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RESEARCH ARTICLE

Stress physiology of onion genotypes: Insights into waterlogging tolerance and susceptibility

Amol R Pawar*, Mayur Patil & Sushant Sukumar Patil

Department of Agronomy, Lovely Professional University, Jalandhar 144 411, Punjab, India

*Correspondence email - amolrp4@gmail.com

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Abstract

Waterlogging is a major abiotic stress that significantly impairs onion *(Allium cepa* L.*)* productivity, particularly during critical growth stages such as seedling establishment, vegetative growth (including leaf and bulb development) and bulbing (bulb formation). This study evaluated the physiological and yield responses of multiple onion genotypes under waterlogging conditions. Various genotypes viz. Bhima Dark Red, Accession 1666, Accession 1630, W-355, Bhima Super, Bhima Shubhra, Bhima Red and Phule Samarth were evaluated. The genotypes Bhima Dark Red, Acc. 1666 demonstrated high tolerance capacity as evident through parameters such as plant height, leaf retention, chlorophyll content, Membrane Stability Index (MSI) and bulb yield under stress. In contrast, cultivars like Bhima Shubhra and Bhima Super, exhibited susceptibility *via* pronounced reductions in growth and yield parameters. In contrast, susceptible genotypes suffered from oxidative damage, metabolic disruption, showed poor assimilate allocation, resulting in significant yield reduction. The findings highlight the importance of genotype selection and targeted agronomic interventions for mitigating waterlogging-induced yield losses in flood-prone regions. These insights provide a foundation for breeding programs with an aim of enhancing waterlogging tolerance in onion, thereby supporting sustainable production in the context of increasing climate variability.

Keywords: antioxidant; genotype; onion; transcriptome; waterlogging; yield

Introduction

Onion production of 98 million tons has been reported from an area of about 4.3 million hectares in 2019 (1). India is the second-largest producer of onions in the world, accounting for around 20 % of global output. The finest grade onions are cultivated in the Deccan Plateau region. This region accounts for more than half of India's onion crop production (2). Onions are cultivated using rainwater or irrigation (3). Climate change has led to more frequent and extended periods of waterlogging, particularly during the monsoon season, which has significantly impacted onion output (4). Flooding causes damage to crop on a global scale equal to around 1 million km^2 every year (5). Heavy rains in India cause flooding on about 14 million acres of crop land every year (6).

Pests and diseases, insufficient soil nutrients and waterlogging are among the biotic and abiotic factors that reduce onion yield and productivity, with waterlogging being one of the most significant abiotic stresses affecting onion development and production (1). Onions are susceptible to water stress because of their shallow root systems (4). Heavy rainfall affects the growth of bulbs reducing the yield by about 50 %-70 % (7). The extent of yield loss is determined by a combination of factors, not solely by the presence of waterlogging. Key contributing variables include the intensity and duration of rainfall, the crop's developmental stage at the time of stress, the specific genotype's tolerance and the timing of the event (8). Soil oxygen depletion caused by waterlogging causes plants to produce harmful compounds that stunt their development and diminish their yield (9). The primary cause of plant mortality leading to decline in productivity is the lack of oxygen in the soil due to waterlogging (6). Insufficient oxygen at the root level causes leaves to become chlorotic and reduces net carbon absorption (9), which in turn impairs plant growth, photosynthesis, nutrient absorption and other developmental processes, ultimately leading to reduced crop yield (10). The growth, leaf area and yield of onion plants are all negatively affected by waterlogging (11). In addition, photosynthesis, nutrient absorption and nutrient translocation are all severely affected by waterlogging, which has a knock-on effect on onion growth and production (12).

Several agronomic practices may be implemented to reduce the effects of waterlogging on onion yields (11). Since the yield losses are high (between 50 % and 70 %) due to waterlogging during monsoon season, onion prices shoot up significantly in the domestic market (12). Most onion cultivars recommended for cultivation during the monsoon season are highly susceptible to waterlogging, making them especially prone to damage when excessive rainfall causes soil to become saturated (2, 13).

India leads in production of onions. The states of Maharashtra, Karnataka, Madhya Pradesh, Gujarat, Bihar, Rajasthan and Uttar Pradesh are among the top producers of onions in India. In India, Maharashtra is the top producer of onions (14). India has become a significant player in the global onion market, as over 20 % of the world supply has been coming from India since 2020 (1, 15). China also produces good quantity of onions followed by the United States, Iran and Turkey (1). More than half of all onions grown worldwide are produced in these nations. Flooding, primarily caused by inadequate soil drainage and erratic rainfall happens to be the most severe annual abiotic constraint, significantly affecting agricultural output and efficiency (16). However, different crops grown in various agroclimatic zones are also vulnerable to harm caused by waterlogging or soil flooding (17). The root system and the plant's morphology are significant factors in determining the tolerance and survival of plant exposed to waterlogging stress (18). Plants can tolerate soil flooding for a certain period with the help of adventitious root system (e.g. tomato). A well-developed aerenchyma tissue has been noted in the stems and roots of these plants (e.g. rice and wheat). Hence, the root plays a crucial role in tolerating waterlogging and saving the crop (19).

India's exceptional output is due to favourable meteorological conditions, cultivation methods and use of high-yielding onion cultivars (20). Besides these, the Indian government has developed several schemes, including the Minimum Support Price (MSP) and the Market Intervention Scheme (MIS) to assist farmers and guarantee a reasonable profit (14). Over 100 million tonnes of onions *(A. cepa* L.*)* are grown commercially worldwide (1). Onion production has increased worldwide due to increasing demand because of their nutritional and therapeutic benefits (21). Since the demand of this crop is growing over the years throughout the world, steps need to be taken and strategies should be developed to prevent the huge losses. Research studies are required to develop varieties that can tolerate water stress. In this study, several genotypes were checked for their efficacy to withstand stress caused due to waterlogging.

Materials and Methods

Experimental site

A field experiment was conducted during the *Kharif* seasons of 2023 and 2024 at the ICAR-Directorate of Onion and Garlic Research (ICAR-DOGR), Rajgurunagar, Pune, Maharashtra, India (18.32° N, 73.51° E; 645 m AMSL), which experiences a tropical dry and humid climate. The site receives an average annual rainfall of approximately 820 mm and temperatures range from 9.2 °C to 39.7 °C. The soil at the site is classified as clay loam (34 % clay, 41 % sand, 21 % silt) with a slightly alkaline pH of 7.

Experimental design and genotypes

The experiment was laid out in a split-plot design with two treatments (waterlogging (D1) and control (D2)) and eight onion *(A. cepa L.)* genotypes, replicated three times. Each genotype was grown in area of 48 m^2, with individual plots measuring 6 m × 2 m (12 m^2) and accommodating 400 plants per plot. Plant spacing was maintained at 15 cm between rows and 10 cm between plants. The genotypes evaluated were sourced from the ICAR-DOGR germplasm and categorized as tolerant (Acc. 1666, Acc. 1630, Bhima Dark Red, Acc. 355) and sensitive (Bhima Super, Bhima Shubhra, Bhima Red, Phule Samarth).

Crop management and waterlogging treatment

Irrigation was done after two days under normal conditions. Manual weeding was performed 45 Days After Transplanting (DAT) and standard agronomic as well as plant protection practices were followed throughout the experiment. Waterlogging was imposed at 45 DAT by maintaining a standing water depth of 5 cm above the soil surface for 10 consecutive days, while control plots received irrigation as per recommended practice without excess water.

Treatment details

D1: Waterlogged

D2: Control

T1: Acc. 1666

T2: Acc. 1630

T3: W-355

T4: Bhima Dark Red (BDR)

T5: Bhima Red

T6: Phule Samarth

T7: Bhima Shubhra

T8: Bhima Super

Observations and measurements

Growth and yield parameters

- Plant height and number of leaves were recorded at 45 and 55 DAT from five randomly selected plants per plot. Leaf area was measured on the third fully matured leaf from the top using a portable leaf area meter.
- Bulb size and diameter were measured at harvest, using a Vernier caliper.
- Average bulb weight was recorded 13 - 15 days after curing.
- Harvesting was performed in the first week of November 2023 and 2024 after 50 % neck fall.

Physiological and biochemical parameters

- **MSI:** This parameter was determined at 45 and 55 DAT using 100 mg of 2 cm leaf discs from the third fully developed leaf (22). Discs were placed in two sets of test tubes containing 10 mL double-distilled water. One set was incubated at 40 °C for 30 min to measure initial electrical conductivity (C1) and the other at 100 °C for 10 min to measure final conductivity (C2). MSI was calculated as,

$$\text{MSI}\ \% = [1 - \left(\frac{C1}{C2}\right) \text{x}\ 100]$$

- **Chlorophyll content**: It was estimated using a non-maceration method with dimethyl sulfoxide (DMSO) as the solvent (22). A fresh leaf sample weighing 0.05 g was incubated in 10 mL of DMSO in darkness for 24 hr or until the tissue became colorless. The absorbance of the resulting extract was then measured at 645 nm and 663 nm using a spectrophotometer, with a DMSO blank for calibration.

Total chlorophyll concentration was calculated using the following formula (23) and expressed in mg/g fresh weight (FW).

Total Chlorophyll (mg/g FW) =

(20.2×A645) + (8.02×A663) (20.2×A645) + (8.02×A663) × (V / W)

- **Dry matter yield:** Dry matter yield was assessed at 45 and 55 DAT by harvesting five plants per plot in each replication. Samples were washed, separated into bulbs and leaves, chopped, air-dried and then oven-dried at 60 °C until constant weight. Dry weights of leaves and bulbs were recorded separately and summed to calculate total dry matter yield.

Statistical analysis

All data were compiled in Microsoft Excel to calculate mean values. The data were then subjected to a two-factor analysis of variance (ANOVA) following the statistical model for a split-plot design, using OPSTAT software (HAU, Hisar). This approach was chosen to accurately assess the main effects of the two experimental factors as well as their interaction, while accounting for the different error terms associated with the main plots and subplots. The significance of differences among treatment means was determined at the 5 % probability level ($P < 0.05$). Results are presented with the standard error of the mean (SEm) and the critical difference (CD) values to facilitate comparisons.

Results

Plant height (cm)

Waterlogging stress significantly reduced plant height in all onion genotypes at 55 DAT compared to controls, while at 45 DAT it was found non-significant (Table 1). Under waterlogging treatment (D1), mean plant height decreased substantially from 26.8 cm in 2023 to 30.6 cm in 2024, while control plants (D2) maintained vigorous growth (38.2 cm in 2023; 41.9 cm in 2024). Notably, no significant differences were observed at 45 DAT between treatments in 2024 ($P > 0.05$), indicating that the adverse effects of waterlogging became pronounced only at the later growth stage.

Among the genotypes, T1 (Acc. 1666) consistently recorded the highest plant height at 55 DAT (36.0 cm in 2023; 41.3 cm in 2024), which was statistically superior to all other genotypes as evidenced by the CD values (1.5-1.9). T2, T3 and T4 formed a statistically similar group with moderate plant heights ranging from 33.9 to 34.3 cm in 2023 and 38.1 to 38.5 cm in 2024.

Table 1. Effect of waterlogging on plant height (cm) in onion genotypes at 45 and 55 DAT

Main-plot	45 DAT (cm)		55 DAT (cm)	
	Year 2023	Year 2024	Year 2023	Year 2024
D1	36.40	40.91	26.80	30.60
D2	34.60	39.12	38.20	41.90
SE (m) ±	0.10	0.70	0.30	0.30
CD at 5 %	0.30	NS	0.90	0.90
Sub-plot				
T1	34.60	39.10	36.00	41.30
T2	35.70	40.20	33.90	38.50
T3	35.90	40.40	34.30	38.30
T4	36.00	40.50	34.10	38.10
T5	36.30	40.80	30.30	34.80
T6	35.90	40.40	32.50	35.00
T7	33.60	38.10	29.30	32.10
T8	36.10	40.60	29.20	32.00
SE (m) ±	0.80	1.00	0.50	0.70
CD at 5 %	NS	NS	1.50	1.90
Main x sub-Interaction				
SE (m) ±	1.10	1.40	0.70	0.90
CD at 5 %	NS	NS	2.10	2.70

In contrast, T8 exhibited the lowest plant height (29.2 cm in 2023; 32.0 cm in 2024), closely followed by T7 (29.3 cm in 2023; 32.1 cm in 2024), both showing significant reductions compared to the top-performing genotypes.

Interaction analysis (Table 2 (i & ii)) revealed that under waterlogging conditions (D1), D1T1 (Acc. 1666) achieved the highest plant height in both years (32.0 cm in 2023; 39.0 cm in 2024), demonstrating superior waterlogging tolerance. The poorest performance under waterlogging was observed in D1T7 (22.6 cm in 2023; 25.1 cm in 2024) and D1T8 (23.1 cm in 2023; 24.6 cm in 2024). Control treatments (D2) maintained uniformly higher plant heights across all genotypes, with values ranging from 35.4 to 43.8 cm. Comparing the magnitude of waterlogging impact, D2T1 (Acc. 1666) outperformed its waterlogged counterpart (D1T1) by 8.1 cm in 2023 and 4.6 cm in 2024, while the most sensitive genotypes (T7 and T8) showed dramatic reductions of 13.4-13.9 cm in 2023 and 13.9-14.8 cm in 2024 when subjected to waterlogging, indicating significant genotypic variation in waterlogging tolerance.

Number of leaves

Waterlogging stress caused a significant reduction in the number of leaves in all onion genotypes at 55 DAT compared to 45 DAT (Table 3). Under waterlogging treatment (D1), the number of leaves showed a decline in both the measurements taken after 45 DAT and 55 DAT, while control plants (D2) noted an increase in leaves. The CD values (0.24-0.33) confirmed the statistical significance of these changes. Among the genotypes, Acc. 1666; T1 consistently maintained the highest leaf count at 55 DAT in

Table 2 (i & ii). Interaction effect of plant height (cm) influenced by plant height at 55 DAT in 2023 and 2024

(i)

Main x sub-Interaction (2023)	D1	D2	Mean B
T1	32.00	40.10	36.00
T2	28.40	39.40	33.90
T3	28.80	39.80	34.30
T4	29.70	38.40	34.10
T5	24.50	36.10	30.30
T6	24.90	40.00	32.50
T7	22.60	36.00	29.30
T8	23.10	35.40	29.20
Mean A	26.80	38.20	
SE (m) ±	0.70		
CD at 5 %	2.21		

(ii)

Main x sub-Interaction (2024)	D1	D2	Mean B
T1	39.00	43.60	41.30
T2	33.70	43.40	38.50
T3	32.80	43.80	38.30
T4	34.40	41.90	38.10
T5	28.50	41.10	34.80
T6	26.90	43.00	35.00
T7	25.10	39.00	32.10
T8	24.60	39.40	32.00
Mean A	30.60	41.90	
SE (m) ±	0.90		
CD at 5 %	2.70		

Table 3. Effect of waterlogging on number of leaves in onion genotypes before and after treatment

Main-plot	45 DAT		55 DAT	
	Year 2023	Year 2024	Year 2023	Year 2024
D1	6.89	7.09	3.83	4.63
D2	6.91	7.11	7.76	8.68
SE (m) ±	0.02	0.02	0.04	0.05
CD at 5 %	NS	NS	0.24	0.33
Sub-plot				
T1	6.64	6.84	6.63	8.43
T2	6.98	7.18	5.62	7.12
T3	6.93	7.13	6.18	6.68
T4	6.71	6.91	6.34	7.54
T5	7.20	7.40	5.01	6.21
T6	6.59	6.79	5.39	5.61
T7	7.04	7.24	5.58	5.76
T8	7.13	7.33	5.60	5.85
SE (m) ±	0.15	0.15	0.13	0.14
CD at 5 %	NS	0.43	0.38	0.39
Interaction				
SE (m) ±	0.21	0.21	0.18	0.19
CD at 5 %	NS	NS	0.54	0.55

both years of assessment (6.63 in 2023 and 8.43 in 2024), which was statistically at par with Bhima Dark Red; T4 (6.34 in 2023; 7.54 in 2024) and W 355; T3 (6.18 in 2023). In contrast, Bhima Red; T5 (5.01 in 2023) and Phule Samarth (T6) (5.61 in 2024) recorded the lowest leaf counts under waterlogging.

Interaction analysis revealed that under waterlogging (D1), Acc. 1666 (D1T1) had the highest leaf number, closely followed by Bhima Dark Red. Bhima Shubhra (D1T7) and Bhima Super (D1T8) showed the lowest leaf counts (3.08, 3.00 in 2023; 3.22, 3.29 in 2024) (Table 4 (i & ii)). Control treatments (D2) maintained high leaf numbers across all genotypes, reflecting optimal growth. The difference between D2 and D1 for Acc. 1666 (D2T1 vs. D1T1) was 3.13 leaves in both years. The least-performing D1 genotypes lagged by over five leaves compared to their D2 counterparts, highlighting the severe impact of waterlogging and genotype-specific resilience.

Table 4 (i & ii). Interaction effect of waterlogging condition on number of leaves in onion genotypes at 55 DAT in 2023 and 2024

(i)

Main x sub-Interaction (2023)

Genotypes	D1	D2	Mean B
T1	5.07	8.20	6.63
T2	3.42	7.82	5.62
T3	4.72	7.65	6.18
T4	5.02	7.67	6.34
T5	3.20	6.82	5.01
T6	3.17	7.62	5.39
T7	3.08	8.08	5.58
T8	3.00	8.20	5.60
Mean A	3.83	7.76	
SE (m) ±	0.18		
CD at 5 %	0.54		

(ii)

Main x sub-Interaction (2024)

Genotypes	D1	D2	Mean B
T1	6.87	10.00	8.43
T2	5.52	8.72	7.12
T3	4.92	8.45	6.68
T4	5.92	9.17	7.54
T5	3.90	8.52	6.21
T6	3.39	7.84	5.61
T7	3.22	8.30	5.76
T8	3.29	8.41	5.85
Mean A	4.63	8.68	
SE (m) ±	0.19		
CD at 5 %	0.55		

Leaf area (cm^2)

Waterlogging stress significantly reduced leaf area in all onion genotypes at 55 DAT compared to controls (Table 5). Under waterlogging treatment (D1), leaf area increased only minimally from 20.86 cm^2 in 2023 to 22.93 cm^2 in 2024, while control plants (D2) exhibited robust increases (26.6 cm^2 in 2023; 28.9 cm^2 in 2024). The CD values (0.30-0.45) confirmed the statistical significance of these reductions. Among the genotypes, Acc. 1666 consistently recorded the highest leaf area at 55 DAT under waterlogging (26.1 cm^2 in 2023; 28.3 cm^2 in 2024), which was statistically at par with Acc. 1630 (25.2 cm^2 in 2023) and W 355 (25.0, 26.7 cm^2), as these values fell within the CD range (1.57-1.77). In contrast, Bhima Red exhibited the lowest leaf area (20.2 cm^2 in 2023; 24.4 cm^2 in 2024) under waterlogging conditions.

Interaction analysis (Table 6 (i & ii)) showed that under waterlogging (D1), D1T1 (Acc. 1666) achieved the highest leaf area, closely followed by D1T4 (Bhima Dark Red). The lowest performance was observed in D1T5 (Bhima Red) (16.97 cm^2 in 2023; 20.19 cm^2 in 2024). Control treatments (D2) maintained uniformly high leaf areas across all genotypes. Comparing D2

Table 5. Effect of waterlogging on leaf area (cm^2) in onion genotypes before and after treatment

Main-plot	45 DAT (cm^2)		55 DAT (cm^2)	
	Year 2023	Year 2024	Year 2023	Year 2024
D1	19.53	24.15	20.86	22.93
D2	19.89	21.60	26.58	28.89
SE (m) ±	0.45	0.45	0.05	0.07
CD at 5 %	NS	NS	0.30	0.45
Sub-plot				
T1	19.74	23.22	26.08	28.31
T2	19.36	22.16	25.17	26.70
T3	19.98	22.83	24.97	26.75
T4	19.72	23.42	24.86	26.64
T5	19.27	21.83	20.22	24.45
T6	20.55	23.19	23.11	24.74
T7	19.83	23.46	22.36	24.99
T8	19.24	22.91	22.96	24.70
SE (m) ±	0.52	0.60	0.54	0.61
CD at 5 %	NS	NS	1.57	1.77
Main x sub-Interaction				
SE (m) ±	0.73	0.85	0.77	0.86
CD at 5 %	NS	NS	2.22	2.50

Table 6 (i & ii). Interaction effect of waterlogging condition on leaf area (cm^2) of onion genotypes at 55 DAT in 2023 and 2024

(i)

Main x sub-Interaction (2023)	D1	D2	Mean B
T1	24.26	27.90	26.08
T2	23.38	26.97	25.17
T3	22.97	26.97	24.97
T4	23.42	26.31	24.86
T5	16.97	23.47	20.22
T6	18.96	27.26	23.11
T7	17.97	26.76	22.36
T8	18.96	26.96	22.96
Mean	20.86	26.58	
SE (m) ±		0.77	
CD at 5 %		2.22	

(ii)

Main x sub-Interaction (2024)	D1	D2	Mean B
T1	26.49	30.13	28.31
T2	24.91	28.50	26.70
T3	24.70	28.80	26.75
T4	25.25	28.04	26.64
T5	20.19	28.70	24.45
T6	20.59	28.89	24.74
T7	21.10	28.89	24.99
T8	20.20	29.19	24.70
Mean	22.93	28.89	25.91
SE (m) ±		0.86	
CD at 5 %		2.50	

with D1, D2T1 (Acc. 1666) outperformed its D1 counterpart by 3.64 cm^2 in both years, while the least-performing D1T5 (Bhima Red) lagged behind its D2 counterpart by 6.50 cm^2 (2023) and 8.51 cm^2 (2024).

MSI percentage

Waterlogging stress significantly reduced the MSI content in all onion genotypes at 55 DAT compared to controls, while no significant effect was observed at 45 DAT (Table 7). Under waterlogging treatment (D1), mean MSI percentage decreased from 61.75 % at 45 DAT in 2023 to 50.43 % at 55 DAT, with similar declines observed in 2024 (59.75 % to 47.77 %), while control plants (D2) maintained higher stability (65.26 % to 66.42 % in 2023; 63.26 % to 63.75 % in 2024). The CD values (1.04-2.18) confirmed the statistical significance of these reductions across both time points and years.

Among the genotypes, T4 consistently recorded the highest MSI percentage at 55 DAT (61.75 % in 2023; 63.08 % in 2024), which was statistically at par with T1 (62.46 % in 2023; 63.79 % in 2024) as these values fell within the CD range (1.44-2.09). T2 and T3 formed a group with moderate MSI percentage (55.54-56.15 % in 2023; 56.87-57.48 % in 2024), showing no significant differences from each other. In contrast, T8 exhibited the lowest MSI percentage (50.51 % in 2023; 51.84 % in 2024), closely followed by T7 (51.95 % in 2023; 53.28 % in 2024), both indicating greater membrane damage compared to the top performers.

Table 7. Effect of waterlogging on MSI % in onion genotypes at 45 and 55 DAT during 2023 and 2024

Main-plot	45 DAT		55 DAT	
	Year 2023	Year 2024	Year 2023	Year 2024
D1	61.75	59.75	50.43	47.77
D2	65.26	63.26	66.42	63.75
SE (m) ±	0.36	0.36	0.37	0.35
CD at 5 %	2.18	2.18	1.10	1.04
Sub-plot				
T1	65.86	63.86	62.46	63.79
T2	59.98	57.98	55.54	56.87
T3	63.40	61.40	56.15	57.48
T4	67.91	65.91	61.75	63.08
T5	64.46	62.46	54.61	55.94
T6	64.08	62.08	53.12	54.45
T7	63.96	61.96	51.95	53.28
T8	58.37	56.37	50.51	51.84
SE (m) ±	0.85	0.85	0.72	0.51
CD at 5 %	2.47	2.47	2.09	1.44
Main x sub-Interaction				
SE (m) ±	1.20	1.02	1.02	0.93
CD at 5 %	NS	NS	3.06	2.80

Interaction analysis (Table 8 (i & ii)) revealed that under waterlogging conditions (D1), D1T1 and D1T4 achieved the highest MSI percentage in both years (59.73 % and 58.57 % in 2023; 57.06 % and 55.91 % in 2024), demonstrating better membrane integrity and tolerance. The poorest performance under waterlogging was observed in D1T7 (42.37 % in 2023; 39.70 % in 2024) and D1T8 (45.31 % in 2023; 42.64 % in 2024). Control treatments (D2) maintained uniformly higher MSI percentage across all genotypes, with values ranging from 58.38 % to 70.52 %. Comparing the magnitude of waterlogging impact, D2T1 outperformed its waterlogged counterpart (D1T1) by 10.79 % in 2023 and 10.79 % in 2024, while the most sensitive genotypes (T7 and T8) showed substantial reductions of 24.49 %-27.16 % in 2023 and 15.74 %-24.49 % in 2024 when subjected to waterlogging, highlighting significant genotypic variation in stress response.

Table 8 (i & ii). Interaction effect of waterlogging condition on MSI % of onion genotypes at 55 DAT in 2023 and 2024

(i)

Main x sub-Interaction (2023)	D1	D2	Mean B
T1	59.73	70.52	65.12
T2	52.22	64.20	58.21
T3	51.19	66.45	58.82
T4	58.57	70.26	64.42
T5	47.96	66.59	57.27
T6	46.12	65.44	55.78
T7	42.37	66.86	54.61
T8	45.31	61.04	53.18
Mean	50.43	66.42	
SE (m) ±		1.02	
CD at 5 %		3.06	

(ii)

Main x sub-Interaction (2024)			
	D1	D2	Mean B
T1	57.06	67.85	62.46
T2	49.55	61.53	55.54
T3	48.52	63.78	56.15
T4	55.91	67.59	61.75
T5	45.29	63.93	54.61
T6	43.45	62.78	53.12
T7	39.70	64.19	51.95
T8	42.64	58.38	50.51
Mean	47.77	63.75	
SE (m) ±	0.93		
CD at 5 %	2.80		

Total chlorophyll

Waterlogging stress significantly reduced the total chlorophyll content in all onion genotypes at 55 DAT compared to controls, while no significant effect was observed at 45 DAT (Table 9). At 55 DAT, the mean chlorophyll content in waterlogged plots (D1) was 4.43 mg/g in 2023 and 3.78 mg/g in 2024, which was significantly lower than in the control plots (D2), where it was 5.94 mg/g and 5.29 mg/g respectively. The CD value of 0.71 confirmed the statistical significance of this reduction in both years.

Among the genotypes, T1 (Acc. 1666) consistently recorded the highest total chlorophyll content at 55 DAT (7.00 mg/g in 2023; 6.35 mg/g in 2024), which was statistically superior to all other genotypes as per the CD values (0.31 - 0.34). T4, T2 and T3 formed a statistically similar group with moderate chlorophyll levels ranging from 5.13 to 5.39 mg/g in 2023 and 4.48 to 4.74 mg/g in 2024. In contrast, T7 exhibited the lowest chlorophyll content (4.37 mg/g in 2023; 3.72 mg/g in 2024), closely followed by T6 (4.65 mg/g in 2023; 4.00 mg/g in 2024), both showing significant reductions.

Interaction analysis (Table 10 (i & ii)) revealed that under waterlogging conditions (D1), D1T1 (Acc. 1666) maintained the highest chlorophyll content in both years (6.82 mg/g in 2023; 6.17 mg/g in 2024), demonstrating superior tolerance to waterlogging -induced chlorosis. The poorest performance under waterlogging was observed in D1T7 (2.88 mg/g in 2023; 2.23 mg/g in 2024) and D1T6 (3.80 mg/g in 2023; 3.15 mg/g in 2024). Control treatments (D2) maintained uniformly higher chlorophyll levels across all genotypes. Comparing the magnitude of the interaction, D2T1 (Acc. 1666) only slightly outperformed its waterlogged counterpart (D1T1) by 0.36 mg/g in both years, whereas the most sensitive genotype, T7, suffered a dramatic reduction of 2.98 mg/g in both years when subjected to waterlogging, indicating significant genotypic variation in maintaining photosynthetic pigments under stress.

Table 9. Effect of waterlogging on total chlorophyll content (mg/g) in onion genotypes at 45 and 55 DAT during 2023 and 2024

Main-plot	45 DAT		55 DAT	
	Year 2023	Year 2024	Year 2023	Year 2024
D1	3.84	3.19	4.43	3.78
D2	3.60	2.95	5.94	5.29
SE (m) ±	0.05	0.05	0.12	0.12
CD at 5 %	NS	NS	0.71	0.71
Sub-plot				
T1	3.63	2.98	7.00	6.35
T2	3.94	3.29	5.13	4.48
T3	3.93	3.28	5.22	4.57
T4	4.22	3.57	5.39	4.74
T5	4.08	3.43	4.98	4.33
T6	3.33	2.68	4.65	4.00
T7	2.82	2.17	4.37	3.72
T8	3.83	3.18	4.73	4.08
SE (m) ±	0.16	0.17	0.11	0.12
CD at 5 %	0.47	0.48	0.31	0.34
Main x sub Interaction				
SE (m) ±	0.23	0.24	0.15	0.17
CD at 5 %	NS	NS	0.44	0.49

Table 10 (i & ii). Interaction effect of genotype and treatment on total chlorophyll content (mg/g) at 55 DAT in 2023 and 2024

(i)

Main x sub-Interaction (2023)			
	D1	D2	Mean B
T1	6.82	7.18	7.00
T2	4.46	5.80	5.13
T3	4.41	6.04	5.22
T4	5.31	5.47	5.39
T5	4.05	5.91	4.98
T6	3.80	5.49	4.65
T7	2.88	5.86	4.37
T8	3.67	5.79	4.73
Mean A	4.43	5.94	
SE (m) ±	0.15		
CD at 5 %	0.44		

(ii)

Main x sub-Interaction (2024)			
	D1	D2	Mean B
T1	6.17	6.53	6.35
T2	3.81	5.15	4.48
T3	3.76	5.39	4.57
T4	4.66	4.82	4.74
T5	3.40	5.26	4.33
T6	3.15	4.84	4.00
T7	2.23	5.21	3.72
T8	3.02	5.14	4.08
Mean A	3.78	5.29	
SE (m) ±	0.17		
CD at 5 %	0.49		

Dry matter yield (g/m^2)

The effect of waterlogging on total dry matter yield became statistically significant at the 55 DAT growth stage, whereas no significant differences among treatments or genotypes were observed at the earlier 45 DAT mark (Table 11). At 55 DAT, waterlogging stress (D1) significantly reduced the mean dry matter yield to 61.92 g/m^2 in 2023 and 65.41 g/m^2 in 2024. These values were substantially lower than those recorded in the control plots (D2), which produced 79.19 g/m^2 and 86.73 g/m^2 respectively. The statistical significance of this reduction at the later stage was confirmed by the CD values (4.71 in 2023; 18.46 in 2024).

Analysis of genotypic performance at 55 DAT revealed that T1 (Acc. 1666) consistently produced the highest total dry matter yield (78.39 g/m^2 in 2023; 90.21 g/m^2 in 2024). This was

Table 11. Effect of waterlogging on total dry matter yield (g/m^2) in onion genotypes at 45 and 55 DAT during 2023 and 2024

Main-plot	45 DAT		55 DAT	
	Year 2023	Year 2024	Year 2023	Year 2024
D1	46.80	54.09	61.92	65.41
D2	50.66	69.88	79.19	86.73
SE (m) ±	0.61	2.93	0.77	3.03
CD at 5 %	3.72	NS	4.71	18.46
Sub-plot				
T1	50.77	69.92	78.39	90.21
T2	51.82	64.48	69.88	70.72
T3	50.83	65.32	68.52	69.73
T4	50.13	65.71	77.71	87.76
T5	48.91	59.67	66.49	70.17
T6	48.82	56.77	68.22	73.98
T7	44.44	58.83	65.10	68.47
T8	44.14	55.20	70.12	77.50
SE (m) ±	1.38	4.64	1.69	4.37
CD at 5 %	3.98	NS	4.90	12.65
Main x sub-Interaction				
SE (m) ±	1.94	6.57	2.39	6.18
CD at 5 %	5.63	NS	6.93	17.89

statistically at par with the yield of T4 (77.71 g/m^2 in 2023; 87.76 g/m^2 in 2024), as their values fell within the CD range (4.90 - 12.65). In contrast, T7 consistently exhibited the lowest dry matter accumulation (65.10 g/m^2 in 2023; 68.47 g/m^2 in 2024), performing significantly poorer than the leading genotypes.

The interaction between waterlogging and genotype was also significant at 55 DAT (Table 12 (i & ii)). Under waterlogging stress (D1), D1T1 (Acc. 1666) demonstrated superior tolerance by achieving the highest dry matter yield in both years (77.31 g/m^2 and 88.09 g/m^2). The most sensitive response to waterlogging was observed in D1T7, which recorded the lowest yields under stress (51.14 g/m^2 and 50.07 g/m^2). A comparison of treatment effects highlights the genetic differences in tolerance; the yield penalty for the tolerant genotype T1 under waterlogging was minimal, with a reduction of only 2.16 g/m^2 in 2023 and 4.24 g/m^2 in 2024 compared to its control. However, the sensitive genotype T7 suffered a drastic yield loss of 27.93 g/m^2 in 2023 and 36.80 g/m^2 in 2024, confirming a strong interaction between genotype and waterlogging stress.

Table 12 (i & ii). Interaction effect of genotype and treatment on total dry matter yield (g/m^2) at 55 DAT in 2023 and 2024

(i)

Main x sub-Interaction (2023)	D1	D2	Mean B
T1	77.31	79.47	78.39
T2	61.74	78.03	69.88
T3	58.58	78.47	68.52
T4	72.38	83.03	77.71
T5	56.94	76.03	66.49
T6	56.86	79.57	68.22
T7	51.14	79.07	65.10
T8	60.41	79.83	70.12
Mean A	61.92	79.19	
SE (m) ±		2.39	
CD at 5 %		6.93	

(ii)

Main x sub-Interaction (2024)	D1	D2	Mean B
T1	88.09	92.33	90.21
T2	62.97	78.47	70.72
T3	58.30	81.17	69.73
T4	76.29	99.23	87.76
T5	57.70	82.63	70.17
T6	62.57	85.40	73.98
T7	50.07	86.87	68.47
T8	67.27	87.73	77.50
Mean A	65.41	86.73	
SE (m) ±		6.18	
CD at 5 %		17.89	

Equatorial and polar bulb diameters (mm)

Waterlogging stress significantly reduced both equatorial and polar bulb diameters in all onion genotypes at harvest compared to controls (Table 13). For equatorial diameter, waterlogging treatment (D1) resulted in substantially smaller bulbs with mean diameters of 37.93 mm in 2023 and 38.77 mm in 2024, which were significantly lower than control plants (D2) that achieved 47.00 mm and 50.42 mm respectively. Similarly, polar diameter under waterlogging was reduced to 33.08 mm in 2023 and 35.56 mm in 2024, compared to 39.76 mm and 44.48 mm in control plots. The CD values (2.94-6.48 for equatorial; 1.03-6.48 for polar) confirmed the statistical significance of these reductions across both parameters and years.

Genotypic analysis revealed distinct performance patterns for bulb dimensions. For equatorial diameter, T1 (Acc. 1666) and T4 consistently recorded the highest values (50.07-52.72 mm), which were statistically at par as evidenced by the CD values (2.27 - 3.20). T2, T3, T7 and T8 formed intermediate groups with moderate diameters, while T5 exhibited consistently poor performance with the lowest equatorial diameter (31.98 mm in

Table 13. Effect of waterlogging on equatorial and polar bulb diameters (mm) in onion genotypes at harvest during 2023 and 2024

Main	Equatorial diameter (mm)		Polar diameter (mm)	
	Year 2023	Year 2024	Year 2023	Year 2024
D1	37.93	38.77	33.08	35.56
D2	47.00	50.42	39.76	44.48
SE (m) ±	0.80	0.48	0.17	1.07
CD at 5 %	4.85	2.94	1.03	6.48
Sub-plot				
T1	50.07	52.72	41.56	44.19
T2	44.07	47.80	41.17	41.05
T3	43.39	45.81	38.12	40.70
T4	50.91	52.15	40.60	43.59
T5	31.98	38.76	25.87	38.85
T6	40.05	39.64	32.73	35.06
T7	36.64	40.87	36.77	38.56
T8	42.59	39.02	34.53	38.12
SE (m) ±	0.78	1.11	0.55	1.15
CD at 5 %	2.27	3.20	1.59	3.35
Main X sub-Interaction				
SE (m) ±	2.27	3.20	0.77	1.63
CD at 5 %	3.07	4.32	2.24	4.73

2023; 38.76 mm in 2024). For polar diameter, T1 again demonstrated superior performance (41.56 mm in 2023; 44.19 mm in 2024), statistically similar to T2 in 2023 (41.17 mm) and T4 in both years (40.60—43.59 mm). T5 showed the most severe reduction in polar diameter, particularly in 2023 (25.87 mm), indicating high sensitivity to stress conditions.

Interaction analysis (Table 14 (i-iv)) revealed significant genotype × treatment effects for both bulb dimensions. Under waterlogging conditions (D1), D1T1 (Acc. 1666) and D1T4 maintained the largest equatorial diameters in both years (45.41 -49.47 mm), demonstrating superior tolerance. The poorest performance under waterlogging was consistently observed in D1T5, which recorded the smallest equatorial diameters (26.86 mm in 2023; 34.95 mm in 2024) and polar diameters (22.44 mm in 2023; 36.60 mm in 2024). Comparing the magnitude of waterlogging impact, the tolerant genotype T1 showed relatively modest reductions of 9.33 mm (equatorial) and 2.09 mm (polar) in 2023, whereas the sensitive genotype T5 suffered dramatic decreases of 10.24 mm (equatorial) and 6.87 mm (polar) in the same year. This differential response pattern confirms significant genetic variation in maintaining bulb size under waterlogging stress, with T1 and T4 demonstrating superior adaptation mechanisms for bulb development under adverse conditions.

Table 14 (i-iv). Interaction effect of genotype and treatment on equatorial and polar bulb diameters (mm) at harvest in 2023 and 2024

(i)

Main X sub-Interaction 2023 Elliptical diameter (mm)	D 1	D 2	Mean A
T 1	45.41	54.74	50.07
T 2	37.76	50.38	44.07
T 3	37.51	49.27	43.39
T 4	47.22	54.61	50.91
T 5	26.86	37.10	31.98
T 6	39.29	40.80	40.05
T 7	33.18	40.09	36.64
T 8	36.18	49.01	42.59
Mean B	37.93	47.00	
SE (m) ±		2.27	
CD at 5 %		3.07	

(ii)

Main X sub-Interaction 2024 Elliptical diameter (mm)	D 1	D 2	Mean A
T 1	49.47	55.97	52.72
T 2	41.19	54.41	47.80
T 3	41.19	50.42	45.81
T 4	47.70	56.60	52.15
T 5	34.95	42.57	38.76
T 6	32.37	46.91	39.64
T 7	34.92	46.82	40.87
T 8	28.37	49.68	39.02
Mean B	38.77	50.42	
SE (m) ±		3.20	
CD at 5 %		4.32	

(iii)

Main X sub-Interaction 2023 Polar diameter (mm)	D 1	D 2	Mean
T 1	40.51	42.60	41.56
T 2	36.64	45.70	41.17
T 3	33.67	42.56	38.12
T 4	38.22	42.98	40.60
T 5	22.44	29.31	25.87
T 6	29.27	36.18	32.73
T 7	33.74	39.79	36.77
T 8	30.12	38.94	34.53
Mean	33.08	39.76	36.42
SE (m) ±		0.77	
CD at 5 %		2.24	

(iv)

Main X sub-Interaction 2024 Polar diameter (mm)	D 1	D 2	Mean
T 1	43.53	44.86	44.19
T 2	36.77	45.34	41.05
T 3	36.20	45.21	40.70
T 4	39.66	47.51	43.59
T 5	36.60	41.09	38.85
T 6	30.54	39.58	35.06
T 7	32.87	44.25	38.56
T 8	28.28	47.96	38.12
Mean	35.56	44.48	40.02
SE (m) ±		1.63	
CD at 5 %		4.73	

Effect of waterlogging on onion yield

Waterlogging stress significantly reduced the final onion bulb yield at harvest in both years (Table 15). In 2023, the mean yield under waterlogging (D1) was 11.26 t/ha, significantly lower than the 12.47 t/ha achieved in the control plots (D2). This negative impact was even more pronounced in 2024, with the waterlogged yield dropping to 7.19 t/ha compared to 12.19 t/ha for the control. The CD values (0.58 in 2023; 0.22 in 2024) confirmed that these reductions were statistically significant.

Among the genotypes, T4 (15.34 t/ha in 2023; 15.28 t/ha in 2024) and T1 (14.70 t/ha in 2023; 12.60 t/ha in 2024) consistently produced the highest bulb yields. In 2023, these two genotypes were statistically at par, while in 2024, T4 significantly outperformed all others, as indicated by the CD values (1.29 in 2023; 0.48 in 2024). In contrast, T7 (9.33 t/ha in 2023; 6.63 t/ha in 2024) and T8 (9.57 t/ha in 2023; 6.66 t/ha in 2024) consistently recorded the lowest yields, performing significantly poorer than all other genotypes in both years.

Table 15. Effect of waterlogging on onion bulb yield (t/ha) in different genotypes at harvest during 2023 and 2024

Yield t/ha		
Main-plot	**Year 2023**	**Year 2024**
D1	11.26	7.19
D2	12.47	12.19
SE (m) ±	0.10	0.04
CD at 5 %	0.58	0.22
Sub-plot		
T1	14.70	12.60
T2	13.32	10.50
T3	12.82	8.51
T4	15.34	15.28
T5	9.56	8.81
T6	10.25	8.55
T7	9.33	6.63
T8	9.57	6.66
SE (m) ±	0.45	0.17
CD at 5 %	1.29	0.48
Main x sub-Interaction		
SE (m) ±	0.63	0.23
CD at 5 %	1.83	0.68

The interaction analysis (Table 16 (i & ii)) revealed a highly significant effect of waterlogging on genotypic performance. The tolerant genotypes T4 and T1 demonstrated remarkable yield stability under waterlogging stress (D1). In 2023, D1T4 and D1T1 yielded 15.60 t/ha and 14.58 t/ha respectively, showing almost no reduction compared to their control plots. In 2024, D1T4 still produced a more yield 13.13 t/ha. Conversely, the sensitive genotypes suffered significantly more yield losses under stress. The most significant effect was seen in D1T7, which yielded only 7.72 t/ha in 2023 and dropped to 3.83 t/ha in 2024. Similarly, D1T6 and D1T8 also showed severe yield reductions, particularly in 2024, with yields dropping to 5.22 t/ha and 4.44 t/ha respectively. This highlights a profound interaction, where waterlogging caused minimal yield loss in tolerant genotypes like T4 and T1 but resulted in a yield collapse for sensitive genotypes like T6, T7 and T8.

Discussion

The differential response of onion genotypes to waterlogging stress underscores a complex interplay of physiological, biochemical and molecular adaptations that determine crop resilience and productivity (2). Among the evaluated genotypes, Acc. 1666 and Bhima Dark Red consistently demonstrate superior tolerance to waterlogging, maintaining robust plant height, leaf retention, leaf area and photosynthetic capacity under stress (19). These genotypes exhibit enhanced adaptive traits such as efficient root oxygen transport, upregulated aerenchyma formation and elevated antioxidant enzyme activity, which collectively mitigate the deleterious effects of hypoxia and oxidative stress (24). In contrast, Bhima Shubhra and Bhima Super display acute susceptibility, with marked declines in growth parameters, leaf senescence and membrane integrity, reflecting systemic failures in metabolic reprogramming, ROS scavenging and resource allocation (13). The resilience of Acc. 1666 and Bhima Dark Red is further evidenced by their ability to sustain high MSI and chlorophyll content, enabling continued carbon assimilation and energy production even under adverse conditions (19).

Table 16 (i & ii). Interaction effect of genotype and treatment on onion bulb yield (t/ha) at harvest in 2023 and 2024

(i)

Main x sub-Interaction (2023)	D1	D2	Mean B
T1	14.58	14.83	14.70
T2	12.62	14.03	13.32
T3	12.90	12.74	12.82
T4	15.60	15.08	15.34
T5	9.48	9.64	9.56
T6	8.78	11.73	10.25
T7	7.72	10.94	9.33
T8	8.39	10.74	9.57
Mean A	11.26	12.47	
SE (m) ±		0.63	
CD at 5 %		1.83	

(ii)

Main x sub-Interaction (2024)	D1	D2	Mean B
T1	11.24	13.95	12.60
T2	7.59	13.41	10.50
T3	6.02	11.01	8.51
T4	13.13	17.43	15.28
T5	6.03	11.58	8.81
T6	5.22	11.88	8.55
T7	3.83	9.42	6.63
T8	4.44	8.87	6.66
Mean A	7.19	12.19	
SE (m) ±		0.23	
CD at 5 %		0.68	

At the biochemical level, waterlogging induces a metabolic shift from aerobic respiration to anaerobic fermentation, a process mediated by hypoxia-responsive genes such as alcohol dehydrogenase (ADH) and pyruvate decarboxylase (PDC) (25). Tolerant genotypes like Acc. 1666 and Bhima Dark Red likely possess enhanced expression of these genes, along with robust aldehyde dehydrogenase (ALDH) activity, which detoxifies cytotoxic fermentation byproducts and preserves cellular integrity (2, 19). Concurrently, tolerant genotypes maintain cellular stability and reduce oxidative damage through enhanced physiological mechanisms that mitigate the effects of hypoxia. These adaptive traits help preserve membrane integrity and photosynthetic efficiency under waterlogging stress, contributing to their better performance compared to susceptible genotypes (26, 27). This integrated defense strategy allows for sustained leaf area, chlorophyll retention and assimilate partitioning to developing bulbs, even under prolonged waterlogging (28, 29). Such coordinated physiological and biochemical adaptations are critical for maintaining onion productivity in flood-prone environments (28). In contrast, susceptible genotypes such as Bhima Shubhra and Bhima Super experience irreversible membrane peroxidation, chlorophyll degradation and accelerated leaf senescence, culminating in reduced photosynthetic output and impaired bulb development (30).

The superior yield performance of Bhima Dark Red and Acc. 1666 under waterlogging is underpinned by their ability to maintain efficient photo assimilate partitioning and cell expansion in storage organs (2). These genotypes exhibit higher dry matter accumulation, larger bulb dimensions and greater marketable yields compared to their sensitive counterparts, which suffer from carbohydrate starvation and poor sink strength (28, 29). The interaction between growth stage and waterlogging stress is also critical, with the bulb initiation and development phases (20-80 DAT) being particularly sensitive to flooding (31). Stress during these stages severely hampers leaf area, chlorophyll content and bulb size, while early vegetative and maturity phases are relatively less affected (32). This highlights the importance of genotype-environment matching and targeted agronomic interventions for minimizing yield losses in flood-prone regions.

The yield performance of onion genotypes under waterlogging stress demonstrates clear differences between tolerant and susceptible cultivars, highlighting the importance of genetic selection for challenging environments (19). Bhima Dark Red consistently emerged as the most resilient genotype, maintaining superior yields under waterlogged conditions, closely followed by Acc. 1666, which also showed robust adaptation to excess moisture stress (2, 31). In contrast, Bhima Shubhra and Bhima Super experienced severe yield penalties, reflecting their high sensitivity and poor adaptation to waterlogged environments (19). The interaction analysis further emphasized these disparities, with Bhima Dark Red achieving the highest yield under waterlogging, while Bhima Shubhra recorded the lowest performance, underscoring the substantial yield advantage of tolerant genotypes over susceptible ones (2, 19, 31). These findings underscore that the ability to sustain yield under waterlogging is a defining trait of tolerant genotypes, making Bhima Dark Red and Acc. 1666 valuable resources for breeding programs, while the poor performance of Bhima Shubhra and Bhima Super highlights the risks of cultivating susceptible varieties in flood-prone areas (28, 31, 32).

Conclusion

The comprehensive evaluation of onion genotypes under waterlogging stress highlights Bhima Dark Red and Acc. 1666 as exemplars of tolerance, exhibiting superior physiological resilience through maintained plant height, leaf retention, chlorophyll content, membrane stability and bulb yield, while Bhima Shubhra and Bhima Super displayed acute susceptibility, with stunted growth, leaf loss and yield collapse. Tolerant onion genotypes exhibit physiological and biochemical traits that help them withstand waterlogging stress, maintaining energy production and cellular stability under hypoxic conditions. In contrast, sensitive genotypes suffer from oxidative damage and impaired metabolic functions, leading to reduced growth and yield. Notably, differences in bulb morphology between genotypes reflect underlying genetic variance influencing carbohydrate partitioning and growth patterns. This study provides valuable genotype-specific insights that can inform breeding programs aimed at enhancing waterlogging tolerance. Future research should focus on exploring the molecular mechanisms underlying these adaptive traits and validating these findings under diverse environmental conditions to support sustainable onion production in flood-prone regions.

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Authors' contributions

ARP conceptualized the study. ARP, MP and SSP contributed to data curation, formal analysis, investigation and methodology. Statistical analysis was done by ARP and SSP. ARP and MP wrote the original draft. The manuscript was reviewed and edited by ARP and SSP. All authors read and approved the manuscript.

Compliance with ethical standards

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