treatments as the main factor. The level of significance was calculated on the basis of the least significant difference value. C: control; HS: heat stress; DS: drought stress; HS + DS: heat and drought stress; LSD: least significant difference; G: genotype; T: treatment; NS: non-significant; **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

Table 3. Effect of heat stress, drought stress and combination of heat and drought stress on photosynthesis, transpiration rate and grain yield of wheat genotypes

Genotypes/ treatments	Photosynthesis ($\mu\text{mol m}^{-2}\text{s}^{-1}$)				Transpiration rate ($\text{m mol m}^{-2}\text{s}^{-1}$)				Grain yield (g plot^{-1})			
	C	HS	DS	HS + DS	C	HS	DS	HS + DS	C	HS	DS	HS + DS
DBW187	17.6 ± 0.4	15.2 ± 0.4	16.8 ± 0.7	8.2 ± 0.2	5.1 ± 0.10	4.3 ± 0.11	4.7 ± 0.18	3.8 ± 0.07	544 ± 11.33	588 ± 15.55	325 ± 13.12	270 ± 7.14
HD2987	21.3 ± 0.7	16.8 ± 0.3	14.1 ± 0.4	7.4 ± 0.2	5.8 ± 0.07	5.1 ± 0.07	4.4 ± 0.09	3.4 ± 0.09	521 ± 15.92	315 ± 4.8	189 ± 5.00	170 ± 4.5
38SAWSN3174	18.3 ± 0.5	12.3 ± 0.4	10.6 ± 0.2	6.8 ± 0.2	5.3 ± 0.05	4.7 ± 0.05	4.5 ± 0.05	2.6 ± 0.04	728 ± 18.32	476 ± 14.54	260 ± 5.41	218 ± 5.76
NEST20-39	18.8 ± 0.5	15.7 ± 0.4	14.5 ± 0.4	9.6 ± 0.1	4.9 ± 0.13	4.2 ± 0.08	3.9 ± 0.03	2.8 ± 0.03	853 ± 22.55	445 ± 11.76	219 ± 6.69	196 ± 3.00
11HPYT433	20.3 ± 0.5	17.4 ± 0.5	12.8 ± 0.3	11.6 ± 0.4	5.5 ± 0.10	4.6 ± 0.12	4.1 ± 0.11	3.1 ± 0.06	559 ± 14.78	305 ± 8.06	194 ± 4.88	179 ± 5.47
G		0.575***				0.170***				16.311***		
T		0.514***				1.010***				14.589***		
G x T		1.150***				2.259***				32.622***		

Analysis of variance (ANOVA) was done with genotypes and treatments as the main factor. The level of significance was calculated on the basis of the least significant difference value. C: control; HS: heat stress; DS: drought stress; HS + DS: heat and drought stress; LSD: least significant difference; G: genotype; T: treatment; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

exhibited maximum and minimum transpiration rate under HS + DS condition respectively (Table 3).

Grain yield

A significant genotype (16.311***), treatment (14.589***), and G x T (32.622***), effect was observed for grain yield. The values varied from 170–853 g plot⁻¹ across the genotypes and treatments. Maximum average values of grain yield were observed in control (853 g plot⁻¹) followed by HS (588 g plot⁻¹), DS (325 g plot⁻¹) and HS + DS (270 g plot⁻¹). Under control conditions genotypes, NEST20-39 (853 g plot⁻¹) and HD2967 (521 g plot⁻¹) recorded maximum and minimum grain yield respectively. Under HS condition genotypes, DBW 14 (588 g plot⁻¹) and 11HPYT433 (305 g plot⁻¹) exhibited maximum and minimum grain yield respectively. Under DS condition genotypes, DBW14 (325 g plot⁻¹) and HD2967 (189 g plot⁻¹) shows maximum and minimum grain yield respectively while genotypes, DBW14 (270 g plot⁻¹) and HD2967 (170 g plot⁻¹) exhibited maximum and minimum grain yield respectively under HS + DS conditions.

Leaf temperature

Leaf temperature was significantly influenced by genotype (1.042) and G x T interaction (2.085), while the treatment effect was non-significant. Leaf temperature ranged from 22.8–29.6 °C across genotypes and treatments. The highest mean leaf temperature was observed under HS + DS (29.6 °C), followed by DS (28.7 °C), HS (28.5 °C) and C (24.8 °C). Under C conditions, genotype 11HPYT433 recorded the maximum leaf temperature (24.8 °C), whereas DBW 14 showed the minimum (22.8 °C). Under HS, 11HPYT433 exhibited the highest leaf temperature (28.5 °C), HD2967 (27 °C) indicated maximum and minimum leaf temperature respectively. Under DS condition genotypes, DBW14 (28.7 °C) and NEST20-39 (26.4 °C) shows maximum and minimum leaf temperature respectively while genotypes, HD2967 (29.6 °C) and 11HPYT433 (27 °C) recorded maximum and minimum leaf temperature under HS + DS condition respectively. Under DS condition genotypes, DBW14 (28.7 °C) and NEST20-39 (26.4 °C) exhibited maximum and minimum leaf temperature respectively while genotypes, HD2967 (29.6 °C) and

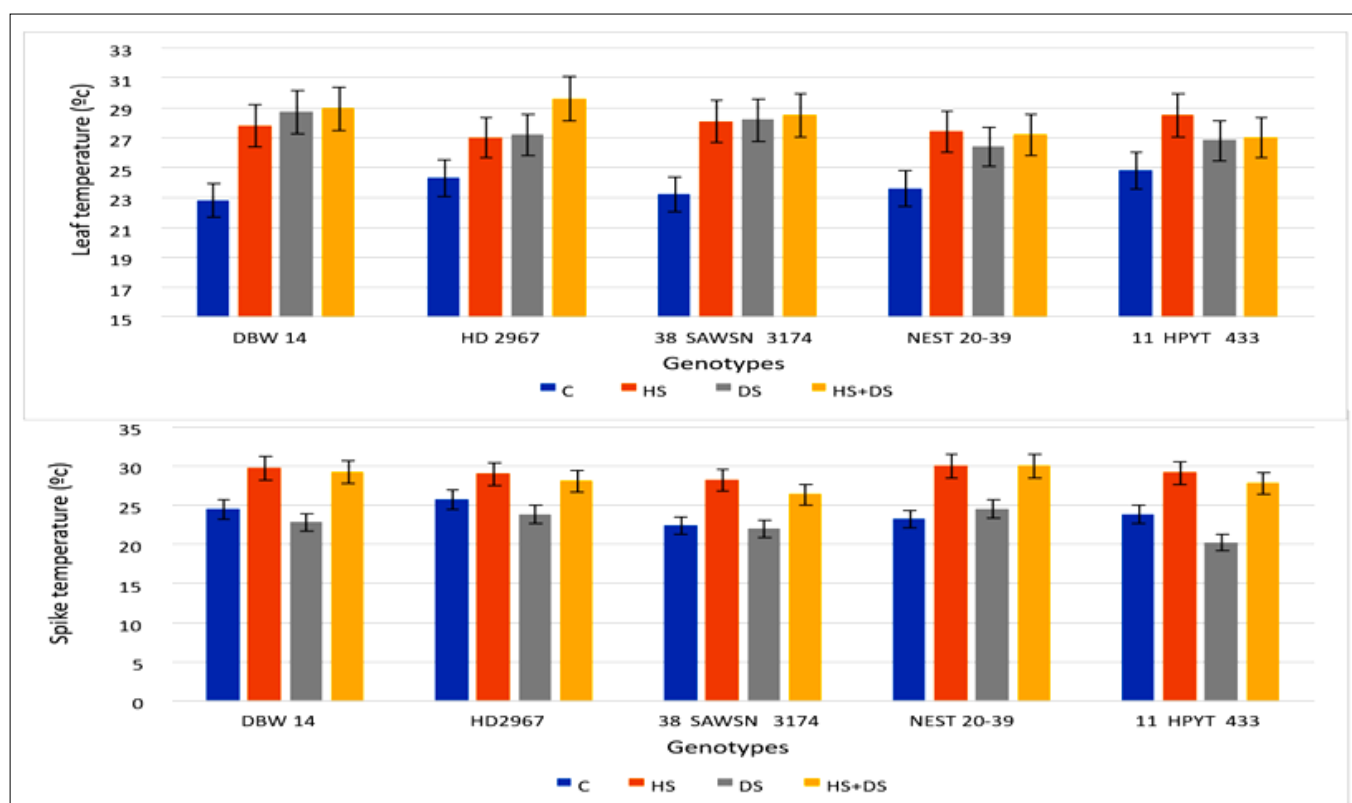


Fig. 1. Graphical representation of heat stress (HS), drought stress (DS) and combination of heat and drought stress (HS + DS) effect on leaf and spike temperature of wheat genotypes.

11HPYT433 (27 °C) exhibited maximum and minimum leaf temperature under HS + DS condition respectively (Fig. 1).

Spike temperature

A significant genotype (1.002***), treatment (0.896***) and G x T (2.003***) effect was observed for spike temperature. The temperatures varied from 20.2–30 °C across the genotypes and treatments. The highest spike temperature was recorded in HS + DS (30 °C) followed by HT (30 °C), C (25.7 °C) and DS (24.5 °C). Under C conditions genotypes, HD2967 (25.7 °C) and 38SAWSN3174 (22.4 °C) shows highest and lowest spike temperature respectively. Similarly, under HS conditions genotypes, NEST20-39 (30 °C) and 38SAWSN 3174 (28.2 °C) shows highest and lowest spike temperature respectively. Under DS condition genotypes, NES 20-39 (24.5 °C) and 11HPYT433 (20.2 °C) exhibited highest and less temperature while genotypes, NEST20-39 (30 °C) and 38SAWSN3174 (26.3 °C) exhibited highest and less temperature under HS + DS condition respectively (Table 4).

Discussions

Root traits under combined heat and drought stress

Roots are often considered organs that absorb water mainly to sustain their own growth and development. Consequently, root tissues generally show lower injury compared to shoots during water stress, frequently resulting in an increased root–shoot ratio. However, severe soil moisture limitation can substantially restrict root elongation and biomass accumulation in wheat (11). In the present study, HS + DS significantly reduced root length, root volume and root area across genotypes, demonstrating the high sensitivity of root growth to simultaneous stress factors.

The growth of superior genotypes under limited water availability is greatly influenced by the adaptive behaviour of their root systems, particularly their ability to explore deeper soil layers while maintaining shoot biomass. Root biomass is known to enhance yield under resource-limited conditions and may reflect genotypic flexibility and plasticity of the root system under stress (12). Beyond water uptake, roots perform multiple functions including mechanical support, nutrient acquisition and signalling and are highly vulnerable to both temperature extremes and water scarcity. Heat stress during reproductive stages has been shown to strongly affect root number, diameter and elongation by limiting carbon allocation belowground (13), which is consistent with our findings.

Physiological responses to drought stress

Drought is one of the most damaging abiotic stresses in wheat and causes significant alterations in plant physiological attributes. Water scarcity restricts cell expansion and photosynthetic activity, leading to reduced plant height and biomass. Terminal drought, occurring during flowering and grain filling, is particularly detrimental and causes substantial yield losses (14). These reductions are primarily attributed to decreased net photosynthesis due to stomatal closure, oxidative damage to chloroplasts and reduced grain set.

Declines in RWC and leaf water potential, accompanied by increased leaf temperature, indicate deteriorating plant water status under drought. Higher photosynthetic rates are associated with increased RWC and lower canopy temperatures (15). Stomatal closure triggered by reduced RWC limits transpiration and CO₂ influx,

Table 4. Effect of heat stress, drought stress and combination of heat and drought stress on spad, relative water content and water use efficiency of wheat genotypes

Genotypes	SPAD				Relative water content (%)				Water use efficiency (kg/m ³)			
	C	HS	DS	HS + DS	C	HS	DS	HS + DS	C	HS	DS	HS + DS
DBW187	49.7 ± 1.03	40.4 ± 1.07	36.5 ± 1.48	32.5 ± 0.86	72.6 ± 1.51	62.4 ± 1.65	65.8 ± 1.37	54.5 ± 1.44	2.07 ± 0.04	1.43 ± 0.04	1.62 ± 0.07	1.07 ± 0.03
HD2987	48.1 ± 1.47	45.4 ± 0.69	37.2 ± 0.98	27.2 ± 0.72	80.5 ± 2.46	67.9 ± 1.04	60.9 ± 1.86	55.2 ± 0.84	1.98 ± 0.06	0.98 ± 0.01	1.37 ± 0.03	0.96 ± 0.03
38SAWSN3174	55.2 ± 1.39	43.1 ± 1.32	34.7 ± 0.72	31.2 ± 0.83	70.8 ± 1.78	65.3 ± 1.99	61.6 ± 1.55	52.8 ± 1.61	2.26 ± 0.06	1.14 ± 0.03	1.56 ± 0.05	1.02 ± 0.02
NEST20-39	48.3 ± 1.28	46.2 ± 1.22	32.8 ± 1.00	29.6 ± 0.45	74.1 ± 1.96	60.5 ± 1.60	58.2 ± 1.54	52.2 ± 1.38	2.18 ± 0.06	1.23 ± 0.03	1.26 ± 0.03	0.92 ± 0.03
11HPYT433	51.8 ± 1.37	46.8 ± 1.24	38.6 ± 0.97	33.5 ± 1.02	71.6 ± 1.89	69.2 ± 1.83	63.1 ± 1.67	56.9 ± 1.51	1.64 ± 0.04	1.18 ± 0.03	0.95 ± 0.03	0.98 ± 0.03
G		1.565***				2.342***					0.056***	
T		1.400***				N/A***					0.050***	
G*T		3.130***				4.685***					0.112***	

Analysis of variance (ANOVA) was done with genotypes and treatments as the main factor. The level of significance was calculated on the basis of the least significant difference value. C: control; HS: heat stress; DS: drought stress; HS + DS: heat and drought stress; LSD: least significant difference; G: genotype; T: treatment; SPAD: soil plant analysis development; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

decreasing stomatal conductance. Drought also alters chloroplast ultrastructure, reduces chlorophyll concentration and disrupts thylakoid stability, ultimately impairing photosynthesis (16). The agronomic trait, physiological and metabolic traits measured, only agronomic traits such as plant height, biomass, seed yield and harvest index were significantly lower in all stress treatments when compared to control. The stress associated genes identified in wheat were indicated unique differentially expressed genes (DEG) involved in adaptive mechanism for plant stress (17). The effects of HS + DS on plant phenotypic characteristics and gluten protein quality traits in eight spring wheat genotypes studied, while DS alone also had negative impacts. However, HS (29 °C) had only mild effects on yield and phenotypic characteristics, although, in field conditions, the impact of HS could be much more severe these findings can support present study in relation to yield and other physiological parameters (18). Heat stress and DS result in the formation of a reactive oxygen species (ROS) signature that mediate cross adaptation. The HS + DS exhibited ROS signature in unique way using various stress regulatory genes and their signalling pathway have already been studied but little information about signalling pathways involved in HS + DS (19).

Effect of combined heat and drought stress

Wheat experiences amplified physiological constraints when heat and DS occur simultaneously. Genotypes differ widely in their ability to withstand these HS + DS. Sensitive genotypes may show poor growth, reduced yield and cellular injury, whereas tolerant genotypes maintain root activity, chlorophyll stability and photosynthetic function.

Chlorophyll degradation is accelerated under heat due to impaired electron transport chains and breakdown of photosynthesis-related enzymes (20). Reduced RWC leads to loss of cell turgor and triggers photorespiration, resulting in the generation of ROS. Heat also enhances proteolytic activity and chloroplast disintegration, which further decreases chlorophyll content and photosynthetic activity (21). Our findings of reduced SPAD values and lowered chlorophyll content under HS + DS agree with earlier studies (22).

In this study, HS + DS caused pronounced reductions in photosynthetic rate, transpiration, stomatal conductance and chlorophyll stability compared to individual stresses. The inability of plants to recover daily transpiration after prolonged HS, as reported previously, is also reflected in our results. Heat and DS significantly reduced yield-related traits in the present study, with HS + DS exerting a greater negative effect on grain yield than DS alone. Previous studies suggest that drought and heat may reduce yield either by directly impairing grain-filling processes or indirectly by limiting photosynthate availability for grain growth (23). Our findings are consistent with earlier reports showing greater yield penalties under HS + DS conditions compared to individual stresses. The yield losses of 42.13–61.06 % under HS + DS in pot experiments, indicating an additive effect (21). However, in the present study, the absence of a clear additive effect on grain yield may reflect the activation of adaptive stress tolerance mechanisms in certain genotypes.

On average, heat and DS resulted in a 35–45 % reduction in grain yield across genotypes and treatments. Biomass production was comparatively less affected, suggesting that biomass partitioning plays a critical role in yield determination under stress conditions. Reduced pollen viability under high temperature and

impaired pistillate flower growth and ovule function under DS have been identified as major contributors to yield loss (22). Consistent with these observations, our results indicate that reduced seed set was the primary cause of yield decline in spring wheat exposed to heat and DS during the heading and grain-filling stages. A 1–3 °C rise in mean global air temperature is suggested to decrease wheat production by up to 28 % (18).

Leaf and spike temperatures, key indicators of plant stress response, increased significantly under stress across all genotypes. Spike temperature consistently exceeded leaf temperature due to greater exposure to environmental extremes, corroborating earlier findings (23). Same findings in one pot experiment observed that all individual, combined and sequential stress changes phytohormone balance and nutrient assimilation pattern leading to oxidative stress as well as reduced growth and yield (24). Combined stress found negative correlation between digital biomass scanned by red, green and blue (RGB) cameras and gluten protein analysed which indicated that protein functioning impaired stress imposed. One interesting finding is the differential accumulation of SA in the flag leaves during HS + DS TaWRKY33 gene characterised in wheat gene data base and studied the expression pattern of some gene in transgenic Arabidopsis lines resulted in lower water loss during drought leads to higher survival rate under exposure to 45 °C (25). This responses to both abscisic acid (ABA) and methyl jasmonate possible involved in signalling and cross adaptation.

It has been demonstrated also in maize. Wheat elucidates effect of HS reduction in photosynthesis and induced the proline accumulation which interact with ethylene. Possibly stomatal closure and ABA production need to be study during HS + DS (26).

Conclusion

Combined heat and drought stress (HS + DS) impacts wheat physiological traits by creating cross adaptive effect related to the adapting mechanism taken place in plant. This combined stress was often detrimental and more intense than individual stress and resulting in significantly reduced rate of photosynthesis, stomatal conductance and transpiration rate mainly. Overall, the HS + DS exerted synergistically negative effects on root architecture, chlorophyll stability, water relations and gas exchange parameters. The study highlights the importance of identifying and utilising genotypes with superior physiological efficiency and root traits improved physiological resilience to improve wheat adaptation under future climate scenarios. The grain yield affected more due to combination of stresses than individual stress. But grain yield was found more in DSW14 genotype affected due to heat stress (HS), drought stress (DS) and HS + DS significant over the other genotype might be selected as inbred line for crop improvement.

Acknowledgements

The authors are sincerely thankful to Dr. Rajendra Prasad Central Agricultural University, Pusa, Bihar, for providing the necessary facilities and financial support to carry out this research work.

Authors' contributions

TMSK conducted the field experiment at the Dr. Rajendra Prasad Central Agricultural University (RPCA), Pusa farm and recorded

observations on physiological, morphological, biochemical, yield and yield-contributing traits. SK conceptualised the study on the combined stress effects under field-grown wheat and supervised the research work. SG contributed to the constructive writing of the manuscript and verified the results. SM supervised the overall research work and provided guidance for conducting the study. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors do not have any conflict of interests to declare.

Ethical issues: None

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Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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