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Soil structural control of partial root-zone drying improves irrigation efficiency and yield stability in maize under deficit water conditions

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Abstract

Partial root-zone drying (PRD) is widely recognized as an effective deficit irrigation strategy to enhance water-use efficiency; however, its performance depends strongly on the soil physical environment. This study investigated how contrasting soil management systems regulate the physiological and biochemical responses of maize to PRD under semi-arid field conditions. A field experiment was conducted using contrasting soil disturbance regimes combined with full irrigation, uniform deficit irrigation, and PRD at two levels of soil water availability. Results showed that the effectiveness of PRD was strongly modulated by soil structural continuity. Under moderate PRD, irrigation water was reduced by approximately 25%, while grain yield remained within 5–8% of full irrigation. In contrast, structurally disturbed soil exhibited significantly greater yield reductions under equivalent water deficit. Improved performance under structurally stable soil conditions was associated with higher relative water content, reduced membrane damage, and sustained photosynthetic activity. Lower sub-stomatal CO_2 concentration together with higher net photosynthesis indicated that photosynthetic limitation remained primarily stomatal rather than metabolic. In addition, PRD combined with improved soil structure reduced excessive accumulation of secondary metabolites while maintaining moderate activation of enzymatic antioxidant defenses, suggesting a more efficient regulation of oxidative stress. Although soil hydraulic conductivity and root-derived hormonal signals were not directly quantified, the integrated physiological responses observed across treatments strongly indicate that soil structural continuity enhances the effectiveness of PRD by stabilizing root-zone water availability and facilitating coordinated plant water regulation. These findings demonstrate that the agronomic success of PRD is contingent upon soil physical conditions and highlight the importance of integrating deficit irrigation strategies with soil-conserving management practices to improve water productivity in water-limited environments.

Keywords: Deficit irrigation; oxidative stress; photosynthetic regulation; soil structure; Water-use efficiency.

Introduction

The relationship between soil water supply and crop productivity in semi-arid irrigated systems is rarely linear, yet agronomic management frequently proceeds as though it were. Decades of irrigation science have optimized water scheduling largely in isolation from the physical medium through which water moves and within which roots respond: the managed soil profile.

This disciplinary separation has produced a body of knowledge that is internally consistent but strategically incomplete. Irrigation strategies developed under idealized soil conditions routinely underperform in real-world field settings where tillage history, residue dynamics, and pore network continuity, rather than theoretical schedules, are the actual determinants of water delivery to active root surfaces (Sadras et al., 2022). The consequences of this incompleteness are acutely felt in maize (Zea mays L.) production. The crop's disproportionate sensitivity to water deficits during reproductive development means that even marginal hydraulic mismatches between irrigation scheduling and root-zone water delivery translate directly into yield loss. Across the semi-arid zones of Central Asia, the Middle East, and sub-Saharan Africa, the combined pressures of groundwater depletion and increasing drought frequency are rendering conventional fully-irrigated maize production economically and hydrologically untenable. This reality compels a fundamental re-examination of how irrigation and soil management practices are designed together rather than in isolation (Zhang et al., 2023a; Liu et al., 2024) .

Among deficit irrigation strategies, partial root-zone drying (PRD) has attracted sustained research interest because it exploits, rather than suppresses, the plant's endogenous stress signaling system. By maintaining spatial heterogeneity within the root zone, alternately wetting and withholding irrigation from opposing root compartments at 10–14 day intervals, PRD sustains a fraction of roots in well-hydrated soil capable of supporting shoot water status. Simultaneously, the progressively drying compartment generates a root-to-shoot chemical signal, predominantly abscisic acid (ABA), which induces partial stomatal closure and reduces transpirational water loss without the bulk leaf water potential decline that triggers non-specific stress responses under uniform deficit (Dodd, 2022). Because this stomatal response is chemically rather than hydraulically mediated, carbon assimilation is preserved at a higher fraction of its potential per unit water consumed. Consequently, PRD yields a more favorable ratio of carbon gain to transpirational loss than equivalent water reductions applied uniformly across the root zone (Romero et al., 2022). Theoretically, PRD decouples water consumption from productivity, a property of extraordinary agronomic value. In practice, however, the evidence is equivocal; published analyses of PRD field trials reveal yield responses spanning from substantial gain to measurable penalty under nominally similar conditions, a variance that irrigation scheduling variables alone cannot explain (Du et al., 2015) .

It is proposed that this unexplained variance reflects a fundamentally underexplored dependency: the hydraulic and structural condition of the soil through which ABA-generating water potential gradients must develop. For the drying root compartment to generate a sustained and quantitatively meaningful ABA flux, soil hydraulic conductivity must decline gradually enough to create a measurable water potential contrast between compartments, while maintaining sufficient pore connectivity for xylem loading and basipetal ABA transport (Chaves and Oliveira, 2004). This hydraulic environment is neither static nor independent of management; it is actively and persistently shaped by tillage intensity. Conventional tillage (CT) disrupts the continuous macropore networks formed by roots, fungal hyphae, and soil fauna, replacing them with a structurally homogenized layer whose biopore architecture and pore continuity do not recover seasonally (Li et al., 2022). In contrast, no-tillage (NT) preserves and progressively accumulates these networks across growing seasons, increasing unsaturated

hydraulic conductivity at the matric potentials typical of moderate water deficit and sustaining more gradual, spatially predictable water potential dynamics between irrigation events (Khan et al., 2022). While the hydraulic benefits of conservation tillage are documented at the system level (Hobbs et al., 2008), the specific mechanistic implication for PRD has received scant attention. NT likely does not merely retain more water but engineers the hydraulic preconditions under which PRD's chemical signaling pathway functions most reliably. Long-term adoption of integrated conservation tillage enhances maize yield by improving soil physical and nutrient environments (Fathi and Zeidali, 2021), suggesting that tillage and irrigation strategies interact through shared soil physical pathways rather than acting independently .

This interaction extends beyond hydraulics into plant stress biochemistry. The intensity and character of oxidative stress experienced by maize under water deficit depend not only on the severity of water limitation but on its predictability and rate of onset, properties governed by the soil's hydraulic architecture (Liu et al., 2024). When soil water potential declines gradually and predictably, as in a well-structured NT soil with preserved pore continuity, the plant's enzymatic antioxidant system, including catalase (CAT) and ascorbate peroxidase (APX), is upregulated proportionally. This contains reactive oxygen species (ROS) within tolerable limits at a modest metabolic cost. Conversely, when potential declines abruptly or unpredictably, as is likely in the macropore-disrupted CT profile, ROS accumulation outpaces enzymatic capacity. The plant must then escalate investment in energetically expensive non-enzymatic secondary metabolites, such as flavonoids and phenolics, as emergency scavengers. This metabolic shift redirects carbon away from productive growth, establishing a mechanistic pathway from tillage-induced hydraulic instability to yield loss that operates through the economics of stress metabolism. Whether PRD-specific induction of enzymatic antioxidant defenses is amplified or attenuated by the tillage-determined soil physical environment carries direct implications for the carbon economy of the crop .

To formalize these proposed interactions, a conceptual framework was developed (Figure 1) positing that no-tillage functions as a hydraulic preconditioner. This preconditioning stabilizes the spatial and temporal dynamics of root-zone water potential under PRD, thereby enabling consistent ABA-mediated stomatal regulation across a wider range of deficit intensities than is achievable in physically disturbed soils. Furthermore, this hydraulic stability attenuates the oxidative stress amplitude experienced by the plant, reducing the metabolic cost of stress tolerance and preserving a greater proportion of assimilated carbon for productive growth. In this framing, conventional tillage does not simply fail to provide the benefits of NT; it actively destabilizes the hydraulic environment, compromising PRD's chemical signaling architecture and imposing a higher biochemical tax on stress management.

Despite the mechanistic coherence of this framework, its empirical evaluation has been obstructed by design limitations in the existing literature. Studies examining PRD and conservation tillage have largely proceeded as parallel research programs. Factorial designs that combine both factors have frequently reported interaction statistics without interrogating the underlying mechanisms (Du et al., 2015; Fathi and Zeidali, 2021). Notably absent is the simultaneous quantification of physiological signatures distinguishing stomatal from non-

stomatal photosynthetic limitation, specifically sub-stomatal CO_2 concentration and net photosynthetic rate data analyzed alongside biochemical markers of enzymatic priming versus secondary metabolite deployment. Without this measurement suite applied across a tillage gradient under PRD conditions, the mechanistic basis for PRD efficacy remains inferential, and the influence of soil structural context cannot be definitively established .

The present study addresses these gaps through a two-year split-plot field experiment intersecting three tillage systems, conventional tillage (CT), reduced tillage (RT), and no-tillage (NT), with five irrigation regimes: full irrigation (FI), deficit irrigation (DI), and partial root-zone drying (PRD), both applied at 75% and 50% field capacity. The objective is to determine how soil structural conditions regulate the physiological effectiveness of PRD, with a specific focus on the interplay between water-use efficiency and plant hydraulic responses. The central hypothesis is that NT amplifies the agronomic efficiency of PRD by stabilizing root-zone hydraulic conductivity, thereby inducing predominantly chemical stomatal regulation and reducing the metabolic cost of stress. It is postulated that this integrated approach will demonstrate that deficit irrigation prescriptions cannot be responsibly formulated independently of soil management history, a conclusion with critical implications for designing climate-resilient cropping systems in water-limited environments.

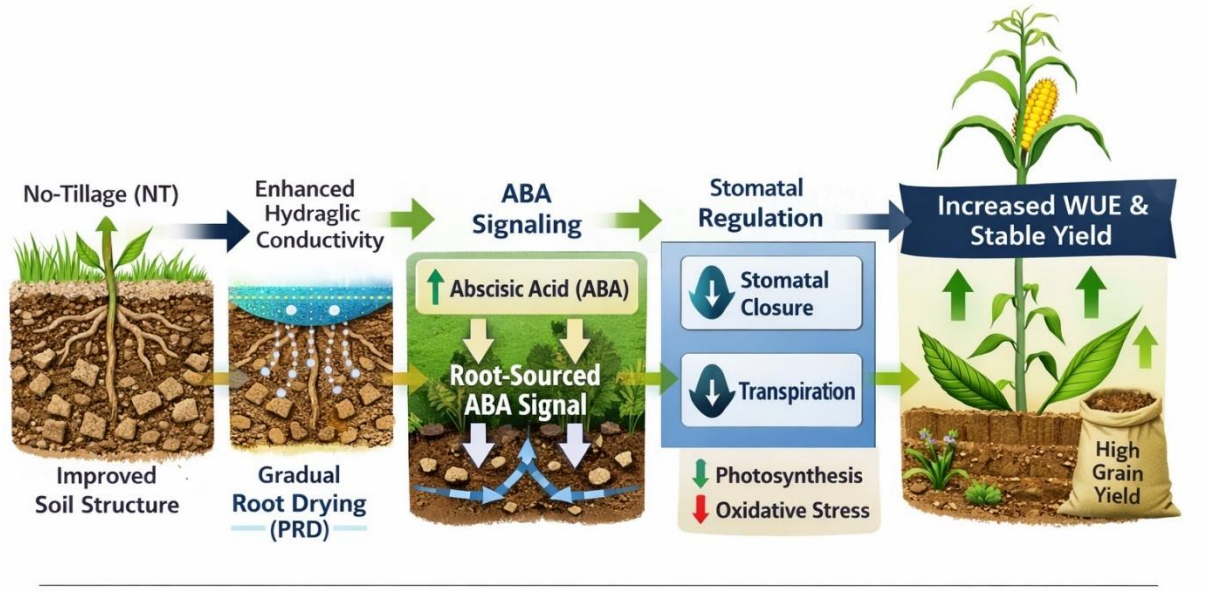


Figure 1- Conceptual model illustrating the mechanistic pathways through which no-tillage (NT) enhances the effectiveness of partial root-zone drying (PRD) in maize. Improved soil structure under NT increases hydraulic conductivity and stabilizes root-zone water gradients, promoting abscisic acid (ABA)-mediated stomatal regulation. This leads to optimized photosynthetic performance, reduced oxidative stress, and ultimately improved water-use efficiency and yield stability under deficit irrigation.

Materials and Methods

Site Description and Experimental

Design A two, year field experiment was conducted during the 2024 and 2025 growing seasons at the research farm of the Faculty of Agriculture, University of Ilam, Iran (33°39′ N, 46°22′ E; 1174 m a.s.l.). The region is characterized by a semi-arid climate, with mean annual precipitation of approximately 300 mm. Long, term meteorological data (30 years) indicate a

mean minimum temperature of 18.6–19.15°C and a maximum of 34.15–34.96°C during the maize growing season. Total potential evapotranspiration was recorded as 2106.9 mm and 1959.3 mm for 2024 and 2025, respectively.

The soil at the experimental site is classified as a clay loam (Calcaric Cambisols). Prior to treatment initiation, composite soil samples (0–30 cm depth) were collected to determine baseline physical and chemical properties (Table 1). The field had been previously cultivated with wheat (*Triticum aestivum* L.) under conventional tillage.

Table 1- Initial soil physical and chemical properties (0–30 cm depth) at the experimental site during the 2024 and 2025 growing seasons.

year	PH	EC ($ds.m^{-1}$)	Sand (%)	Silt (%)	Clay (%)	Soil Texture	Bulk Density ($g\ cm^{-3}$)	Organic Carbon (%)	N (%)	P (ppm)	K (ppm)
2024	7.41	0.185	27	45.5	27.5	clay loam	1.38	0.838	0.072	6.33	471.01
2025	8.1	0.309	27	39.5	31.5	clay loam	1.35	1.2	0.10	7.8	359.3

Baseline soil physical properties, including bulk density (using the core method) and particle size distribution, were determined from composite samples collected prior to treatment initiation.

The experiment was arranged as a split-plot design within a randomized complete block design (RCBD) with three replications. The main plots consisted of three tillage systems: conventional tillage (CT), reduced tillage (RT), and no-tillage (NT). The sub, plots comprised five irrigation regimes: full irrigation (FI) at 100% field capacity (FC), deficit irrigation (DI) at 75% and 50% FC, and partial root-zone drying (PRD) at 75% and 50% FC.

Crop Management and Tillage Practices

Maize (Zea mays L. cv. Astar, FAO 600) was sown on May 31 at a depth of 5 cm with an intra-row spacing of 20 cm, resulting in a plant density of 10 plants m^{-2}. Plot dimensions were 3 m × 3 m, consisting of four rows spaced 50 cm apart. Although the plot size (3 m × 3 m) was constrained by the experimental design requirements for precise irrigation control, border rows and a 1 m buffer strip around each plot were maintained to minimize edge effects and lateral water movement. Buffers of 2 m, 2 m, and 1 m were maintained between blocks, main plots, and subplots, respectively, to minimize lateral water movement and edge effects.

Tillage operations were implemented according to the treatment protocols:

Conventional Tillage (CT): Moldboard plowing to a depth of 25–30 cm, followed by two passes of a disk harrow and furrow formation using a ridger.

Reduced Tillage (RT): Soil chiseling to a depth of 25–30 cm (single pass), retaining approximately 50% of the previous crop residue on the surface.

No-Tillage (NT): Direct seeding into untilled soil using a no, till planter, maintaining 100% surface residue cover to conserve soil moisture and structure.

Fertilization was applied uniformly across all plots based on local soil test recommendations. Nitrogen was applied at a rate of 100 kg ha^{-1} as urea, split equally between sowing and the V6 growth stage (six, leaf stage). Phosphorus (100 kg P_2O_5 ha^{-1}) was applied as triple

superphosphate at sowing. Weeds were controlled mechanically at the 4–6 leaf stage to avoid confounding effects of herbicides on plant physiology.

Irrigation Management and PRD Setup

Irrigation was scheduled based on soil moisture depletion using a precisely calibrated drip irrigation system. Soil volumetric water content (θv) was monitored prior to each irrigation event using a Time Domain Reflectometry (TDR) device (Model R2V/6, Delta-T Devices Ltd., UK). To ensure accuracy, TDR readings were calibrated using gravimetric soil samples. The actual soil moisture content (θ_0) was calculated using the linear calibration equation derived from standard gravimetric methods:

$$(1)\ \theta_0 = 1.087 \times \theta_{TDR} - 0.03$$

Where θ_{TDR} is the volumetric moisture content read by the device.

To facilitate the partial root-zone drying (PRD) strategy, the sub-plots were equipped with two parallel drip tapes per plant row. These tapes were positioned symmetrically, approximately 10–15 cm from the plant base on opposite sides, allowing for independent control of soil wetting on either side of the root system. The volume of water delivered to each sub-plot was strictly monitored using digital flow meters installed at the inlet.

For PRD treatments, irrigation was applied exclusively to one side of the root system at a time, maintaining the opposing side in a drying state. The wetting and drying sides were alternated at fixed intervals of 10–14 days. This switching schedule was designed to allow the soil water potential in the drying compartment to decline sufficiently to stimulate the synthesis of root-sourced chemical signals (predominantly ABA) before the next irrigation cycle. Meanwhile, the irrigated compartment maintained root water uptake, preventing severe hydraulic failure in the shoot. In contrast, Full Irrigation (FI) and Deficit Irrigation (DI) controls received water simultaneously from both drip tapes, ensuring uniform soil moisture distribution across the root zone. All differential irrigation treatments commenced after the crop establishment phase (30 days after sowing) and continued until physiological maturity.

The irrigation water volume (V, m^3) required to replenish the root zone to field capacity was calculated using the following equation:

$$(2)\ V = (\theta_{FC} - \theta_i) \times D_r \times A \times 10$$

Where θ_{FC} is the volumetric soil water content at field capacity (m^3m^{-3}), θ_i is the volumetric soil water content prior to irrigation (m^3m^{-3}), D_r is the effective root zone depth (0.55m), and A is the plot area (m^2). The factor 10 converts the result from liters to decimeter, equivalent depth, ensuring unit consistency.

For deficit irrigation and partial root-zone drying (PRD) treatments, the calculated irrigation volume (V) was adjusted by applying coefficients of 0.75 or 0.50 relative to full irrigation. In PRD treatments, irrigation was applied to only one side of the plant row during each irrigation event, while the opposite side was allowed too progressively dry. This created a distinct spatial heterogeneity in soil moisture within the root zone. The wetted and sides were alternated at 10–

14 day intervals to maintain a sustained contrast in soil water availability and to stimulate root-to-shoot chemical signaling. To ensure a clear hydraulic separation between the two compartments, drip lines and emitters were positioned to minimize lateral water movement across the root zone. The spatial configuration of the irrigation system and the implementation of PRD are illustrated schematically in Figure 2.

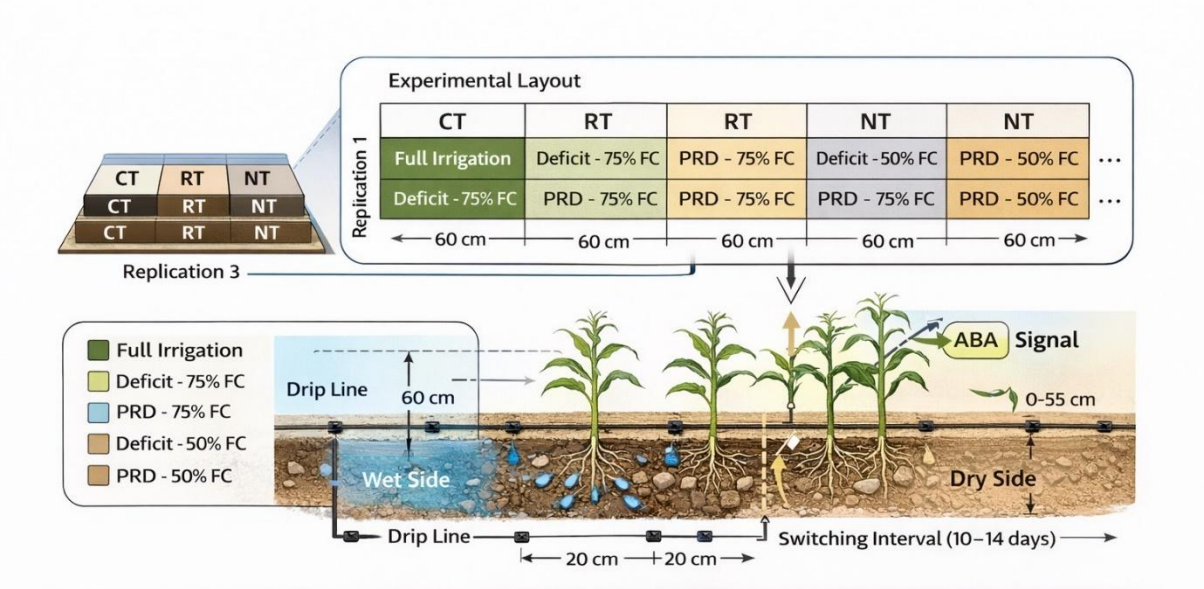


Figure 2- Schematic representation of the experimental design and irrigation configuration. The split-plot layout included tillage systems (conventional tillage, CT; reduced tillage, RT; and no-tillage, NT) as main plots and irrigation regimes as subplots. The diagram illustrates the implementation of partial root-zone drying (PRD), where irrigation was alternately applied to one side of the root zone while the opposite side was allowed to dry, with switching intervals of 10–14 days. The positioning of drip irrigation lines, emitters, and the effective root-zone depth are also depicted.

The total seasonal water applied for each treatment is summarized in Table 2.

Table 2- Total volume of irrigation water applied (m^3 ha^{-1}) for different irrigation treatments during the growing seasons.

	Irrigation level				
Irrigation treatments	**PRD 50% of the water requirement**	**PRD 75% of the water requirement**	**50% of the water requirement**	**75% of the water requirement**	**100% of water requirement**
Irrigation rate	4436.5	6655	4436.5	6655	8873

Physiological and Biochemical Measurements

Leaf Water Status and Membrane Stability

Relative water content (RWC) of the ear leaf was assessed one day before irrigation (peak stress) between 08:00 and 09:00 h. Leaf discs were excised, immediately weighed for fresh weight (FW), floated on distilled water for 24 h at 4°C in the dark to obtain turgid weight (TW), and then oven, dried at 85°C for 24 h to determine dry weight (DW). RWC was calculated as:

$$(3)\ \mathrm{RWC}(\%) = \frac{\mathrm{FW}-\mathrm{DW}}{\mathrm{TW}-\mathrm{DW}} \times 100$$

Electrolyte leakage (EL), an indicator of membrane integrity, was measured by washing leaf discs in deionized water to remove surface electrolytes. The discs were then placed in test tubes containing 10 mL of distilled water and incubated on a shaker for 24 h at 25°C. After incubation, the initial electrical conductivity (C_1) was measured using a conductivity meter. Samples were subsequently autoclaved at 120°C for 20 min to completely rupture the cells and release all electrolytes. After cooling to room temperature, the final electrical conductivity (C_2) was recorded. The EL percentage was calculated as:

$$(4)\ \mathrm{EL}(\%) = \frac{\mathrm{C1}}{\mathrm{C2}} \times 100$$

Photosynthetic Gas Exchange

Gas exchange parameters, including net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (C_i), were measured on the sun, exposed ear leaf at the flowering stage using a portable infrared gas analyzer (KR8700, KoreaTech, South Korea). Measurements were taken between 11:00 and 13:00 h under clear sky conditions with ambient CO_2 concentration and photosynthetic photon flux density > 1200 µmol m^{-2} s^{-1}. Instantaneous water-use efficiency (WU_{Einst}) was calculated as the ratio of P_n to E using the following equation:

$$(5)\ \mathrm{WUEinst} = \frac{\mathrm{Pn}}{\mathrm{E}}$$

Where Pn is the net photosynthetic rate (µmol$CO2m^{-2}s^{-1}$) and E is the transpiration rate (mmol$H2Om^{-2}s^{-1}$).

Antioxidant Enzyme Activity and Oxidative Damage

Fresh leaf tissue (0.5 g) was homogenized in ice, cold extraction buffer (50 mM phosphate buffer, pH 7.0, containing 1 mM EDTA and 1% polyvinylpyrrolidone) and centrifuged at 12,000 × g for 15 min at 4°C. The supernatant was used for enzyme assays. Catalase (CAT) activity was determined by monitoring the decomposition of H_2O_2 at 240 nm (extinction coefficient 39.4 mM^{-1} cm^{-1}) as described by Aebi (1984). One unit of CAT was defined as the amount of enzyme that decomposes 1 µmol H_2O_2 per minute. Ascorbate peroxidase (APX) activity was measured by following the oxidation of ascorbate at 290 nm (extinction coefficient 2.8 mM^{-1} cm^{-1}) in a reaction mixture containing phosphate buffer, ascorbate, H_2O_2, and enzyme extract (Nakano and Asada, 1981). Lipid peroxidation was estimated by quantifying malondialdehyde (MDA) content using the thiobarbituric acid (TBA) method (Heath and Packer, 1968). Absorbance was recorded at 532 nm and 600 nm, and MDA concentration was calculated using an extinction coefficient of 155 mM^{-1} cm^{-1}.

Osmolyte and Secondary Metabolite Accumulation

Proline content was determined using the acid, ninhydrin method (Bates et al., 1973). Absorbance was measured at 520 nm, and concentration was calculated using an L, proline standard curve. Total phenolic content was assayed using the Folin, Ciocalteu reagent, with

results expressed as mg gallic acid equivalents (GAE) per gram fresh weight (Singleton & Rossi, 1965). Total flavonoid content was determined via the aluminum chloride colorimetric method and expressed as mg quercetin equivalents (QE) per gram dry weight (Chang et al. 2002).

Yield and Statistical Analysis

At physiological maturity, plants from the central rows (e.g., 2 m^2 area*)* of each sub, plot were harvested to determine biological yield (above, ground biomass) and grain yield (adjusted to 14% moisture content). Harvest index (HI) was calculated as the ratio of grain yield to biological yield.

Data were subjected to analysis of variance (ANOVA) using SAS software (version 9.4). Normality and homogeneity of variances were tested using Shapiro, Wilk and Levene's tests, respectively. Since the year effect was non, significant for most agronomic traits (Table 3), data were pooled across years for analysis. Mean comparisons were performed using the least significant difference (LSD) test at a probability level of 0.05. Graphical representations were generated using SigmaPlot software (version 14.0).

Results

Grain yield, biomass production, and carbon allocation

A strong interaction between soil management and irrigation strategy was detected for grain yield ($P < 0.01$; Table 3), indicating that crop productivity was jointly regulated by water availability and the soil physical environment governing root water uptake.

Under non-limiting water supply, grain yield remained statistically similar between inversion-based tillage and residue-retaining systems, averaging approximately 10,200 kg ha^{-1} (Figure 3; Table 3). This convergence suggests that enhanced nutrient mineralization in tilled soil compensated for the structural advantages of undisturbed systems when water was not limiting. However, this equivalence rapidly diverged under water deficit.

As irrigation declined, yield reductions were substantially greater in tilled soil, whereas residue-retaining systems maintained significantly higher productivity. Under moderate deficit imposed through spatial root-zone drying at 75% of field capacity, grain yield remained close to the fully irrigated control (9,650 kg ha^{-1}), while tilled soil exhibited a marked yield penalty (8,150 kg ha^{-1}; Figure 3; Table 3). This divergence widened further under severe deficit, where residue-retaining systems sustained 7,200 kg ha^{-1} compared with 6,000 kg ha^{-1} in tilled soil (Figure 3).

Biomass production followed a similar interaction pattern ($P < 0.01$; Table 3). While tilled soil maximized aboveground biomass under full irrigation (24,500 kg ha^{-1}), its performance declined sharply under water deficit. In contrast, residue-retaining systems maintained significantly greater biomass under severe deficit (18,200 vs. 13,800 kg ha^{-1}; Figure 4), indicating improved resilience of growth processes under water limitation.

Harvest index was primarily regulated by irrigation ($P < 0.01$; Table 3). The highest value was observed under full irrigation (~44.5%; Figure 5). Importantly, moderate deficit imposed

through partial root-zone drying maintained harvest index at ~41%, statistically comparable to the control (Figure 5), indicating stable assimilate partitioning. In contrast, severe deficit reduced harvest index to ~36% (Figure 5), reflecting a shift toward survival-oriented allocation.

Plant water status and membrane stability

Leaf water status was significantly influenced by both soil management and irrigation ($P < 0.01$; Table 3). Full irrigation resulted in the highest relative water content (~86%; Figure 6). Residue-retaining systems consistently maintained higher leaf hydration (~82%) compared to tilled soil (~78%; Figure 6)

Under irrigation treatments, partial root-zone drying at 75% of field capacity maintained relative water content (~80.5%) at levels statistically comparable to uniform irrigation at the same level (Figure 6; Table 3), confirming its efficiency in preserving plant water status.

Membrane stability showed clear sensitivity to both factors ($P < 0.01$; Table 3). Electrolyte leakage was highest in tilled soil (~28.5%) and lowest in residue-retaining systems (~19.2%; Figure 7). Water deficit intensified membrane damage, with maximum leakage observed under severe uniform deficit (~32.4%; Figure 8). However, partial root-zone drying significantly mitigated this damage under equivalent water supply (22.1% vs. 25.6%; Figure 8), highlighting its protective physiological effect.

Biochemical regulation: antioxidant systems and secondary metabolism

Flavonoid and total phenolic contents were significantly affected by the three-way interaction of soil management, irrigation, and year ($P < 0.01$; Table 3). In both years, these metabolites increased progressively with water deficit (Table 4).

The highest flavonoid accumulation was observed under severe deficit conditions in tilled soil (up to 4.10 mg QE g^{-1} DW in 2025; Table 4), whereas residue-retaining systems exhibited a more moderate increase (3.70 mg QE g^{-1} DW). A similar pattern was observed for total phenolics, which reached 6.80 mg GAE g^{-1} FW in tilled soil under severe deficit, compared with 6.40 mg GAE g^{-1} FW in residue-retaining systems (Table 4).

Catalase activity was significantly influenced by soil management, irrigation, and their interaction (Table 3). The highest activity was recorded under severe partial root-zone drying (1.30 μmol H_2O_2 min^{-1} mg^{-1} protein; Figures 9 and 10), while full irrigation resulted in the lowest values.

Proline accumulation increased significantly under water deficit (Table 3), reaching maximum values under severe uniform deficit (~2.10 μmol g^{-1} FW; Figures 11 and 12). Intermediate soil disturbance induced greater proline accumulation than either extreme (Figure 11), suggesting increased osmotic stress under less stable soil conditions.

Ascorbate peroxidase activity was also significantly affected by irrigation and its interaction with soil management (Table 3). The highest values were observed under severe deficit conditions (Figures 13 and 14), with strong responses also recorded under partial root-zone drying.

Oxidative damage and photosynthetic function

Lipid peroxidation, measured as malondialdehyde content, was significantly influenced by irrigation ($P < 0.01$; Table 3). The highest levels were observed under severe uniform deficit (~1.65 nmol g^{-1} FW; Figure 15), whereas partial root-zone drying significantly reduced oxidative damage (~1.15 nmol g^{-1} FW; Figure 15).

Photosynthetic performance was strongly affected by the interaction between soil management and irrigation ($P < 0.01$; Table 3). Under moderate deficit with spatial root-zone drying, net photosynthesis remained significantly higher (4.85 µmol CO_2 m^{-2} s^{-1}) than in tilled soil (3.50 µmol CO_2 m^{-2} s^{-1}; Figure 16). Even under severe stress, residue-retaining systems sustained higher photosynthetic activity (Figure 16).

Sub-stomatal CO_2 concentration increased under water deficit (Figure 18), particularly in tilled soil, indicating a shift toward non-stomatal limitations. In contrast, residue-retaining systems maintained lower internal CO_2 levels (Figure 17), suggesting preservation of photosynthetic capacity.

Transpiration dynamics and water-use efficiency

Transpiration rate was primarily influenced by irrigation ($P < 0.01$; Table 5). Full irrigation resulted in the highest transpiration (~5.60 mmol H_2O m^{-2} s^{-1}), while partial root-zone drying significantly reduced transpiration relative to uniform irrigation at the same level (Figure 21).

This reduction translated into improved instantaneous water-use efficiency, which was significantly affected by the interaction of soil management and irrigation ($P < 0.05$; Table 5). The highest efficiency was observed under severe partial root-zone drying in residue-retaining systems (~4.10 µmol CO_2 mol^{-1} H_2O; Figure 22), followed by moderate deficit under similar conditions.

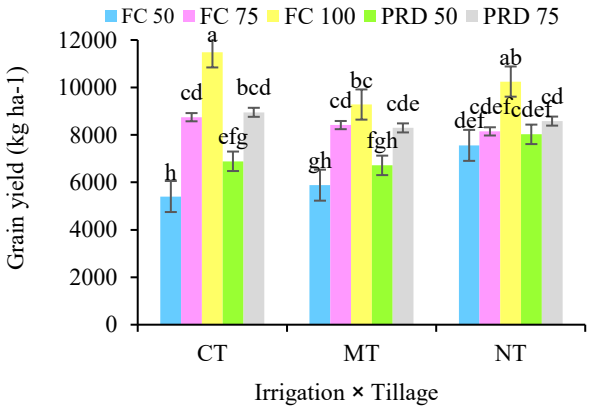


Figure 2- Comparison of the average interaction effect of tillage and irrigation levels on grain yield
No Tillage NT, Reduced tillage RT, Conventional Tillage CT. Different letters indicate statistically significant differences according to Fisher's LSD test ($P \leq 0.05$).

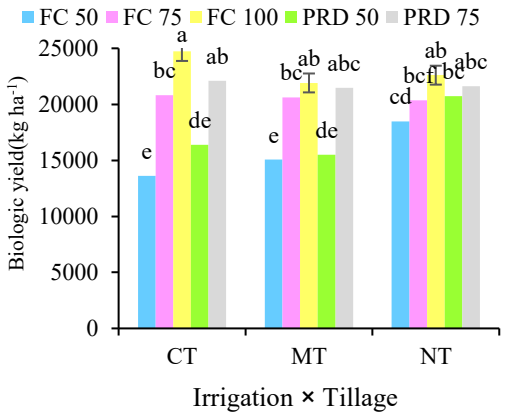


Figure 3- Comparison of the average interaction effect of tillage and irrigation levels on biological yield
No Tillage NT, Reduced tillage RT, Conventional Tillage CT

Table 3- Analysis of variance (mean squares) for the effects of tillage, irrigation, and year on maize agronomic and physiological traits.

Source of variation	df	Grain yield	Biologic yield	Harvest index	Relative water content	Electrolyte leakage	Flavonoid	Total phenol	Catalase	Proline	ascorbate peroxidases	Malon dialdehyde	Pn	Ci (µmol CO_2 mol^{-1})
year	1	884467.6ns	159257.6ns	25.11ns	17.55ns	1.02ns	0.58*	4.5**	4.06 **	7.98 **	0.09*	0.3ns	0.1ns	899.33ns
Rep(year)	4	15188412	33118002.4	110.49	38.75	7.52	0.208	1.8	0.13	0.29	0.02	0.57	0.29	4403.92
Tillage	2	5033562.2**	26372035.7**	15.93ns	80.57**	33.66**	7.34**	10.07 **	0.33 **	1.28**	0.05 ns	0.08 ns	2.45**	77194.26**
Tillage× year	2	121897.3ns	1019049.2ns	18.46ns	4.15ns	0.0009ns	11.8**	12.82 **	0.03 ns	0.25ns	0.001 ns	0.32 ns	0.00013ns	0.46ns
Rep× (year)	8	357618.7	7351698.9	17.16	27.14	0.67	0.52	1.08	0.17	0.23	0.06	0.21	0.02	3153.27
Irrigation Level	4	42309271.4**	165631322.9**	70.53**	1055.45**	1891.96**	1.28**	6.49 **	1.14 **	0.98 **	1.13 **	2.13 **	50.93**	21088.38**
Tillage× Irrigation	8	3489779.7**	17889768.4**	13.46ns	3.22ns	0.33ns	0.86**	1.95 **	0.16 *	0.1 ns	0.05*	0.09 ns	0.21**	255.63ns
Irrigation × year	4	77420.7ns	2164681.9ns	18.37ns	3.12ns	0.0012ns	0.4**	2.51 **	0.8 **	0.42 **	0.02ns	0.35 ns	0.001ns	0.71ns
Tillage× Irrigation × year	8	113733.4ns	1597908.9ns	8.29ns	2.71ns	0.0009ns	0.68**	1.12 **	0.12ns	0.12 ns	0.005 ns	0.07 ns	0.00007ns	0.3ns
Total Error	48	499189.9	2620590	14.36	15.80	0.92	0.097	0.38	0.06	0.08	0.02	0.16	0.04	229.09
C.V. (%)	,	8.64	8.20	9.16	5.23	1.40	10.67	14.81	17.18	13.76	11.03	13.93	7.47	3.45

ns: not significant. * and **: significant at the 0.05 and 0.01 probability level, respectively.

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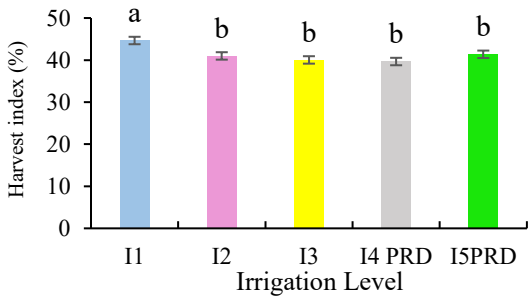


Figure 4- Effect of irrigation levels on harvest index
I1 100% irrigation, I2 75% irrigation, I3 50% irrigation, I4 75% PRD irrigation, I5 50% PRD irrigation

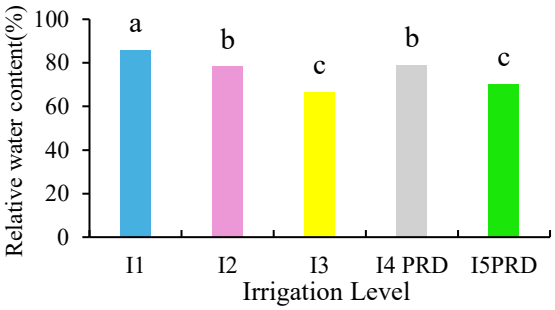


Figure 5- Effect of irrigation levels on relative water content
I1 100% irrigation, I2 75% irrigation, I3 50% irrigation, I4 75% PRD irrigation, I5 50% PRD irrigation.

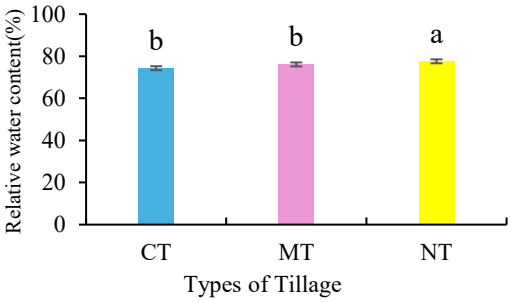


Figure 6- Effect of tillage methods on relative water content
No Tillage NT, Reduced tillage RT, Conventional Tillage CT

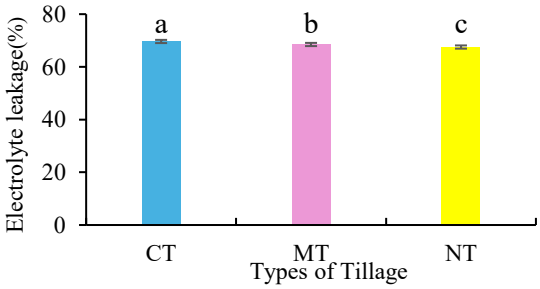


Figure 7- Effect of tillage methods on electrolyte leakage
No Tillage NT, Reduced tillage RT, Conventional Tillage CT

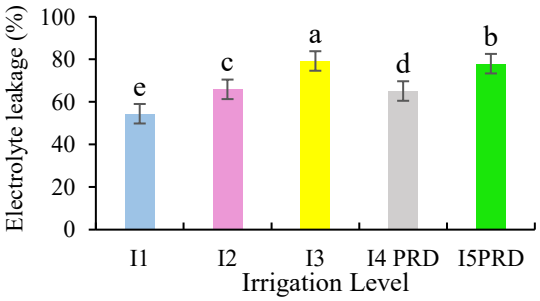


Figure 8- Effect of irrigation levels on electrolyte leakage
I1 100% irrigation, I2 75% irrigation, I3 50% irrigation, I4 75% PRD irrigation, I5 50% PRD irrigation

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Table 4-Comparison of the effect of tillage on agronomic and biochemical traits of corn during two cropping years

Tillage	Irrigation	Flavonoid (mg QE/g DW)		Total phenol (mg GAE/g FW)	
		2024	2025	2024	2025
	I1	1.85e	1.92e	4.20f	4.35f
	I2	2.45d	2.50d	5.10d	5.25d

CT	I3	3.10c	3.20c	6.05b	6.15b
	I4	3.60b	3.65b	6.50a	6.60a
	I5	4.05a	4.10a	6.70a	6.80a
	I1	1.70f	1.75f	3.90g	4.00g
	I2	2.20e	2.25e	4.80e	4.90e
	I3	2.95cd	3.05cd	5.60c	5.70c
RT	I4	3.40bc	3.45bc	6.10b	6.20b
	I5	3.80ab	3.85ab	6.40ab	6.50ab
	I1	1.55g	1.60g	3.65h	3.75h
	I2	2.10ef	2.15ef	4.55f	4.65f
NT	I3	2.80de	2.90de	5.30d	5.40d
	I4	3.25cd	3.30cd	5.85c	5.95c
	I5	3.65b	3.70b	6.30b	6.40b

In each column, means followed by a common letter do not differ significantly at the 5% probability level using LSD test.

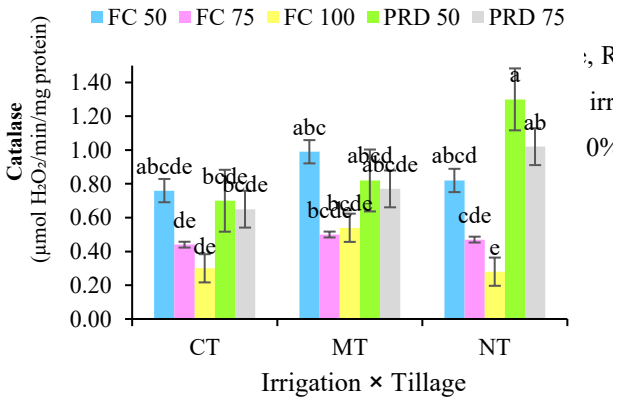


Figure 9- Comparison of the interaction effect of tillage and irrigation levels on catalase

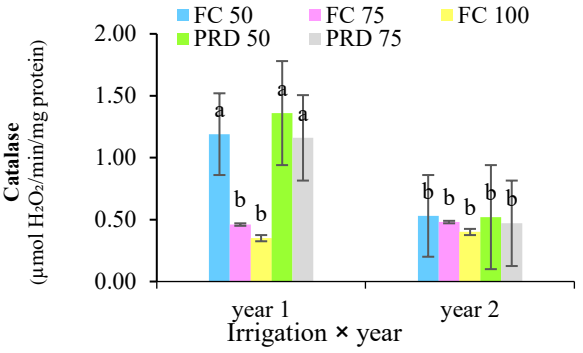


Figure 10- Comparison of the average interaction effect of year and irrigation levels on catalase content

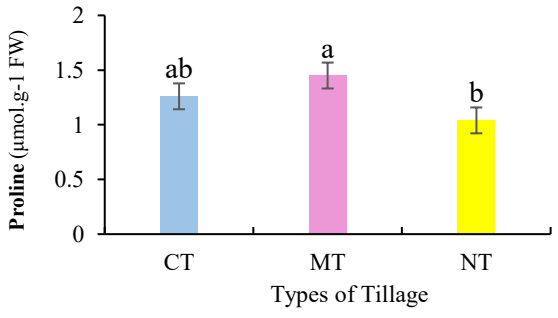


Figure 11- Effect of tillage methods on proline

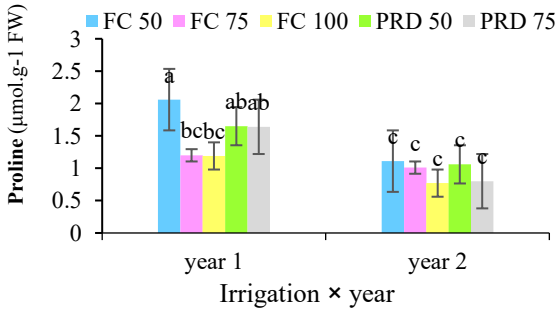


Figure 12- Interaction effect of year and irrigation levels on proline

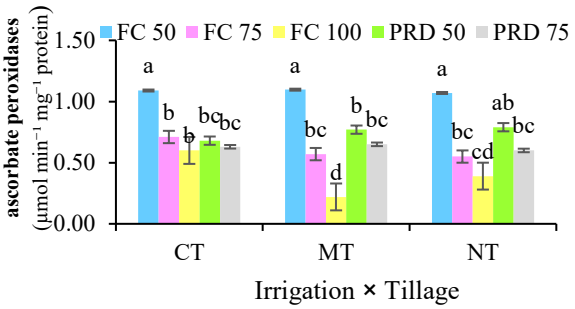


Figure13- Comparison of the average interaction effect of tillage methods and irrigation levels on ascorbate peroxidase content

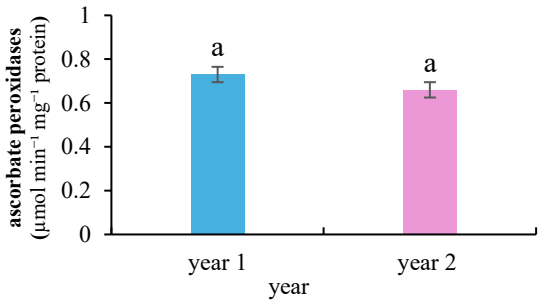


Figure 14 - Comparison of the average effect of year on ascorbate peroxidase content

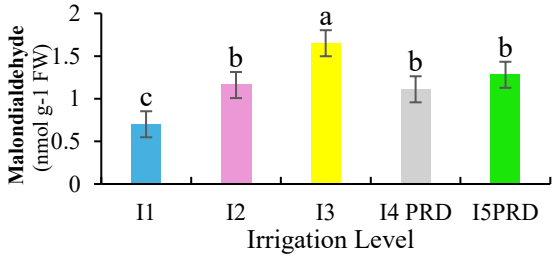


Figure 15- Effect of irrigation levels on malondialdehyde

I1 100% irrigation, I2 75% irrigation, I3 50% irrigation, I4 75% PRD irrigation, I5 50% PRD irrigation
No Tillage NT, Reduced tillage RT, Conventional Tillage CT

400

401

402

Table 5- Analysis of variance (mean squares) for the effects of tillage, irrigation, and year on maize leaf temperature, transpiration rate, and photosynthetic water-use efficiency.

Source of variation	df	TL	transpiration Rate	PWUE
year	1	0.74ns	0.05ns	0.05ns
rep(year)	4	16.35	1.24	1.49
Tillage	2	158.61**	0.04ns	1.16**
Tillage× year	2	0.0007ns	0.00001ns	0.0003ns
rep× (year)	8	5.43	0.02	0.03
Irrigation Level	4	9.43**	81.05**	20.76**
Tillage× Irrigation	8	0.03ns	0.06ns	0.14*
Irrigation × year	4	0.0007ns	0.003ns	0.01ns
Tillage× Irrigation × year	8	0.0002ns	0.00001ns	0.0006ns
Total Error	48	0.19	0.07	0.05
C.V. (%)	,	1.22	14.59	10.04

ns: not significant. * and **: significant at the 0.05 and 0.01 probability level, respectively.

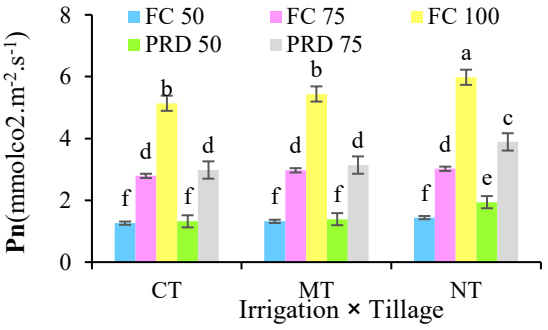


Figure 16- Interaction effects of irrigation and tillage levels on net photosynthesis rate

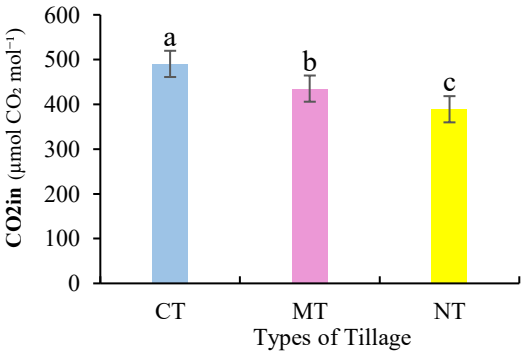


Figure 17- Effect of tillage method on CO2 in

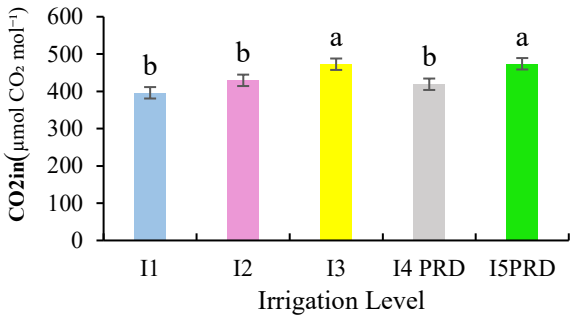


Figure 18- Effect of irrigation levels on CO2 in

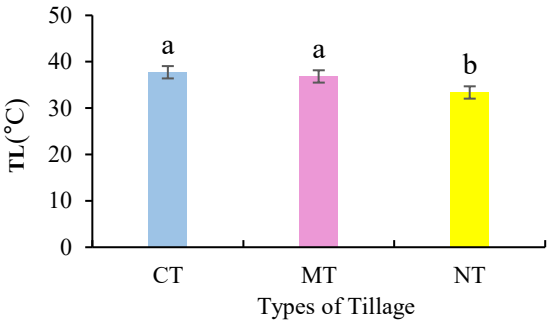


Figure 19- Effect of tillage method on leaf temperature

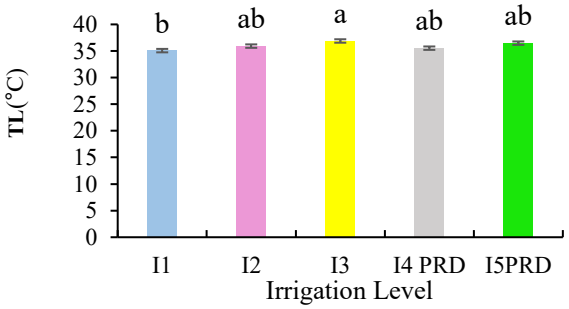


Figure 20- Effect of irrigation levels on leaf temperature

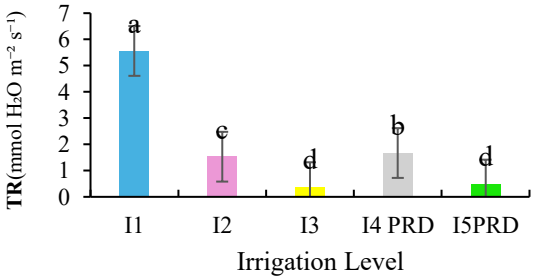


Figure 21- Effect of irrigation levels on transpiration rate

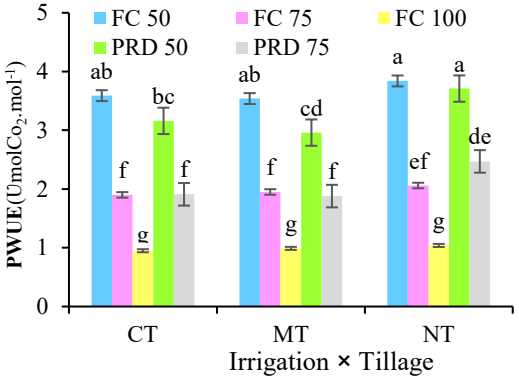


Figure 22- Interaction effect of tillage method and irrigation levels on photosynthetic water use efficiency

I1 100% irrigation, I2 75% irrigation, I3 50% irrigation, I4 75% PRD irrigation, I5 50% PRD irrigation
No Tillage NT, Reduced tillage RT, Conventional Tillage CT

Discussion

Grain yield, biomass production, and source-sink regulation

The yield advantage observed under conventional tillage (CT) in the absence of water limitation is likely attributable to the transient pulse of nitrogen mineralization following soil inversion, a phenomenon that enhances nutrient availability during critical reproductive stages (Hobbs et al., 2008). However, this apparent agronomic benefit is structurally fragile. The disruption of macropore continuity and the exacerbation of evaporative losses under tilled conditions impose a steep, unfavorable yield–water relationship that rapidly deteriorates as water availability declines (Niu et al., 2022).

In contrast, no-tillage (NT) fundamentally alters this hydraulic paradigm by stabilizing the soil's physical architecture. By preserving continuous pore networks, NT enhances unsaturated

hydraulic conductivity at low matric potentials, thereby sustaining effective water flux to roots during periods of peak atmospheric demand (Li et al., 2022). This hydraulic buffering elucidates why yield reductions under NT were disproportionately smaller than the reduction in applied water volume, indicating a partial decoupling of biomass production from total water consumption. From an agronomic perspective, this shift is significant, as it prioritizes water productivity over absolute yield maximization. Although soil hydraulic conductivity was not directly quantified in this study, the divergent physiological responses across management systems, specifically the disparities in leaf water status, transpiration dynamics, and photosynthetic regulation, serve as robust functional proxies indicating that soil structural continuity critically governed water transport to the root zone (Wang et al., 2024). Consequently, these integrated plant responses suggest that management-induced variations in pore connectivity were the primary drivers of water uptake efficiency under partial root-zone drying (PRD) (Yan et al., 2023).

The harvest index (HI) responses further underscore a vital physiological distinction between irrigation strategies. Under uniform deficit irrigation (DI), stomatal closure is primarily driven by declining leaf water potential, a hydraulic signal that simultaneously constrains photosynthesis and assimilate transport. Conversely, the maintenance of HI under PRD implies regulation mediated by root-sourced chemical signals, most plausibly abscisic acid (ABA), generated in the drying soil compartment prior to critical shoot water deficit (Dodd, 2022). This response aligns with the established chemical signaling pathway characteristic of PRD (Dodd, 2022; Zhao et al., 2024). While ABA was not directly quantified here, the coordinated phenotype of reduced stomatal conductance, preserved leaf water status, and stable photosynthetic performance is widely recognized as the functional signature of PRD-induced signaling (Zhao et al., 2024). The preservation of assimilate partitioning under these conditions suggests that reproductive sinks remained functionally prioritized. When coupled with NT, this mechanism appears to maintain the hormonal hierarchy necessary for efficient grain filling under reduced water input (Peng et al., 2023). The comparable yields achieved under moderate PRD and conventional deficit irrigation further highlight the efficiency of this integrated strategy in sustaining carbon allocation to reproductive tissues (Razzaghi et al., 2023).

Plant water relations and membrane stability

The consistently higher relative water content (RWC) observed under NT cannot be ascribed solely to enhanced soil water storage. Rather, it reflects improved root system functionality arising from a superior physical environment. In tilled soils, mechanical impedance and structural instability can restrict root proliferation, limiting access to deeper moisture reserves. By preserving soil structure, NT facilitates deeper, more continuous root penetration, effectively increasing the exploitable soil volume and enabling plants to maintain turgor under deficit conditions (Bai et al., 2023).

Electrolyte leakage (EL) patterns provide complementary insights into stress mitigation pathways. NT appears to mitigate membrane damage primarily through physical buffering, dampening temperature fluctuations and minimizing rapid wetting–drying cycles in the rhizosphere. In contrast, PRD operates through a physiological preconditioning mechanism,

upregulating antioxidant defenses before oxidative stress reaches damaging levels (Ahmad et al., 2023). The significant reduction in membrane damage observed when these two strategies are combined suggests their effects are additive rather than redundant, operating through distinct yet convergent pathways of stress alleviation.

Biochemical regulation and the metabolic cost of stress

The accumulation of flavonoids and phenolics under water deficit represents more than a generalized stress response; it reveals critical differences in stress management efficiency between soil systems. The elevated concentrations observed under CT likely indicate repeated exposure to oxidative stress driven by amplified soil temperature fluctuations and surface exposure. Each stress cycle necessitates the renewed synthesis of non-enzymatic secondary metabolites, imposing a cumulative metabolic tax on the plant (Sharma et al., 2019). This repeated carbon diversion may partially explain the accelerated yield decline observed in tilled soils under water deficit (Zhang et al., 2023b).

Conversely, NT attenuates the frequency and intensity of oxidative perturbations at their source. Surface residues moderate soil temperature and moisture variability, thereby lowering the demand for sustained secondary metabolite production. Consequently, plants achieve oxidative homeostasis with a lower metabolic expenditure, preserving carbon resources for growth and yield formation (Ibrahim et al., 2020).

The observed enzymatic antioxidant activity supports this interpretation. The moderate yet sustained elevation of catalase (CAT) and ascorbate peroxidase (APX) activity under the combined NT and PRD treatment, alongside reduced lipid peroxidation, suggests a "primed" physiological state. In this state, antioxidant defenses are sufficiently activated to maintain redox balance without triggering the energetically expensive escalation of secondary metabolism typical of severe or fluctuating stress (Anjum et al., 2016; Bazrgar et al., 2023).

Interestingly, the elevated proline accumulation under reduced tillage (RT) highlights the physiological consequences of intermediate soil disturbance. While partial residue cover reduces evaporative loss, the lack of continuous pore networks may result in spatially and temporally inconsistent water availability. Such hydraulic variability likely generates a less predictable stress signal, forcing the plant to rely more heavily on osmotic adjustment. Given the high energetic cost of proline synthesis, its accumulation in this system reflects a compensatory strategy to maintain cellular hydration under unstable hydraulic conditions (Bates et al., 1973; Sikuku et al., 2023).

Photosynthetic regulation and water-use efficiency

The dynamics of sub-stomatal CO_2 concentration (Ci) provide a key mechanistic distinction between soil management systems. Under CT, increasing Ci despite reduced stomatal conductance indicates the onset of non-stomatal limitations, suggesting impairment of the photosynthetic apparatus, likely due to oxidative damage to thylakoid membranes (Hu et al., 2024). In contrast, lower Ci coupled with higher photosynthetic rates under NT indicates that biochemical capacity is largely preserved, and photosynthesis is regulated primarily through controlled stomatal limitation. This distinction is critical: stomatal limitation is generally

reversible upon rehydration, whereas non-stomatal damage often leads to prolonged or irreversible reductions in photosynthetic capacity. Agronomically, this translates into resilience; systems limited primarily by stomatal regulation can recover rapidly following rewatering, whereas systems dominated by non-stomatal limitations accumulate damage over successive stress cycles, leading to progressive yield decline.

Study limitations and future perspectives

While the results provide compelling evidence for the interaction between soil management and irrigation strategy, several limitations must be acknowledged. First, the inference of root-to-shoot signaling relies on indirect physiological indicators, including stomatal conductance, intercellular CO_2 concentration, and antioxidant activity. The absence of direct quantification of abscisic acid limits the ability to conclusively attribute the observed responses to hormonal pathways; thus, our interpretation of PRD-induced signaling remains inferential rather than confirmatory. Second, the proposed linkage between soil structure and PRD effectiveness, while strongly supported by plant physiological data, requires direct physical validation. Measurements of soil hydraulic properties, such as conductivity functions and water retention characteristics, were not conducted. Future research should integrate high-resolution soil physical measurements with simultaneous quantification of root-sourced signaling compounds to empirically validate the soil-plant interaction mechanisms proposed here. Collectively, however, these findings demonstrate that integrated plant physiological responses offer a robust framework for inferring soil-plant hydraulic dynamics in field environments where direct physical measurements may be constrained.

Conclusion

This study demonstrates that the effectiveness of deficit irrigation strategies in semi-arid maize systems is fundamentally governed by the soil physical environment created by tillage practices. While conventional tillage maximizes yield under optimal water supply, its structural instability leads to a rapid decline in productivity under water limitation. In contrast, no-tillage establishes a more resilient yield-water relationship by stabilizing soil hydraulic properties and sustaining plant water uptake under deficit conditions.

The combination of no-tillage and partial root-zone drying at moderate deficit emerged as the most efficient management strategy, achieving substantial water savings with minimal yield penalty. This system maintained photosynthetic performance primarily through regulated stomatal limitation rather than irreversible metabolic damage, while simultaneously reducing the metabolic cost of stress through a balanced antioxidant response.

Collectively, these findings indicate that the benefits of deficit irrigation are strongly context-dependent and are maximized when coupled with soil management practices that enhance hydraulic continuity and physiological stability. Advancing this integrative framework will require direct quantification of soil–plant hydraulic interactions and hormonal signaling dynamics, providing a more mechanistic basis for designing climate-resilient cropping systems.

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Competing interests

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Data availability

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