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Effect of *Phalaris minor* and *Medicago denticulata* on Wheat Growth and Yield Under Drought Stress: Physiological and Biochemical Insights

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Abstract

Weed infestation is a major biotic stress that remarkably impacts agricultural productivity worldwide, leading to reduced crop yields and increased management costs. Annually, weeds cause an estimated economic loss of USD 32 billion on a global scale. Additionally, drought is one of the most severe abiotic stresses, restricting plant growth and reducing global agricultural productivity by ~ 50%, threatening food security. Wheat's physiological response to drought stress is well documented; however, its physiological, biochemical, and yield responses to the combined effects of biotic (weed interference) and abiotic (drought) stress remain less understood. To ensure global food security (SDG-2) and develop adaptive strategies against climate threats (SDG-13), understanding the impact of weed interference on wheat physiological, biochemical, and yield responses under drought stress is crucial. Therefore, this study, conducted over two years (2022 and 2023), evaluated the biochemical, physiological, and yield responses of wheat in the presence of its major weeds, *Phalaris minor* and *Medicago denticulata*, at critical competitive period (20 days after sowing) under drought stress. The results revealed that *M. denticulata* interference induced excessive oxidative stress in wheat, as indicated by elevated levels of malondialdehyde (WW: 3.62-fold; DS: 6.58-fold), superoxide ion (Well-Watered: 2.33-fold; Drought Stress: 3.75-fold), and H_2O_2 (WW: 5.82-fold; DS: 8.87-fold). Similarly, *P. minor* interference also triggered oxidative stress, with malondialdehyde (WW: 2.13-fold; DS:

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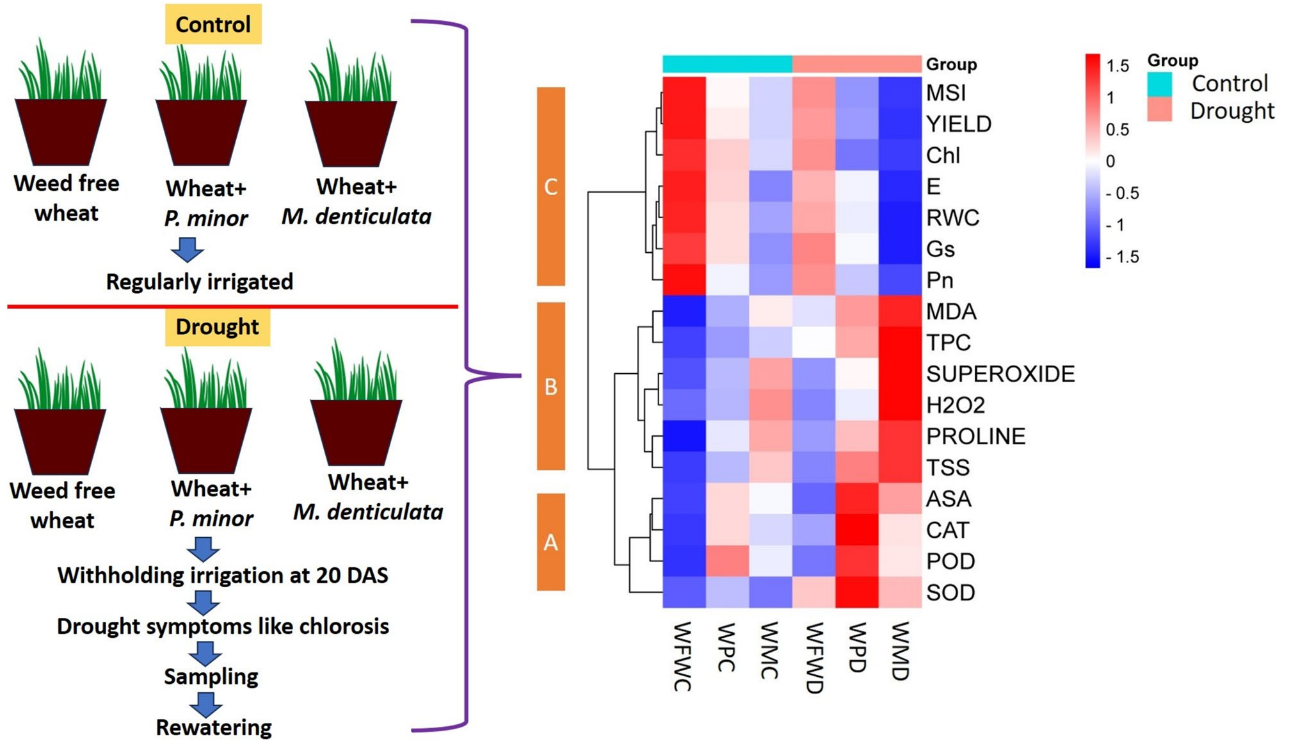
4.79-fold), superoxide ion (WW: 88.76%; DS: 1.58-fold), and H_2O_2 (WW: 1.62-fold; DS: 2.95-fold) accumulation. Reductions in relative water content, membrane stability index, photosynthetic rate, and yield accompanied this oxidative stress. Notably, *M. denticulata* interference caused more significant oxidative stress and yield reduction than *P. minor* under both well-watered (WW) and drought stress (DS) conditions. These findings highlight wheat's higher sensitivity to *M. denticulata* competition, underscoring the need for targeted weed management strategies to mitigate yield losses under both optimal and drought-stressed environments.

Graphical Abstract



Keywords Drought stress · Crop–weed interaction · *Medicago denticulata* · *Phalaris minor* · Oxidative stress · Climate change

Introduction

Climate change profoundly affects agricultural soils and crop productivity worldwide. Crops are increasingly subjected to various stresses, including biotic stresses such as weed interference (Sreekanth et al. 2024) and abiotic stresses, i.e., drought, etc. (Alkhateeb et al. 2024; Abdelaal et al. 2020), which collectively threaten global food security (Farouk et al. 2024; El-Sorady et al. 2022; Omara et al. 2023; Sheasha et al. 2023; Seliem et al. 2024). The drought is further aggravated by ongoing climate change, which is forecasted to exaggerate the hydrological cycle and rise the frequency of extreme weather events, including prolonged droughts (Cambridge University Press 2021). Currently, about 66% of the world's arable land is affected by drought, and this situation is expected to rise due to climate change (Ullah et al. 2021). Consequently, global crop productivity has already declined by nearly 50% due to drought (Lamaoui et al. 2018). This challenge is compounded by the swiftly growing world population, which is projected to exceed 9 billion by 2050 and reach 11 billion by the end of the century (Bonaccorsi et al. 2020). Subsequently, the escalating demand for food is likely to strain the food supply chain further, hindering the achievement of sustainable development goals, specially zero hunger (SDG-2) (United Nations 2023).

Weed infestation is a major biotic stress limiting wheat yield in India (Das et al. 2014) and globally (Li et al. 2016; Abbas et al. 2017). Weed species worldwide lead to a 31.5% drop in plant productivity, resulting an economic loss of USD 32 billion annually (Kubiak et al. 2022). At the national level, weed interference leads to an estimated loss of 2.7 million tons of grain annually. In India, the economic impact of weeds is even more severe, costing over USD 11 billion each year in agricultural production losses (Gharde et al. 2018). Yield losses attributed to weed competition are substantial across various crops, with reductions estimated at 31% in soybean, 25% in maize, and 18.6% in wheat (Gharde et al. 2018). These significant yield losses underscore the urgent need for effective weed management strategies to enhance agricultural productivity and ensure food security.

Wheat (*Triticum aestivum* L.) is a widely grown cereal crop globally, serving as a primary dietary staple for the global population (Arzani and Ashraf 2017). It is grown on approximately 220 million hectares, with an annual production of 778 million metric tons, contributing nearly 10% to global agricultural value addition (Khan et al. 2020). However, wheat production is increasingly vulnerable to multiple abiotic and biotic stresses. For instances, drought alone causes an average yield reduction of 50–60% (Zhao et al. 2020). If current trends persist, further declines in wheat productivity could severely impact global food and nutritional security (Mansour et al. 2020). In India, weed infestation exacerbates this challenge, leading to wheat yield losses of approximately 18.6%, translating to economic losses of ~ USD 3376 million annually (Gharde et al. 2018). Hence, reducing these losses by half could enhance global wheat production by an additional 100 million metric tons, significantly contributing to hunger reduction worldwide. To meet the growing food demands of an estimated 9 billion people by 2050, global wheat production should rise by at least 60% (Borisjuk et al. 2019). Achieving this requires sustainable intensification strategies, as a 50% yield increase is necessary to combat hunger and malnutrition effectively (Poudel et al. 2020). Tackling these challenges necessitates rigorous attempts from researchers, policymakers, and stakeholders to build resilient and efficient wheat production systems for future food security.

Problematic weeds in wheat fields include *Phalaris minor* Retz. (Jabran et al. 2017) and *Medicago denticulata* (Singh et al. 1995; Chhokar et al. 2012) competing with wheat for water, nutrients, and space. This competition is influenced by climatic parameters like light and temperature (Guillemin et al. 2013) and is most intense when weeds and crops emerge together, especially under resource-limited conditions (Zimdahl 2007; Hussain et al. 2015). This competition is particularly severe under water-limited conditions, where weeds exhibit a competitive advantage over crops (Griffin et al. 1989; Orwick and Schreiber 1979). In managed cropping systems, the competition for soil water and various resources among crops and weeds intensifies water stress, reducing soil water within the crop root region (Sun et al. 2020). Consequently, understanding weed–crop competition dynamics is vital for formulating efficient weed control approaches to boost wheat productivity.

Drought stress triggers a cascade of morpho, physio, biochemical, and molecular variations in crops (Sallam et al. 2019; Shelake et al. 2022). When combined with weed interference, these stresses amplify oxidative stress markers, through the extensive synthesis of reactive oxygen species (ROS), cellular damage, lipid peroxidation, and compromised membrane stability (Kar 2011; Sabagh et al. 2021; Sreekanth et al. 2024). Such oxidative stress disrupts vital cellular functions, leading to diminished growth and development, ultimately causing significant reductions in crop yields (Farooq et al. 2014; Shelake et al. 2022). Understanding the relationship between drought stress and weed competition is key to develop appropriate management strategies that minimize yield losses and ensure sustainable agriculture.

Despite frequent drought stress, extensively researchers focused on insights into the adaptability of several weeds to water stress (Chahal et al. 2018). Further, wheat's physiological response to drought stress is well documented, nevertheless wheat's physiological, biochemical, and yield responses to combined biotic (weed interference) and abiotic (drought) stress remain less understood. Previous studies have focused on either drought stress or weed competition separately, with a few exceptions examining their combined effects in rice (Sreekanth et al. 2024). However, similar studies in wheat, especially involving simultaneous competition from weeds like *P. minor* and *M. denticulata*, remain scarce. Bridging this research gap is essential for formulating effective mitigation plans to enhance wheat resilience under changing climatic conditions. Furthermore, gaining deeper insights into these interactions is essential for achieving global sustainable development goals, mainly SDG-2 (Zero Hunger) and SDG-13 (Climate Action) (United Nations 2023). Therefore, we hypothesize that weed interference significantly influences wheat's physiological, biochemical, and yield responses under drought stress. A deeper understanding of these responses will aid in devising targeted management strategies to minimize yield losses and ensure sustainable wheat production. To address this, a two-year (2022–2023) experiment has been conducted with the following objectives: (i) to assess the physiological and biochemical responses of wheat to weed competition under drought stress, and (ii) to compare wheat's response to individual and interactive effects of weed interference and drought in terms of physiology, biochemistry, and yield.

Material and Methods

Experimental site Description and Treatment Details

A two-year pot experiment was carried out during the *Rabi* seasons of 2022 and 2023 at the greenhouse of

ICAR-Directorate of Weed Research, Jabalpur, India. The study aimed to evaluate the effect of weed competition on wheat variety GW-322 physiological, biochemical, and yield responses. Throughout the experimentation, 12-h photoperiod, a temperature of 28 ± 2 °C, relative humidity ranging from 60 to 75%, and illuminance between 500 and 1000 µmol photons m^{-2} s^{-1} was maintained in the greenhouse. These conditions ensured uniform growth and minimized environmental variability. The experiment was executed in a completely randomized design (CRD) with five biological replicates. The treatments included wheat grown solely and wheat grown in competition with its major problematic weeds, *Medicago denticulata* and *Phalaris minor*. The experiment was carried out in large earthen pots, each with a diameter of 46 cm and a height of 42 cm, filled with 58 kg of soil. Wheat and weed seeds were sown, and after the emergence of the weed seedlings, they were thinned to maintain densities of 25 plants/m^2 for *M. denticulata* (5 weeds per pot) and 50 plants/m^2 for *P. minor* (10 weeds per pot). Excess weed seedlings were uprooted seven days after emergence to ensure uniform competition throughout the study period. Crop management practices, including irrigation and fertilizer application, were carried out following standard agronomic guidelines to optimize wheat growth. In addition, weed-free wheat pots were maintained by manually uprooting any emerging weeds at 5–7-day intervals, ensuring the absence of weed competition. Pot-based setups have certain limitations, notably root confinement, which can influence plant growth and alter below-ground competition dynamics compared to open-field conditions. Root restriction may intensify or underrepresent competition, depending on species interactions. Details of the treatments are presented in Table 1.

Imposition of Drought Stress and Soil Moisture Content Measurement

The experiment contains two irrigation regimes: well-watered (WW) and drought stress (DS). In the well-watered (WW) treatment, pots were irrigated regularly to maintain optimal soil moisture levels throughout the experiment. In contrast, drought stress (DS) was imposed by withholding irrigation at 20 days after sowing (DAS) for 15 days. During this period, plants in the DS treatment were closely monitored, and rewatering was performed upon observing visible drought symptoms such as chlorosis, leaf drying, and rolling. Soil moisture content was measured before rewatering the DS plants to assess soil moisture depletion under WW and DS conditions. Soil samples were collected using a sampling auger and placed in pre-weighed containers for precise moisture determination. Samples were taken from each pot at different depths: the top 5 cm and the bottom 5 cm of the soil profile. Triplicate samples were collected from each pot to ensure accuracy and reliability. Immediately after collection, the soil samples were weighed to determine their fresh weight. They were then oven-dried at 105°–110 °C until a constant weight was achieved. Once thoroughly dried, the final dry weight of the samples was noted. Soil moisture content was calculated with the following formula (Schmugge et al. 1980):

Table 1 Experimental treatment conditions

Treatments	Crop and Weed combinations
Control (Well-watered)	Weed-free wheat-Control (WFWC)
	Wheat + *P. minor*-Control (WPC)
	Wheat + *M. denticulata*-Control (WMC)
Drought (Drought stress)	Weed-free wheat-Drought (WFWD)
	Wheat + *P. minor*- Drought (WPD)
	Wheat + *M. denticulata*- Drought (WMD)

$$\text{Soil moisture content} = \left[\text{Weight of wet soil (Ww)} - \text{Weight of dry soil (Wd)} / \text{Weight of wet soil (Ww)}\right] \times 100$$

Sampling and Assessment of Physiological and Biochemical Parameters

Physiological and biochemical traits were evaluated before rewatering to determine the influence of drought on wheat.

Estimation of Relative Water Content (RWC) and Membrane Stability Index (MSI):

RWC was measured using the Barrs and Weatherly (1962) method, while MSI was assessed following the (Sairam 1994) method.

Estimation of Total Chlorophyll Content:

A 0.1 g leaf sample was extracted in 10 mL of 80% acetone, and O.D. was measured at 663 and 645 nm (Lichtenthaler 1987).

Assessment of Leaf Gas Exchange Parameters:

LI-COR 6400 IRGA (10:00–12:00 h) instrument was used to assess photosynthetic rate (PN), stomatal conductance (gs), and transpiration rate (E) by following the protocol of (Leakey et al. 2004).

Estimation of Oxidative Stress Indicators

MDA Content:

Lipid peroxidation was assessed via MDA estimation (Heath and Packer 1968), measured absorbance at 532 and 600 nm.

Superoxide Anions ($O_2{\cdot}^-$):

Superoxide anion levels were assessed using the (Wu et al. 2010) method with a sodium nitrate standard, recorded absorbance at 530 nm.

Hydrogen Peroxide (H_2O_2) Content:

H_2O_2 levels were measured at 415 nm and calculated using a standard H_2O_2 curve (Mukherjee and Choudhuri 1983).

Antioxidant Enzyme Assay

Enzyme Extraction

Fresh leaf samples (0.5 g) were extracted in 50 mM phosphate buffer (pH 7.0) with EDTA, PVPP, and PMSF, then centrifuged at 12,000 × g for 20 min at 4 °C. The supernatant was used for enzymatic analysis.

Superoxide Dismutase (SOD, E.C. 1.15.1.1):

SOD activity was assessed following (Beauchamp and Fridovich 1971) by its inhibition of nitroblue tetrazolium (NBT) photoreduction at 560 nm. One unit of SOD was specified as the amount required to hinder NBT reduction by 50%, specified as units mg^{-1} protein min^{-1}.

Catalase (CAT, E.C. 1.11.1.6):

CAT activity was assessed using (Aebi 1974) method by tracking the decline in O.D. at 240 nm due to H_2O_2 consumption.

Peroxidase (POD, E.C. 1.11.1.7):

POD activity was assessed following (Kar and Mishra 1976) method by tracking purpurogallin formation at 420 nm, specified as absorbance units mg^{-1} protein min^{-1}.

Non-Enzymatic Antioxidants and Total Soluble Sugars

The non-enzymatic antioxidant defence under drought stress was evaluated by measuring proline, total phenolics (TPC), ascorbic acid (AsA), and total soluble sugars (TSS) as follows:

Proline Content:

Proline was evaluated following the method of (Bates et al. 1973), which was homogenizing 0.5 g leaf samples in 3% sulfosalicylic acid. The filtrate was used for analysis, with absorbance noted at 520 nm.

Total Phenolic Content (TPC):

TPC was measured following (Singleton and Rossi 1965) method by recording extract absorbance at 765 nm using a spectrophotometer.

Ascorbic Acid (AsA) Content:

AsA content was measured following the (Hodges et al. 1996) method by recording O.D. at 525 nm and calculating concentration using an L-ascorbic acid standard curve.

Total Soluble Sugars (TSS):

TSS content was measured following (McCready et al. 1950) by extracting 0.1 g leaf samples in 80% ethanol, centrifuging, and recording the absorbance at 630 nm. Values were specified as mg g^{-1} FW using glucose as a standard.

Grain Yield and Weed Parameters

At harvest, five plants per treatment were carefully uprooted, and the grain yield was recorded. Weed indices, including plant height, fresh biomass, root length, and leaf area, were measured 45 days after sowing (DAS) to assess weed growth and competition.

Data Analysis

Results were presented as means ± SE. Treatment differences were calculated with Duncan's multiple range test ($p \leq 0.05$). ANOVA was performed in SPSS 16.0 (SPSS Inc., Chicago, IL, USA), while graphs with GraphPad Prism 9.0.0 and Excel-2007. Principal component and correlation analyses were conducted using GRAPES software.

Results

Soil Moisture Content (SMC)

SMC was remarkably affected by weed presence and drought stress. In weed-free wheat, SMC was 19.11% (top 5 cm) and 21.02% (below 5 cm) under well-watered (WW) environment but declined to 14.25% and 15.26%, respectively, under drought stress (DS). The presence of *P. minor*

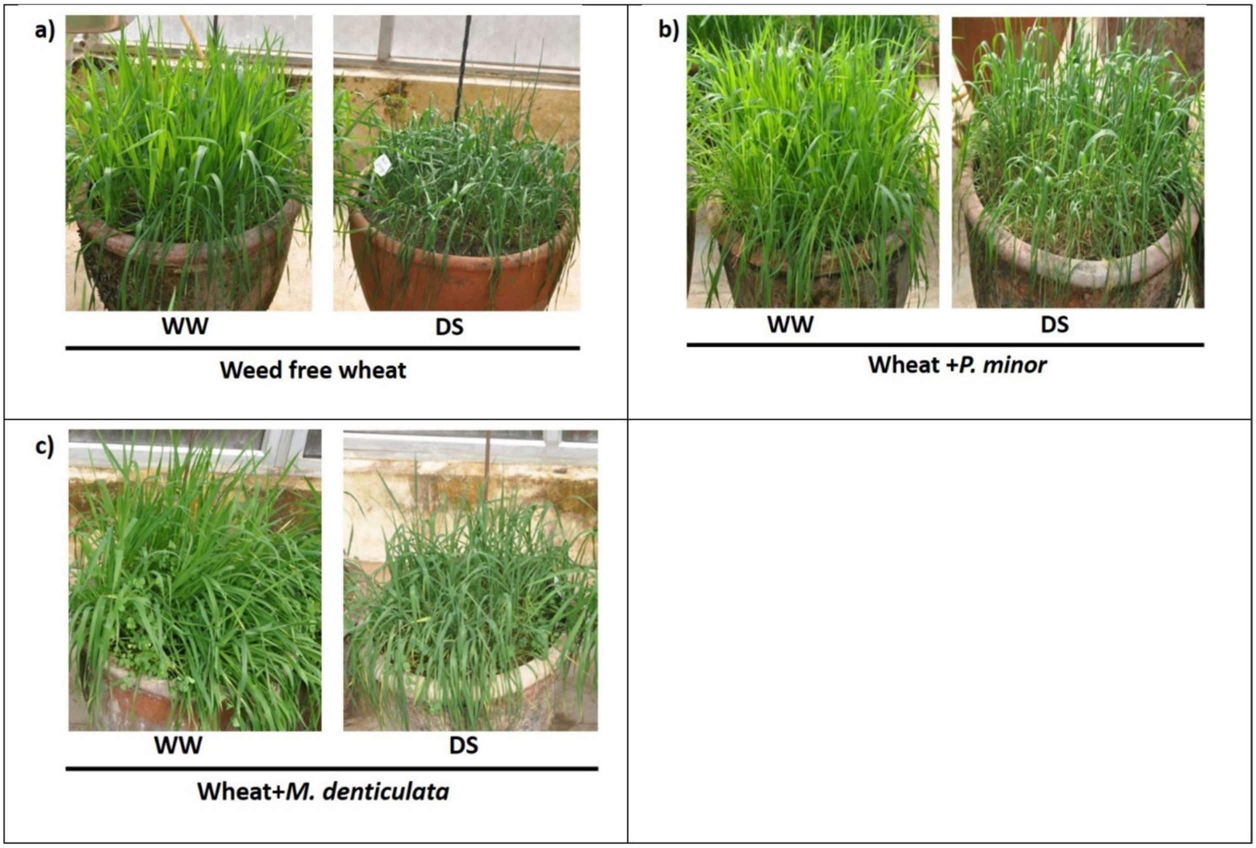


Fig. 1 Effect of weed interference by *P. minor* and *M. denticulata* on morphological and physiological responses of wheat (a, b, and c) under well-watered (WW) and drought stress (DS) conditions

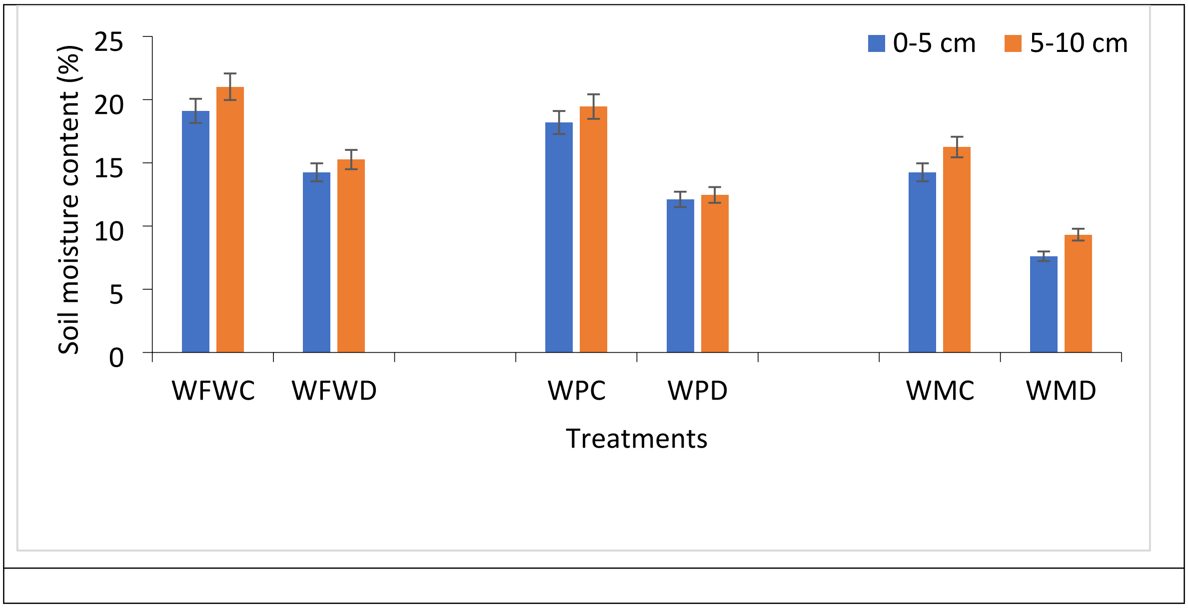


Fig. 2 Soil moisture content at 0–5 cm and 5–10 cm depths in wheat rhizosphere under weed interference by *P. minor* and *M. denticulata* under well-watered (WW) and drought stress (DS) conditions. *WFWC* weed-free wheat control; *WFWD* weed-free wheat drought; *WPC* wheat + *P. minor control*; *WPD* wheat + + *P. minor* Drought; *WMC* wheat + *M. denticulata* control; *WMD M. denticulata* drought. The data shown above denote the Mean ± SE (n = 5)

further reduced SMC to 18.19% (top) and 19.45% (below) under WW, with a sharper decline under DS to 12.11% and 12.46%. Weed *M. denticulata* interference led to a greater reduction, with SMC dropping to 14.25% (top) and 16.25% (below) under WW and plummeting to 7.61% and 9.32% under DS. The most severe moisture depletion occurred with *M. denticulata* under DS, highlighting its strong competitive impact on wheat (Fig. 1 and Fig. 2).

RWC, MSI, and Total Chlorophyll Content

Analysis of variance (ANOVA) has shown that weed interference (*P. minor* and *M. denticulata*) under drought stress has a statistically significant effect ($P < 0.001$) on most of the important wheat physiological parameters (Fig. 3). Weed interference significantly lowered the wheat RWC, MSI, and total chlorophyll content compared to weed-free wheat under both WW (Well-watered) and DS (Drought stress). A significant reduction in wheat RWC (WW: 78.20%; DS: 71.18%), MSI (WW: 64.85%; DS: 56.20%), and total chlorophyll content (WW: 2.73 mg/g FW; DS: 1.82 mg/g FW) has been noticed in the presence of *M. denticulata.* At the same time, *P. minor* interference had a moderate effect on wheat RWC (WW: 84.76%; DS: 81.99%), MSI (WW: 67.66%; DS: 61.22), and total chlorophyll content (WW: 3.25 mg/g FW; DS:2.14 mg/g FW). A substantial decline in RWC, MSI, and total chlorophyll content under both WW and DS conditions suggests that wheat experienced severe drought stress due to competition from both weeds. However, reduction was more pronounced in the presence of *M. denticulata* than *P. minor*.

Gas exchange Parameters

Weed interference under drought stress has a significant ($P < 0.001$) influence on most of the gas exchange parameters, including rate of photosynthesis (P_N), stomatal conductance (g*s*), and rate of transpiration (E) (Fig. 4). Weed interference significantly lowered the wheat P_N, g*s*, and E compared to weed-free wheat under both WW (Well-watered) and DS (Drought stress). A significant reduction in wheat P_N (WW: 9.91; DS: 7.89), g*s* (WW: 0.47; DS: 0.33), and E (WW: 2.83; DS: 1.72) has been noticed in the presence of *M. denticulata.* However, *P. minor* interference had a moderate effect on wheat P_N (WW: 12.18; DS: 11.18), g*s*

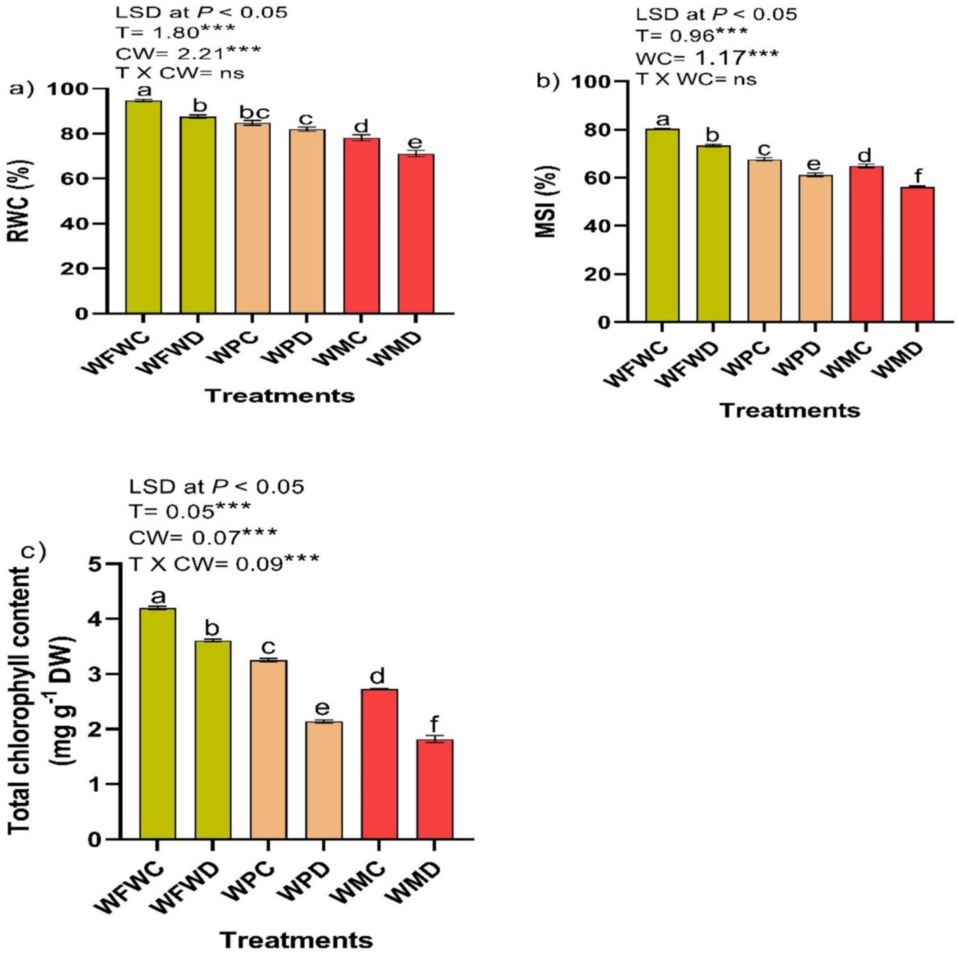


Fig. 3 Effect of weed interference (*P. minor* and *M. denticulata*) on wheat RWC **a**, MSI **b**, and total chlorophyll content **c** under control drought stress. Data are expressed as Mean ± SE ($n = 5$). *WFWC* weed-free wheat control; *WFWD* weed-free wheat drought; *WPC* wheat + *P. minor control*; *WPD* wheat + + *P. minor* Drought; *WMC* wheat + *M. denticulata* control; *WMD M. denticulata* drought. Distinct alphabets on error bars depict significant variations ($p = 0.05$). LSD at $p < 0.05$, 0.01, and 0.001 is marked by *, **, and ***, respectively; ns represent non-significance. CW: crop–weed combinations, T: treatment, CW × T: interaction effect

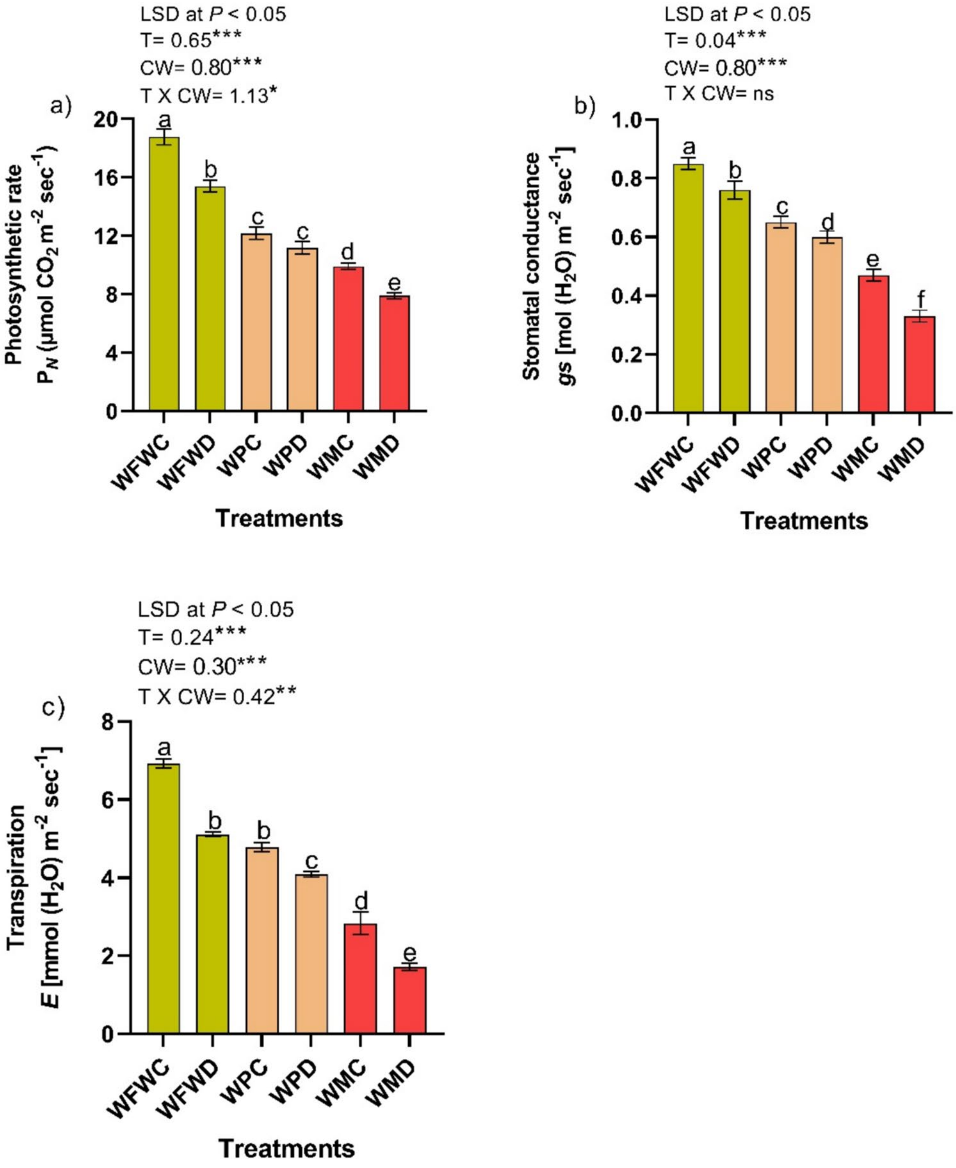


Fig. 4 Effect of weed interference (*P. minor* and *M. denticulata*) on wheat gaseous exchange parameters **a-c** under control drought stress. Data are expressed as Mean ± SE ($n = 5$). *WFWC* weed-free wheat control; *WFWD* weed-free wheat drought; *WPC* wheat + *P. minor control*; *WPD* wheat + + *P. minor* Drought; *WMC* wheat + *M. denticulata* control; *WMD M. denticulata* drought. Distinct alphabets on error bars depict significant variations ($p = 0.05$). LSD at $p < 0.05$, 0.01, and 0.001 is marked by *, **, and ***, respectively; ns represent non-significance. CW: crop–weed combinations, T: treatment, CW × T: interaction effect

(WW: 0.65; DS: 0.60), and *E* (WW:4.78; DS:4.09). A notable decrease in Pn, gs, and E under both WW and DS environments specifies that wheat experienced severe drought stress due to competition from both weeds. The reduction was more pronounced in the presence of *M. denticulata* than *P. minor*.

Oxidative Stress Markers

Weed interference significantly ($P < 0.001$) increased the wheat oxidative stress markers like MDA levels, superoxide ion levels, and H_2O_2 levels under both WW and DS conditions (Fig. 5). A significant enhancement in wheat MDA (WW: 3.62-fold; DS: 6.58-fold), Superoxide ion (WW: 2.33-fold; DS: 3.75-fold), and H_2O_2 (WW: 5.82-fold; DS: 8.87-fold) has been noticed in the presence of *M. denticulata.* In comparison, *P. minor* interference had a moderate effect on wheat MDA (WW: 2.13-fold; DS: 4.79-fold), Superoxide ion (WW: 88.76%; DS: 1.58-fold), and H_2O_2 (WW: 1.62-fold; DS: 2.95-fold). A substantial increase in MDA, superoxide ions, and H_2O_2 under both WW and DS conditions suggests that wheat experienced severe drought stress due to competition from both weeds. The ROS levels were more pronounced in the presence of *M. denticulata* than *P. minor*.

Enzymatic and Non-Enzymatic Antioxidants

SOD, CAT, and POD and non-enzymatic antioxidants like proline, total phenolic content, and AsA showed significant differences ($P < 0.001$) due to weed interference under both WW and DS environments (Fig. 6 a,b,c). Weed interference significantly enhanced the antioxidant

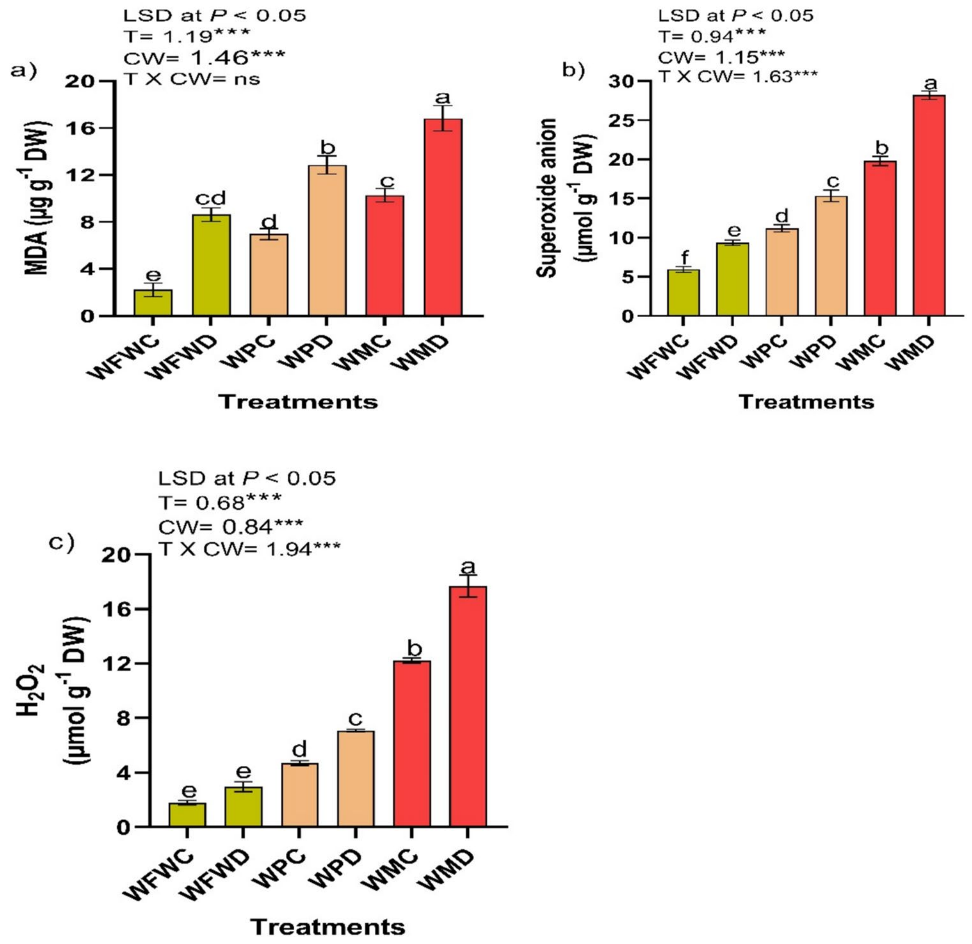


Fig. 5 Effect of weed interference (*P. minor* and *M. denticulata*) on wheat oxidative stress markers **(a-c)** under control drought stress. Data are expressed as Mean ± SE ($n = 5$). *WFWC* weed-free wheat control; *WFWD* weed-free wheat drought; *WPC* wheat + *P. minor control*; *WPD* wheat + + *P. minor* Drought; *WMC* wheat + *M. denticulata* control; *WMD M. denticulata* drought. Distinct alphabets on error bars depict significant variations ($p = 0.05$). LSD at $p < 0.05$, 0.01, and 0.001 is marked by *, **, and ***, respectively; ns indicates non-significance. CW: crop–weed combinations, T: treatment, CW × T: interaction effect

enzymes under both WW and DS environments. A significant enhancement in wheat SOD (WW: 5.55%; DS: 51.50%), CAT (WW: 22.10%; DS: 31.10%), and POD (WW: 1.65-fold; DS: 2.04-fold) has been noticed in the presence of *M. denticulata.* At the same time, *P. minor* interference had a moderate effect on wheat SOD (WW: 21.95%; DS: 91.11%), CAT (WW: 32.40%; DS: 62.43%), and POD (WW: 2.96-fold; DS: 3.66-fold).

In a similar trend, weed interference also enhanced the non-enzymatic antioxidants under both WW and DS conditions (Fig. 6 d,e,f). A significant enhancement in wheat Proline (WW: 1.53-fold; DS: 2.09-fold), TPC (WW: 91.06%; DS: 2.85-fold), and AsA (WW: 1.58-fold; DS: 2.46-fold) has been noticed in the presence of *M. denticulata.* However, *P. minor* interference had a moderate effect on wheat proline (WW: 1.02-fold; DS: 1.44-fold), TPC (WW: 57.67%; DS: 1.76-fold), and AsA (WW: 1.96-fold; DS: 3.56-fold).

Total Soluble Sugars (TSS) and Grain Yield

TSS and grain yield were significantly ($P < 0.001$) affected by weed interference under both WW and DS conditions (Fig. 7a, b). *P. minor* presence led to an increase of 11.60% and 30.38% in total soluble sugars, while *M. denticulata* interference enhanced TSS by 23.38% and 37.74% under WW and DS, respectively, in contrast to the weed-free control. Yield significantly declined under DS in the presence of weeds. *P. minor* reduced yield by 28.91% under WW and 44.49% under DS in contrast to the weed-free control. Similarly, *M. denticulata* interference led to yield reductions of 36.58% and 57.87% under WW and DS, respectively. The reduction was more pronounced in the presence of *M. denticulata* than *P. minor*.

Effect of Drought Stress on Weed Biomass Traits

Drought stress significantly altered the biomass-related traits of the weed species, as well as all measured parameters showed a decline under stress conditions. The reduction in biomass was more pronounced in *P. minor* compared to *M.*

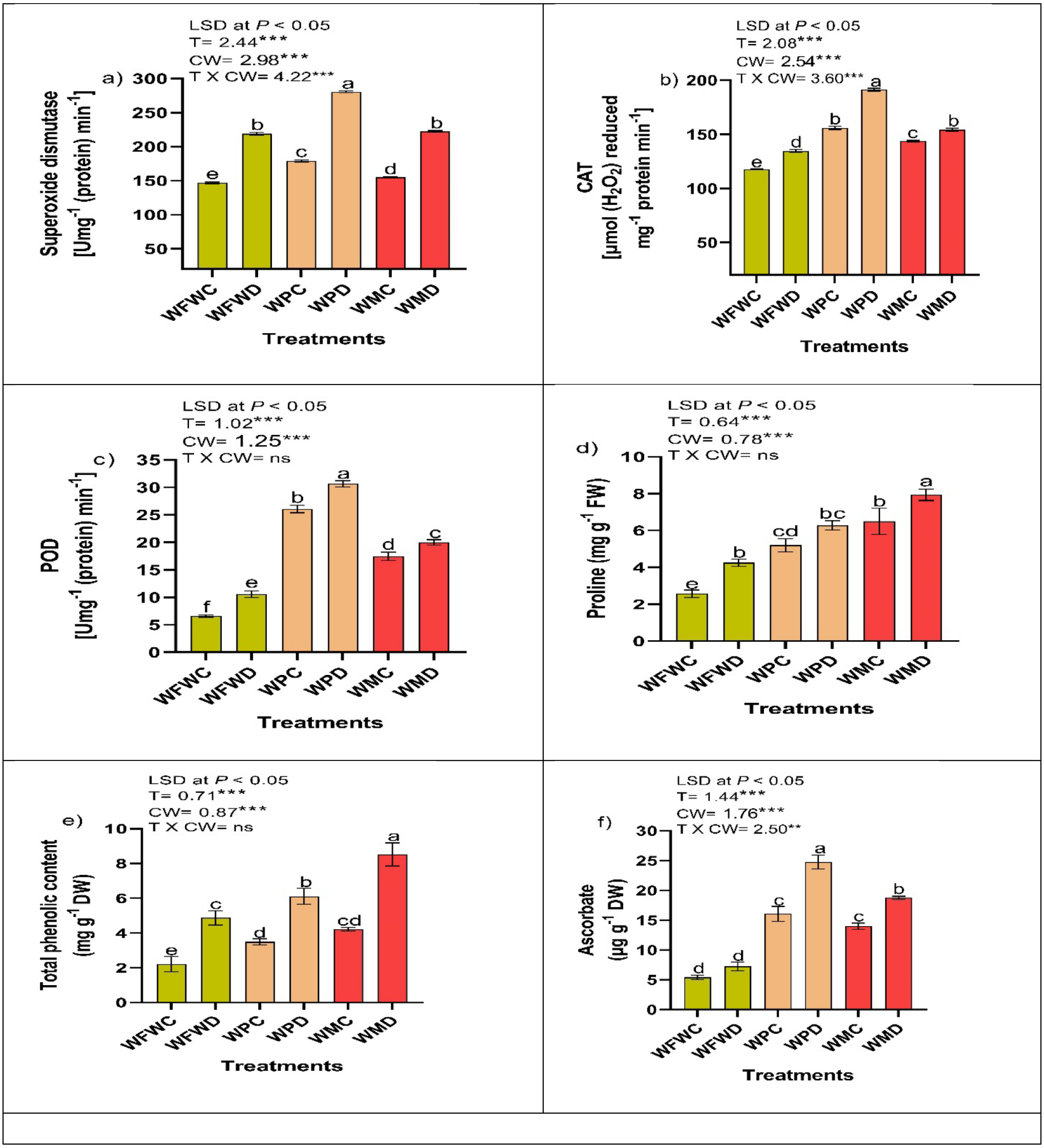


Fig. 6 Effect of weed interference (*P. minor* and *M. denticulata*) on wheat enzymatic and non-enzymatic antioxidants **(a-f)** under control drought stress. Data are expressed as Mean ± SE ($n=5$). *WFWC* weed-free wheat control; *WFWD* weed-free wheat drought; *WPC* wheat + *P. minor control*; *WPD* wheat + +*P. minor* Drought; *WMC* wheat + *M. denticulata* control; *WMD M. denticulata* drought. Distinct alphabets on error bars depict significant variations ($p=0.05$). LSD at $p<0.05$, 0.01, and 0.001 is marked by *, **, and ***, respectively; ns indicates non-significance. CW: crop–weed combinations, T: treatment, CW × T: interaction effect

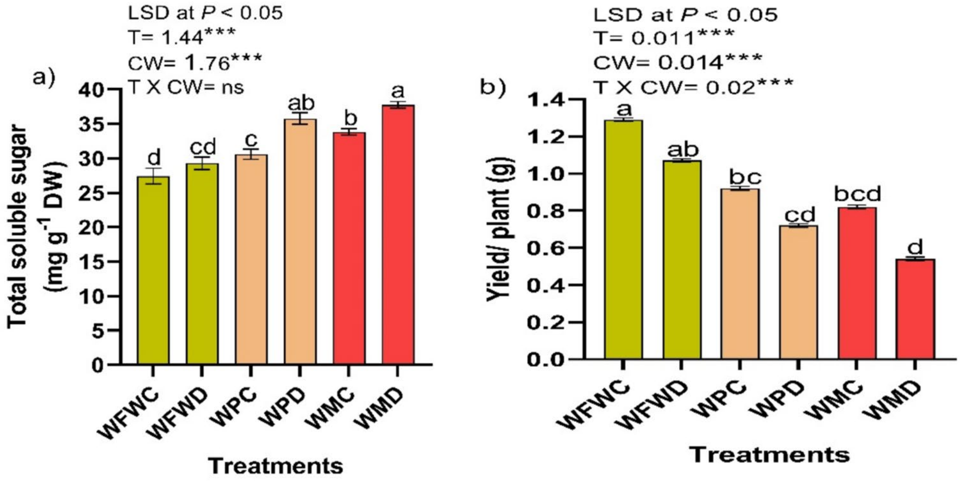


Fig. 7 Effect of weed interference (*P. minor* and *M. denticulata*) on wheat total soluble sugars and yield **(a-b)** under control drought stress. Data are expressed as Mean ± SE ($n = 5$). *WFWC* weed-free wheat control; *WFWD* weed-free wheat drought; *WPC* wheat + *P. minor control*; *WPD* wheat + + *P. minor* Drought; *WMC* wheat + *M. denticulata* control; *WMD M. denticulata* drought. Distinct alphabets on error bars depict significant variations ($p = 0.05$). LSD at $p < 0.05$, 0.01, and 0.001 is marked by *, **, and ***, respectively; ns indicates non-significance. CW: crop–weed combinations, T: treatment, CW × T: interaction effect

Table 2 Impact of drought stress on growth and biomass characteristics of *P. minor* and *M. denticulata*

Weed and Crop	Treatment	Plant height (cm)	Fresh weight (g)	Leaf area (cm^2)	Root length (cm)
P. minor	WW	42.00 ± 0.47^{c}	0.36 ± 0.02^{a}	2.19 ± 0.18^{c}	3.56 ± 0.28^{c}
	DS	35.70 ± 0.97^{d}	0.31 ± 0.03^{a}	1.45 ± 0.24^{d}	3.92 ± 0.32^{c}
M. denticulata	WW	59.00 ± 0.95^{a}	4.60 ± 0.52^{a}	32.85 ± 0.53a	11.60 ± 0.75^{b}
	DS	55.20 ± 0.58^{b}	3.84 ± 0.81^{b}	23.27 ± 0.65b	14.20 ± 0.58^{a}

Data are presented as Mean ± SE (n = 5). WW: well-watered condition; DS: drought stress. Values represent the mean of replicates. Means sharing the same letter within a column do not contrast significantly at $P = 0.05$, as assessed by Duncan's test

denticulata, indicating a higher sensitivity of *P. minor* to drought. In contrast, the relatively lower reduction in growth traits of *M. denticulata* suggests its better adaptability and competitive interaction with wheat under drought conditions. Traits such as plant height, fresh weight, and leaf area of both weeds were reduced under drought stress over their respective controls. Meanwhile, *M. denticulata* exhibited a greater root length than *P. minor* in both well-watered and drought-stressed situations. This suggests that *M. denticulata* possesses more effective tolerant traits to cope with drought compared to *P. minor* (Table 2).

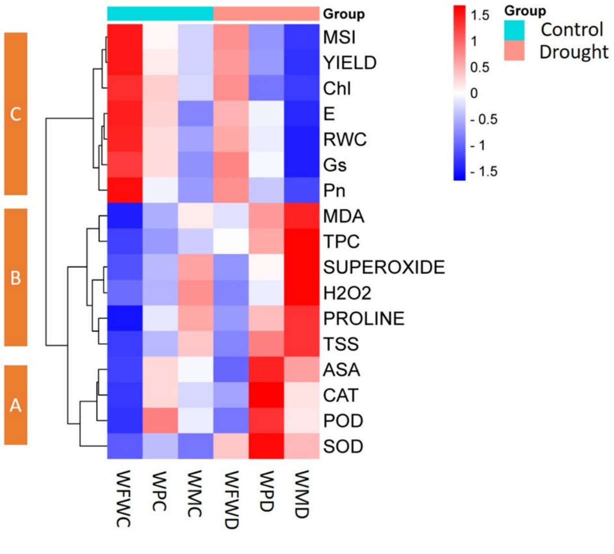


Fig. 8 A heatmap with clustering visually represents the interactions among all investigated components and treatments, displaying the scaled average values of the examined wheat traits

Assessment of Treatment–Variable Interactions Using Heatmap, PCA, and Correlation Analysis

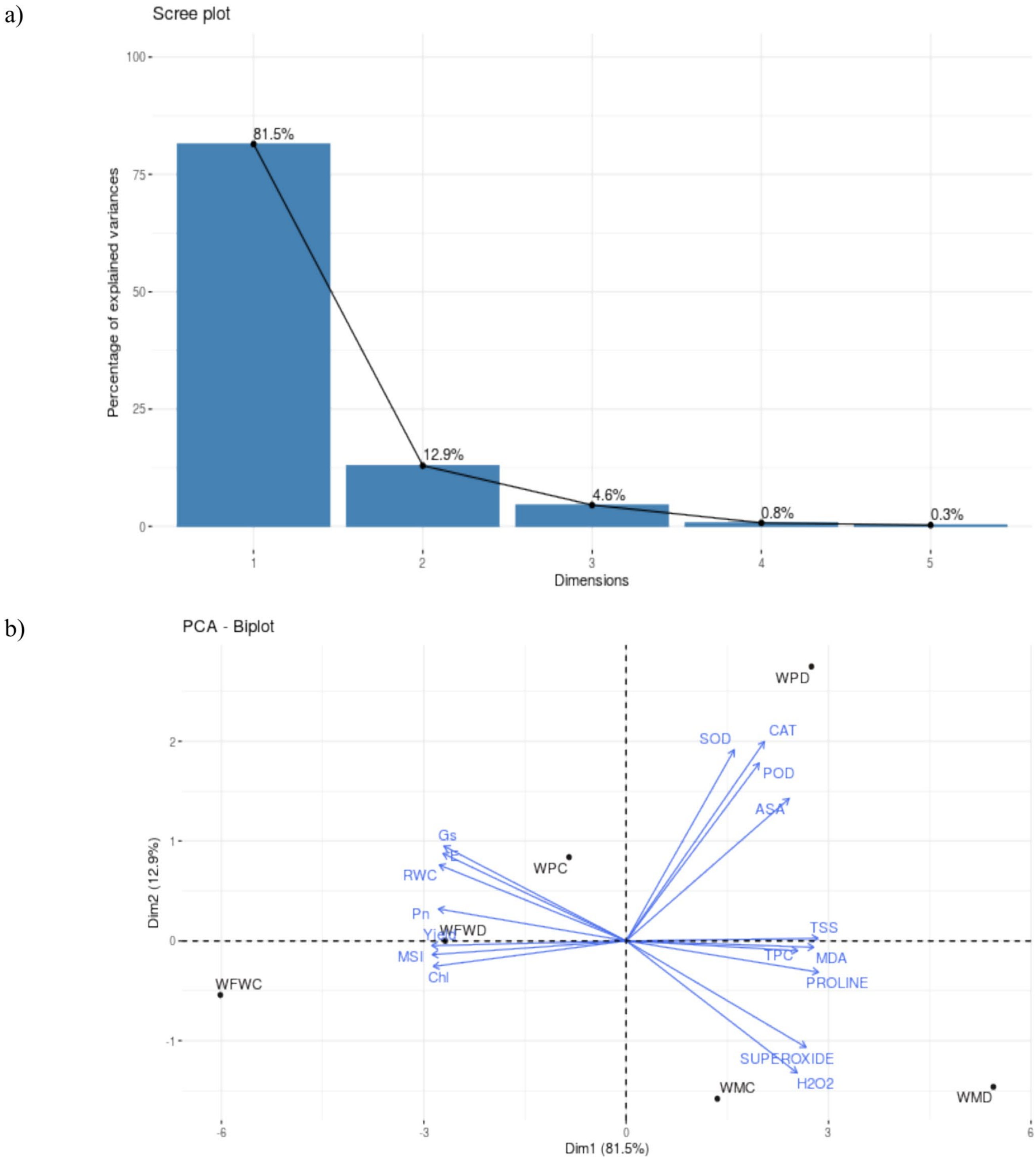


Fig. 9 Principal Component Analysis (PCA) illustrating the association between wheat physiological and biochemical traits under weed interference in well-watered and drought stress conditions**.** **a** Scree plot diplaying the percentage of variance described by each PC; **b** Biplot representing the interrelationship among physiological and biochemical traits; **c** Contribution of each variable to total variability in PC1 and PC2, along with their correlations; **d** Correlation plot depicting relationships between variables and principal components

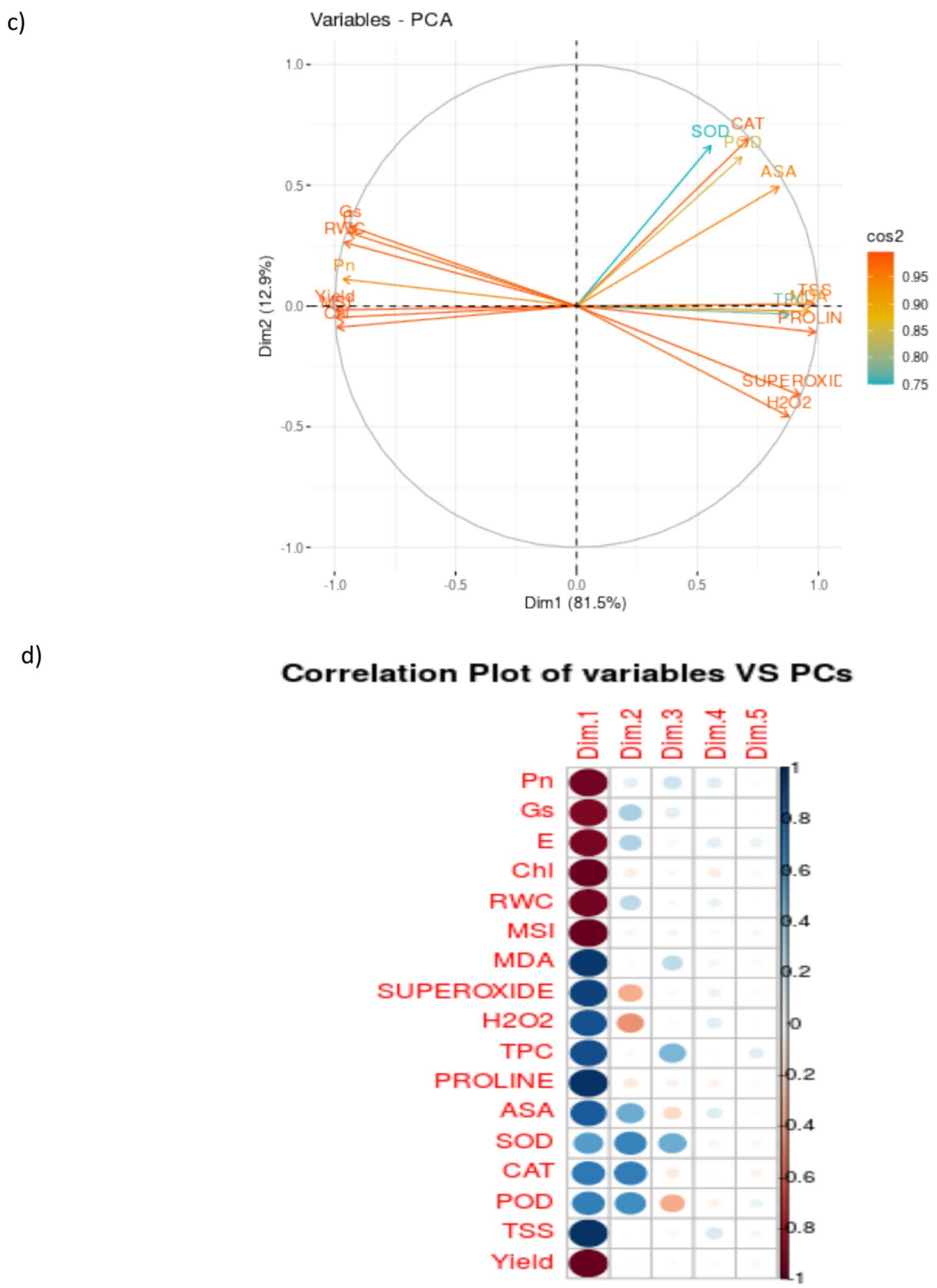


Fig. 9 (continued)

Hierarchical Clustering, Heatmap Analysis

In this study, physio-biochemical parameters under control and drought stress were analyzed for each treatment and subjected to hierarchical clustering, heatmap analysis, correlation, and PCA (Fig. 8). Hierarchical clustering categorized the variables into three distinct groups (Clusters A, B, and C) (Fig. 8). The parameters like AsA, SOD, CAT, and POD are gathered in Cluster-A. The Cluster-A attributes displayed an increased pattern in wheat with *P. minor* (WPD) under drought stress, while dropping in weed-free wheat under control (WFWC) and drought (WFWD) conditions. Cluster-B variables included MDA, TPC, superoxide ion, H_2O_2, proline, and TSS. Cluste-B traits were shown to be decreasing in weed-free wheat under control (WFWC) and drought (WFWD) conditions and increasing in wheat with *M. denticulata* (WMD) under drought stress. Furthermore, Cluster-C included traits like MSI, yield, total chlorophyll content, transpiration, RWC, stomatal conductance, and rate of photosynthesis. Cluster-C parameters displayed an increased trend in weed-free wheat under control conditions (WFWC) and showed decreased trend in wheat with *M. denticulata* under drought stress (WPD).

Principal Component Analysis (PCA)

PCA was executed to recognize the physio-biochemical traits that best explained the wheat's response to weed interference *(P. minor* and *M. denticulata*) under drought stress (Fig. 9). The PCA analysis identified two principal components (PCs), with PC1 (81.5%) and PC2 (12.9%) together explaining 94.4% of the total variation (Fig. 9). In PC1, the major contributing traits included MSI, total chlorophyll, proline, TSS, and yield, while AsA, SOD, CAT, and POD influenced PC2. The biplot analysis showed that SOD, CAT, POD, AsA, TSS, TPC, MDA, proline, superoxide ion, and H_2O_2 aligned with PC1, indicating a positive correlation. Wheat grown with *P. minor* under drought (WPD), *M. denticulata* under control (WMC), and *M. denticulata* under drought (WMD) were positioned on the positive side of PC1, highlighting the competitive nature of these weeds under drought stress. Conversely, total chlorophyll, stomatal conductance, photosynthetic rate, transpiration rate, RWC, MSI, and yield were negatively associated with PC1. Weed-free wheat under control (WFWC) and drought (WFWD), along with wheat with *P. minor* under control (WPC), were located in the opposite direction of PC1, suggesting reduced sensitivity of wheat to *P. minor* under well-watered conditions. Vector lengths indicated the relative importance of different traits. Among them, CAT contributed most to the increased competitiveness of *P. minor* with wheat under drought (WPD), while superoxide ion and H_2O_2 levels played a significant role in *M. denticulata* competitiveness under both control and drought conditions.

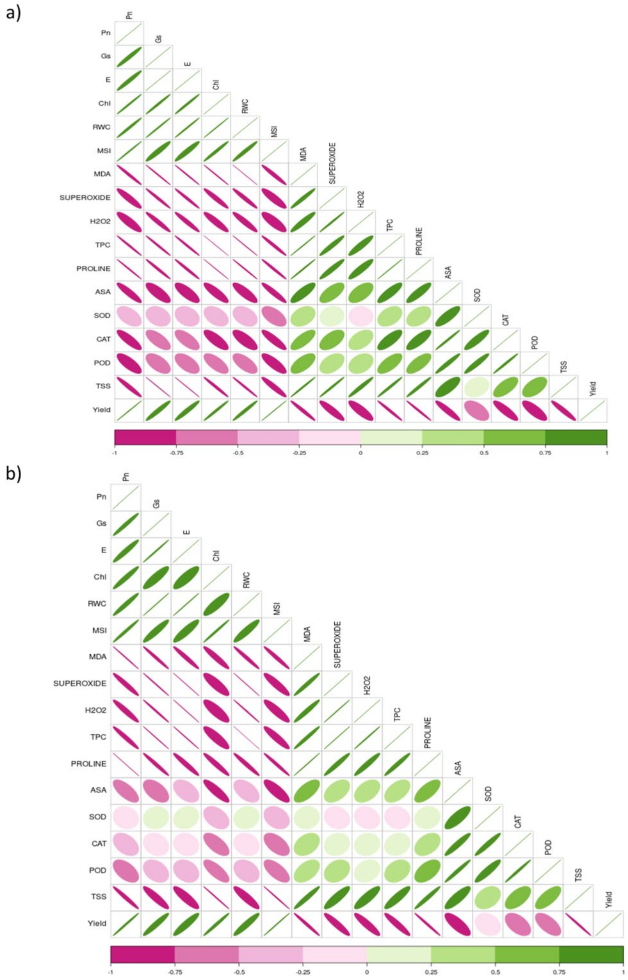


Fig. 10 The correlation coefficient between changes in physiological and biochemical parameters under well-watered **a** and drought stress condition **b.** *Pn* rate of photosynthesis; *Gs* stomatal conductance; *E* rate of transpiration; *Chl* total chlorophyll content; *RWC* relative water content, *MSI* membrane stability index; *MDA* malondialdehyde content; *Superoxide* superoxide ion levels, H_2O_2 hydrogen peroxide levels, *TPC* total phenolic content; *AsA* ascorbic acid levels; *TSS* total soluble sugar levels; and *Yield* grain yield

Pearson Correlation

A correlation analysis was conducted to assess the relationships among various physio-biochemical parameters under both control and drought stress conditions, and the results are illustrated in a correlogram (Fig. 10). Under control conditions, traits such as MDA, superoxide ion, H_2O_2, TPC, proline, AsA, CAT, POD, and TSS demonstrated a strong negative correlation with yield (r = − 0.75 to − 1), while SOD exhibited a moderate negative association ($r = -0.77$ to − 0.5). Conversely, photosynthesis rate (Pn), stomatal conductance (Gs), transpiration rate (E), RWC, total chlorophyll content, and MSI were positively correlated with yield (Fig. 10a). Similarly, under drought stress, Pn, Gs, E, total chlorophyll content, and RWC maintained a strong positive correlation with yield ($r = 0.5$ to 1). In contrast, MDA, superoxide ion, H_2O_2, TPC, proline, AsA, and TSS exhibited a strong negative correlation ($r = -0.75$ to − 1). POD and CAT had a moderate negative correlation ($r = -0.77$ to − 0.5), while SOD indicated a weak negative correlation ($r = -0.25$) under drought stress (Fig. 10b).

Discussion

The current study comprehensively evaluated the effect of weed interference, specifically *Phalaris minor* and *Medicago denticulata*, on the physiological, biochemical, and yield attributes of wheat under well-watered (WW) and drought stress (DS) environments. To the best of our knowledge, this is the first of its kind study that focuses on both the interaction of wheat with biotic stress (weeds) and abiotic stress (drought). Further, the present study sheds light on how drought stresses in the presence of weeds influence wheat growth, physiology and, eventually, affect yield. The findings revealed that weed competition significantly influenced all measured physiological traits, including RWC, MSI, total chlorophyll content, and gas exchange parameters. Similarly, biochemical responses, such as enzymatic and non-enzymatic antioxidant activities, along with yield-related parameters, exhibited notable variations under both water regimes. Notably, *M. denticulata* interference induced more significant physiological and biochemical disruptions in wheat compared to *P. minor*, irrespective of water availability. These results align with the understanding that drought stress elicits complex physiological, morphological, and biochemical responses in plants (Sreekanth et al. 2024), further amplifying the adverse effects of weed competition on wheat performance.

The findings of this study demonstrated that wheat physiological traits, including RWC, MSI, and total chlorophyll content, were significantly reduced by weed interference under both WW and DS conditions. The reduction was more pronounced in the presence of *M. denticulata* than *P. minor*, indicating a more substantial competitive effect of *M. denticulata* on wheat. The decline in chlorophyll content under drought stress can be attributed to the disruption of enzymes associated with chlorophyll formation and the enhanced activity of chlorophyll-damaging enzymes, a similar mechanism was also reported by (Shah et al. 2022) in wheat genotypes under drought conditions. Additionally, drought-induced damage to thylakoid membranes negatively affects chlorophyll synthesis, as well as the distribution and accumulation of photoassimilates (Medrano et al. 2002; Rana et al. 2017).

RWC is widely recognized as a reliable indicator of plant water status under drought stress (Farooq et al. 2019), and its reduction has been linked to the accumulation of osmoprotectants that help plants counteract stress effects (Rivero et al. 2014). Drought stress also compromises membrane stability, results in cell wall injury (Mubarik et al. 2021), as membranes are primary sites of cellular injury where reactive oxygen species (ROS) trigger lipid peroxidation, resulting in leakage of cell contents and cell death (Candan and Tarhan 2003; Smirnof 2005); Basu et al. 2021). Significant reductions in RWC and MSI under drought stress have also been stated in various assessments (Bangar et al. 2019). The current study further supports these findings, as wheat exposed to *P. minor* and *M. denticulata* under DS displayed a remarkable reduction in RWC and MSI compared to WW conditions. The remarkable drop in wheat RWC and MSI in the presence of *M. denticulata* suggests a higher competitive pressure from this weed under drought stress. Similar trends were observed in rice, where the presence of *A. paronychioides* and *E. colona* resulted in significant reductions in RWC and MSI under DS compared to WW (Sreekanth et al. 2024). These results emphasize the compounded impact of drought stress and weed competition on plant physiological integrity, highlighting the necessity for effective weed management strategies, particularly in water-scarce environments.

In the present study, weed interference further exacerbated these effects, leading to significant alterations in gas exchange parameters, like PN, gs, and E, under both WW and DS conditions. The disruption of physiological processes due to stress-induced changes has been previously described by (Sattar et al. 2020), who highlighted that disturbances in plant physiological machinery can alter interconnected mechanisms such as photosynthesis, stomatal conductance, and transpiration. Moreover, the decline in photosynthesis under drought is not solely associated with stomatal closure but also with disruptions in photosynthetic metabolism (Lawlor and Cornic 2020). A similar trend was described by (Sreekanth et al. 2024) in rice, where gas exchange parameters were significantly reduced due to weed interference under both WW and DS conditions. These findings suggest that weed competition further amplifies the detrimental consequences of drought stress on photosynthetic efficiency, emphasizing the need for integrated weed and drought management strategies to sustain crop productivity under changing climatic conditions.

Drought stress triggers the regulation of several oxidative stress factors, like the generation of ROS, cellular injury, lipid peroxidation, and membrane instability (Rahman et al. 2015; Sabagh et al. 2021). Oxidative stress induced by drought disrupts biochemical and physiological homeostasis, ultimately leading to plant cell death (Mittler 2002). Malondialdehyde (MDA), a lipid peroxidation byproduct, serves as a reliable marker of oxidative damage (Quagliata et al. 2023; Sallam et al. 2019). In the present study, excessive ROS production was noticed in wheat under both WW and DS conditions due to weed interference. The intensity of ROS accumulation was higher in wheat subjected to *M. denticulata* competition than in the presence of *P. minor* under both WW and DS conditions.

Weed interference significantly alters antioxidant gene expression and activity (Afifi and Swanton 2012; Gal et al. 2015; Agostinetto et al. 2017). Previous studies have demonstrated that key antioxidant enzymes, including ascorbate peroxidase, catalase, and SOD, were notably reduced in soybean competing with purple nutsedge (*Cyperus rotundus*) (Darmanti et al. 2016). In contrast, the present study observed a notable increase in both enzymatic antioxidants (SOD, CAT, and POD) and non-enzymatic antioxidants (proline, TPC, and AsA) in wheat under *P. minor* and *M. denticulata* interference in both WW and DS environments.

However, this increase was more pronounced under *P. minor* interference compared to *M. denticulata*. These findings are reliable with those of (Sreekanth et al. 2024), who reported lower oxidative stress marker levels in weed-free rice and in the presence of *A. paronychioides*, which was associated with increased antioxidant enzyme activity. Similarly, in rice, SOD, CAT, and POD levels were enhanced in weed-free conditions and the presence of *A. paronychioides* under drought stress compared to competition with *E. colona*. These results underscore the impact of weed competition on oxidative stress responses in crops, highlighting the critical role of effective weed management in mitigating stress-induced oxidative damage in wheat and rice.

Drought stress is known to induce the synthesis of osmoprotectants like proline and soluble sugars, which play a vibrant role in maintaining cellular redox and ionic homeostasis (Loutfy et al. 2012; Rivero et al. 2014). (Sattar et al. 2020) observed a remarkable rise in TSS and proline levels in wheat when subjected to combined drought and heat, rather than to their distinct stress. Similarly, the present study demonstrated a marked accumulation of TSS and proline due to weed interference under both WW and DS conditions. This response is likely an adaptive strategy that helps strengthen the cell membrane and plant parts by scavenging free radicals, thereby mitigating oxidative damage (Shah et al. 2017). Ascorbic acid (AsA) plays a pivotal role in plant defence by directly reacting with hydrogen peroxide (H_2O_2) and facilitating the regeneration of α-tocopherol from its oxidized form (Noctor and Foyer 1998; Gallie 2013). Elevated AsA levels have been shown to protect proteins and lipids from oxidative damage in water-stressed plants (Tambussi et al. 2000; Aly and Latif 2011). Interestingly, these protective mechanisms are typically upregulated under mild stress conditions, enhancing plant tolerance as stress severity increases. The extent of acquired stress tolerance varies widely among genotypes and is influenced by the type and time of stress exposure (Rizhsky et al. 2004; Choudhury et al. 2017). In alignment with these reports, the present assessment also found that total phenolic content, proline, TSS, and AsA levels were significantly elevated in rice under weed interference across both WW and DS conditions (Sreekanth et al. 2024). These findings highlight the importance of antioxidant and osmoprotectant accumulation in plants as a key adaptive response to weed competition and drought stress.

The current study observed a significant drop in wheat grain yield due to weed interference under both WW and DS conditions. Notably, oxidative stress induced by *M. denticulata* was more severe, as evidenced by the excessive accumulation of malondialdehyde, superoxide ions, and H_2O_2. This heightened oxidative stress corresponded with significant reductions in key physiological traits, including RWC, MSI, total chlorophyll content, photosynthetic rate, and yield attributes. Interestingly, the degree of yield reduction was more pronounced under *M. denticulata* interference compared to *P. minor* interference in both WW and DS conditions. This suggests that *M. denticulata* poses a greater competitive threat to wheat growth and productivity. It is important to highlight that the ultimate plant yield is influenced by the interplay of various biochemical and physiological processes that determine overall plant performance (Alsamadany 2022; Shah et al. 2022). The adverse effect of weed interference on yield can be attributed to the disruption of these essential processes, such as photosynthesis, water relations, and nutrient uptake. Similarly, in rice, the grain yield was higher in the presence of weeds under both WW and DS conditions, indicating a comparable influence of weed interference on crop yield in different species (Sreekanth et al. 2024). This highlights the complex interactions between weeds and crops under varying water availability conditions and underscores the importance of effective weed management strategies for maintaining crop productivity.

(Sreekanth et al. 2024) reported that *E. colona* exerted a more pronounced negative impact on rice than *A. paronychioides*. Consistent with this, the present study revealed that *M. denticulata* had a greater adverse effect on wheat under DS compared to WW conditions. This heightened impact under DS is likely due to the enhanced root growth observed in *M. denticulata*, which was significantly greater than that of *P. minor* under both WW and DS conditions. This increased root length may confer a competitive advantage by facilitating improved water uptake under moisture-limited environments. These deeper and more developed roots likely confer a competitive advantage in accessing subsurface moisture and nutrients, particularly when surface soil layers become dry under drought conditions. This increased resource uptake by *M. denticulata* may further exacerbate stress in wheat by intensifying belowground competition, reducing the water and nutrients available to the crop during a critical growth stage. Weeds generally possess several competitive advantages over crops due to their phenotypic plasticity, enabling them to morphological and physiological variations in response to various stresses (Duke 2018). These short- and long-term adaptive responses enhance their survival and fitness, allowing them to tolerate and avoid environmental limitations such as drought more effectively than crops. The superior adaptability of *M. denticulata* under drought conditions highlights the need for targeted management strategies to mitigate its competitive effects on wheat productivity.

Conclusion

This study highlights the impact of weed interference on wheat's physiological, biochemical, and yield responses under drought stress. The findings reveal that wheat exhibits greater sensitivity to *Medicago denticulata* than *Phalaris minor* under both well-watered and drought conditions. Notably, oxidative stress induced by *M. denticulata* was more severe, as evidenced by the excessive accumulation of malondialdehyde, superoxide ions, and H_2O_2. This heightened oxidative stress corresponded with significant reductions in key physiological traits, including RWC, MSI, total chlorophyll content, photosynthetic rate, and yield attributes. The magnitude of decline was consistently greater in the presence of *M. denticulata* compared to *P. minor*, underscoring its more substantial competitive impact on wheat. These insights provide a foundation for breeding programs aimed at developing weed-competitive crop varieties with enhanced tolerance to abiotic stresses such as drought. Additionally, the study informs weed management strategies, helping policymakers assess and mitigate crop yield losses under water-limited conditions. Understanding the interplay between weed interference and drought stress is also crucial in addressing broader global challenges, particularly the impact of climate change on agricultural productivity. Future research should prioritize identifying tolerant growth stages and optimal drought durations to develop effective mitigation strategies in the context of a changing climate (SDG-13), food security and sustainable agricultural production (SDG-2), particularly in regions with low-intensity rainfall.

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Declarations

Conflict of interest The authors declare that they do not have any conflict of interest.

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