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Enhancing growth and tolerance traits in pepper (*Capsicum annuum* L.) through water-saving irrigation practices

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Abstract

Due to their intensive cultivation, horticultural crops are particularly susceptible and vulnerable to the detrimental effects of drought stress, necessitating significant water inputs for optimal growth and yield. Accordingly, water-saving irrigation strategies, i.e., Partial Root zone Drying (PRD) and Regulated Deficit Irrigation (RDI) emerge as pivotal tools for bolstering the resilience of the horticultural sector. The current study aims to evaluate the impact of PRD and RDI strategies on pepper (*Capsicum annuum* L.) growth, and physio-biochemical attributes under semi-controlled greenhouse conditions. Research findings revealed pronounced enhancements in stem length under both irrigation strategies, with PRD exhibiting superior effects on shoot fresh and dry biomass (increases of 57.2% and 61.1%, respectively) compared to full irrigation. At the physiological level, PRD and RDI induced a significant reduction in stomatal conductance in pepper plants relative to full irrigation, while maintaining leaf water potential and relative water content. Biochemically, plants subjected to PRD and RDI methods exhibited significant accumulation of free proline, particularly pronounced with PRD (approximately 115.9% increase compared to full irrigation). Furthermore, Chl a and carotenoid concentration significantly increased under PRD, indicating sustained photosynthetic functionality. Comparatively, PRD appears as the more effective technique, offering the potential to conserve agricultural water about 50 without compromising growth parameters, while simultaneously enhancing tolerance traits in *C. annuum*. Nonetheless, further investigations on other traits across diverse soil types, climates, and cultivars under field conditions are imperative to ascertain the broader applicability of PRD and optimize its implementation.

Keywords: *Capsicum annuum*; irrigation management; partial rootzone drying (PRD); regulated deficit irrigation (RDI); stomatal conductance; proline; water-use efficiency

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Introduction

Irrigation consumes around 70% of the world's freshwater withdrawals, supporting global agricultural production and guaranteeing food security (Rockström *et al*., 2017; FAO, 2019). Notably, irrigated lands constitute 20% of the total global cropland area, yet they contribute to approximately 40% of the global food output (Borsato *et al*., 2020). Simultaneously, 40% of irrigation practices worldwide exhibit unsustainability due to their impact on environmental flows and/or depletion of groundwater reserves (Rosa *et al*., 2018). The interaction between economic agricultural productivity and water resource requirements necessitates the assessment of drought stress for sustainable agriculture, especially in semi-arid and arid regions. Irrigation rationalization has emerged as a key strategy to minimize the adverse effects of climate variations, especially in regions where agriculture holds paramount economic importance (Borsato *et al*., 2020). In this context, water-efficient irrigation methods have been developed to address this challenge. Among these water applications through the adoption of water-saving irrigation (WSI) practices are regulated deficit irrigation (RDI) and partial root drying (PRD) (Slamini *et al*., 2020). These methods help in reduce water consumption while maintaining crop productivity. By adopting these practices, farmers can enhance water use efficiency while minimizing the environmental impacts associated with excessive water use (Slamini *et al*., 2020).

RDI and PRD represents effective management strategies for improving water use efficiency in agriculture (Tahi *et al*., 2007). The choice of an irrigation approach depends, to a large extent, on the different responses of species and cultivars to water deficit (Lamaoui *et al*., 2018). Unlike RDI, which is advantageous when well managed by applying mild water deficit throughout the root system, PRD is an alternative irrigation method that allows the plant to obtain sufficient water from the well-watered side of the root system while the other side is exposed to soil drying. This drought-perceiving side reduces stomatal opening by producing root chemical signals, primarily abscisic acid, to enhance water use efficiency and plant growth (Slamini *et al*., 2022). In addition, several research reported that the uptake of plant nutrients reaches its peak with PRD compared to full irrigation, across a variety of arable crops, including potatoes (Shahnazari et al., 2008; Wang et al., 2009) and maize (Krida *et al*., 2005; Li *et al*., 2007). Indeed, the implementation of this mild deficit stimulates root development and increases the root-to-shoot ratio, thereby equipping plants better to cope with soil water deficit in later stages (Iqbal *et al*., 2020). The effect of these two deficit irrigation techniques on eco-physiological and biochemical behavior has been studied in several plant species, including common bean (Wakrim *et al*., 2005), tomato (Tahi *et al*., 2007), olive tree (Aganchich *et al*., 2007), and melon (Lamaoui *et al*., 2018).

Pepper (*Capsicum annuum* L.) is a major economic importance crop, widely cultivated in numerous countries. The total global production of pepper is estimated at 34 million tons per year (Penella and Calatayud, 2018). In Morocco, its yield varies depending on the variety, cultivation type, management practices, and production region (Ellatir *et al*., 2003). Its cultivation within the framework of the vegetable sector plays a significant role socioeconomically. This sector in Morocco serves as a foreign exchange earner with over 1.2 billion US$ annually (42% of agricultural exports) (MAPMDREF, 2024). However, several countries worldwide, including Morocco, are facing the issue of freshwater availability (Hssaisoune *et al*., 2020).

In this context, the study is conducted to assess the effect of two water-saving irrigation methods, namely PRD and RDI, on the main growth traits and physio-biochemical responses in *C. annuum* plants grown under semi-controlled greenhouse conditions.

Materials and Methods

Plant material and growth conditions

The roots of two-month-old plants were divided into two and transplanted into plastic pots (25 cm in length and 12 cm in diameter) filled with a substrate mixture composed of 50% peat, 25% sand, and 25% compost (Figure 1a). Each plant was transplanted into two plastic pots of equal volume placed side by side, and each root portion was placed in a separate pot filled with 500 g of the substrate mixture. Before initiating our experiment, the plants were regularly irrigated every 48 hours for one month according to the field capacity (FC) determined beforehand in pots without plants containing the same substrate mixture. Subsequently, the plants were divided into 3 blocks as follows: block A: control plants maintained at 100% field capacity for both adjacent pots, block B: plants irrigated using the RDI technique, which involves reducing irrigation to 50% of the field capacity for the entire root system, and block C: plants irrigated using the PRD technique, which involves irrigating only half of the root system at 50% of the field capacity (Figure 1b). This study was conducted in pots to simulate field conditions (Figure 1c). The experiment was carried out in a greenhouse under semi-controlled conditions (28±3 °C, 60-65% relative humidity, and natural photoperiod of approximately 12 hours of light per 24 hours), for 40 days, at the Higher Normal School of Marrakech (-8.05014220°/W, 31.62912560°/N, and 442.26 m a.s.l).

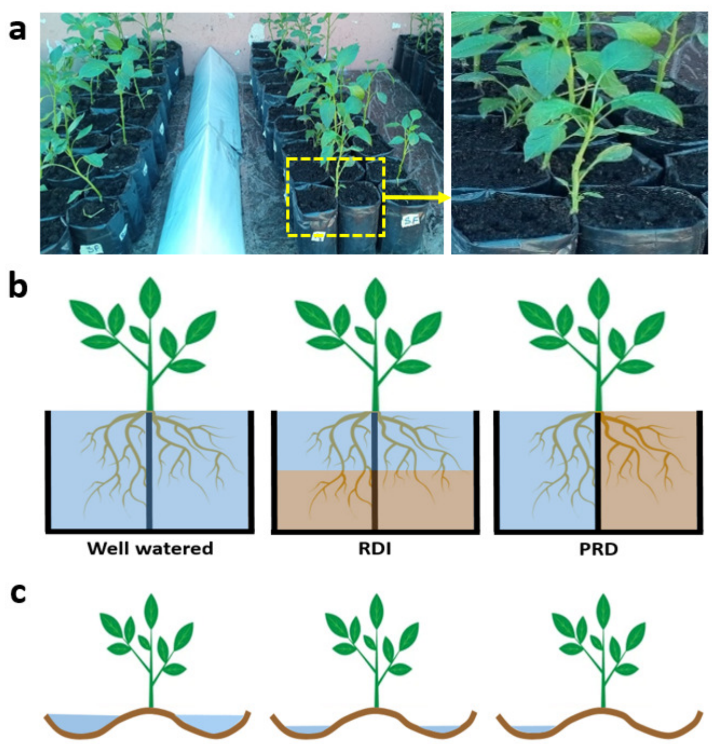

Figure 1. Experimental layout a) transplantation of *C. annuum* plants roots into plastic pots, b) schematic diagram of the irrigation pattern in Well-watered, RDI (regulated deficit irrigation), and PRD (partial root-zone drying) (pot implication), and c) schematic representation of the irrigation pattern in Well-watered, RDI, and PRD (field implication)

Growth traits measurement

The maximum length of the stem (LS) and the internode distance (IND) (between the 3rd and 4th node) of *C. annuum* plants were measured using a ruler graduated in cm. The total number of leaves (NL) was counted. The fresh and dry biomass of the shoots (FBS and DBS) was measured using a digital precision balance in mg. The dry biomass was measured after drying the fresh plant material in an oven at 70 °C for 48 hours. For all blocks, the leaf area (LA) at the 4^{th} node was determined in cm^2 according to the method of Paul *et al.* (1979). These measurements were performed with 5 repetitions per treatment (plant per repetition).

Physio-biochemical traits

Determination of water potential, stomatal conductance, and relative water content

The predawn leaf water potential (Ψ_{pd}) of *C. annuum* plants was assessed using a pressure chamber (SKPD 1400, Instruments Skye, Powys, United Kingdom). Stomatal conductance (g_s) was determined with a portable porometer (Leaf Porometer LP1989, Decagon Device, Inc., Washington, USA). Leaf relative water content (RWC) was measured and computed as follows: RWC (%) = (FW−DW) / (SW−DW) × 100, where FW, SW, and DW represent fresh weight, saturated weight (after 24 hours of rehydration in distilled water at 4 °C), and dry weight (after oven drying for 48 hours at 80 °C), respectively. These measurements were performed with 5 repetitions per treatment (plant per repetition).

Photosynthetic pigments

Chlorophyll (Chl a and Chl b) and total carotenoid (Car) concentrations in *C. annuum* leaves (100 mg) were quantified using 80% acetone extracts following the procedure outlined by Arnon (1949). Absorbance readings were taken at wavelengths of 663 nm, 645 nm, and 440 nm, employing a digital spectrophotometer (J.P SELECTA, s.a. model VR-2000). The concentrations of Chl a, Chl b, and Car were calculated and expressed as mg g-1 dry weight, utilizing the following equations: Chl a = [12.7(A663) – 2.69(A645)] × (V/1000)W, Chl b = [22.9(A645) – 4.68(A663)] × × (V/1000)W, and Car = 46.95 × A440 – 0.268 × Chl (a+b); where A represents the optical density, V denotes the volume (in mL), and W indicates the sample weight. The measurements were performed with 3-4 repetitions per treatment (plant per repetition).

Organic osmolytes

For proline concentration (Pro), the leaf samples of *C. annuum* (200 mg) were homogenized with 2 mL of 40% ethanol and heated at 85 °C for 60 minutes. Subsequently, the homogenate was centrifuged at 1788 × g for 10 minutes, and proline concentration was quantified in the supernatant following the method described by Monneveux and Nemmar (1986). To the supernatant (1 mL), 1 mL of glacial acetic acid and 1 mL of acid ninhydrin solution were added, and the resulting mixture was heated for 1 hour in a boiling water bath. Following this, 5 mL of toluene was added to the mixture, and after shaking, the upper phase was recovered. The absorbance at 528 nm was then measured, and expressed as mg g^{-1} DW.

Soluble sugar (SS) concentration was assessed using the procedure outlined by Dubois et al. (1956). Leaf samples (100 mg) were homogenized with 80% acetone and subsequently centrifuged at 2795 × g for 10 minutes. The resulting supernatant (1 mL) was mixed with 1 mL of a 5% phenol solution and 5 mL of concentrated sulfuric acid. Absorbance readings were taken at 485 nm using a digital spectrophotometer, and the concentration of soluble sugars (µg g^{-1} DW) was determined using a standard curve generated with glucose.

These measurements were performed with 4 repetitions per treatment (plant per repetition).

Statistical analysis

All experimental data were subjected to analysis of variance (ANOVA) to assess the impact of both PRD and RDI on the morpho-physio-biochemical traits under investigation. Statistical comparisons of means were performed at a significance level of 5% using Tukey's post hoc test. A Principal Component Analysis (PCA) was established to identify and distinguish discriminatory variables between different irrigation regimes. All statistical analyses were conducted using SPSS version 25 for Microsoft Windows.

Results

The results related to growth traits measured in pepper plants subjected to different irrigation systems are presented in Table 1. Statistical analysis of these results revealed significant differences among the irrigation systems for certain traits ($p \leq 0.05$). Stem length significantly increased by approximately 21.5% under RDI and 25.8% under PRD compared to the control, without exhibiting a statistically significant difference between these two deficit irrigation systems. Relative to the control, the highest leaf number was recorded under RDI with an improvement of about 23.8%, while under PRD, we noted the highest shoot biomass, approximately 57.2% for fresh biomass and 61.1% for dry biomass. However, no significant difference was recorded among the studied irrigation systems for internode distance and leaf area ($p \leq 0.05$).

Table 1. Change of growth traits (stem length, internode distance, number of leaves, leaf area, and shoot fresh and dry biomass in three-month-old *C. annuum* plants under both RDI and PRD for 40 days

Parameter	Control	RDI	PRD
Stem length	16.50±0.41b	20.05±1.05a	20.75±0.96a
Internode distance	2.48±0.13a	2.83±0.24a	2.73±0.34a
Number of leaves	15.75±1.71b	19.50±1.29a	18.75±1.71ab
Leaf area	19.08±4.69a	22.54±10.02a	23.65±7.87a
Shoot fresh biomass	3.25±0.73b	4.26±1.16ab	5.11±0.44a
Shoot dry biomass	0.36±0.07b	0.50±0.13ab	0.58±0.06a

Means with different lowercase letters are significantly different according to Tukey's test ($p \leq 0.05$)

The results regarding chlorophyll a and b as well as carotenoid concentration revealed significant ($p \leq 0.05$) differences between PRD and RDI (Table 2). Indeed, PRD induced a significant increase in Chl a by approximately 24.8%, Chl b by 34.6%, and Car by about 25.0% compared to RDI. Nonetheless, in comparison to the control, there was a significant increase of 51.7% in Chl a, 39.1% in Chl b, and 36.4% in Car under PRD conditions ($p \leq 0.05$).

Table 2. Change of Chl a, Chl b, and Car concentration in three-month-old *C. annuum* plants under both RDI and PRD for 40 days

Parameter	Control	RDI	PRD
Chl a (µg/mg)	14.48±3.05b	17.61±0.79b	21.97±0.65a
Chl b (µg/mg)	13.39±0.34b	13.83±0.49b	18.62±2.23a
Car (µg/mg)	0.11 ±0.01b	0.12±0.00b	0.15 ±0.01a

Means with different lowercase letters are significantly different according to Tukey's test ($p \leq 0.05$)

Except for g_s (Figure 2), results of Ψ_{pd} and RWC showed no significant ($p \leq 0.05$) difference among *C. annuum* plants subjected to different irrigation systems (Figures 3 and 4). The values of Ψ_{pd} ranged from -1.25 MPa (control irrigation) to -1.42 (PRD) (Figure 3), while those of RWC varied from 56.7 for PRD to 70.16 for the control (Figure 4). Nonetheless, both RDI and PRD induced a significant decrease in g_s in *C. annuum* plants. Compared to the control, RDI reduced g_s by 26.4%, while PRD reduced it by 15.1% ($p \leq 0.05$). The significant ($p \leq 0.05$) difference in g_s between PRD and RDI was approximately 15.3% (Figure 2).

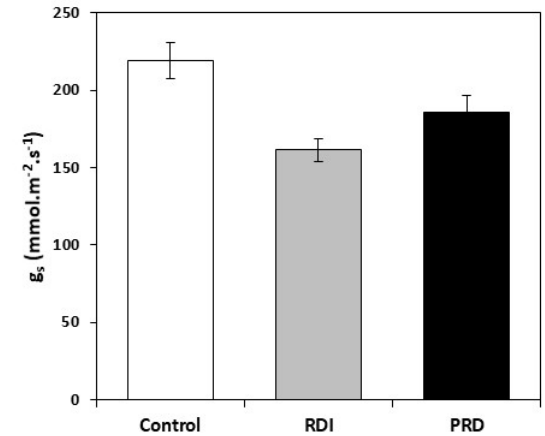

Figure 2. Change of stomatal conductance in three-month-old *C. annuum* plants under both RDI and PRD for 40 days
Means with different lowercase letters are significantly different according to Tukey's test ($p \leq 0.05$)

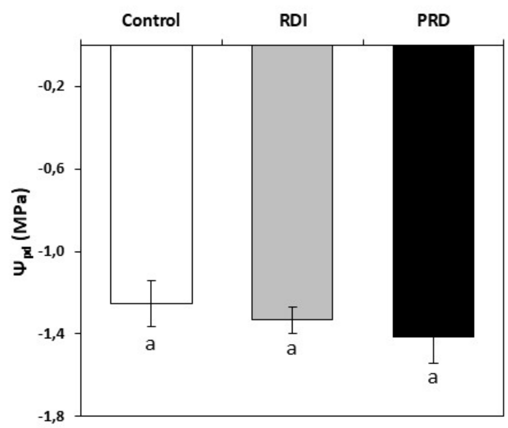

Figure 3. Change of Ψ_{pd} in three-month-old *C. annuum* plants under both RDI and PRD for 40 days
Means with different lowercase letters are significantly different according to Tukey's test ($p \leq 0.05$)

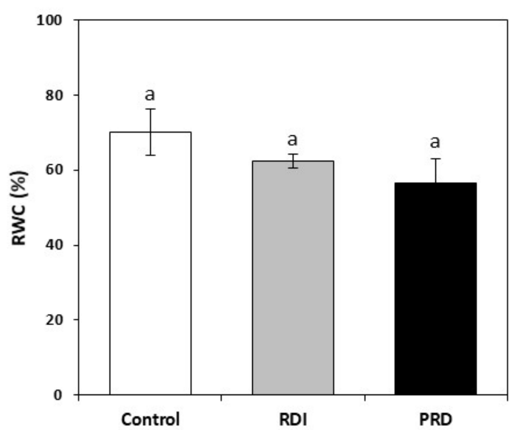

Figure 4. Change of RWC in three-month-old *C. annuum* plants under both RDI and PRD for 40 days.
Means with different lowercase letters are significantly different according to Tukey's test ($p \leq 0.05$)

Both irrigation methods investigated, RDI and PRD, significantly ($p \leq 0.05$) increased the concentration of free proline in *C. annuum* plant leaves compared to the control irrigation regime (Figure 5). This increase was estimated at 39.5% under RDI and 115.9% under PRD compared to the control. Moreover, the difference in proline concentration induced by RDI and PRD was about 54.8%, indicating a pronounced accumulation of proline in *C. annuum* plants subjected to PRD. However, no significant difference was observed between the studied irrigation methods regarding the total soluble sugar concentration (Figure 6). The recorded values ranged from 2.41 μg/mg (control regime) to 2.79 μg/mg (RDI). The recorded values ranged from 2.41 μg/mg (control treatment) to 2.79 μg/mg (RDI).

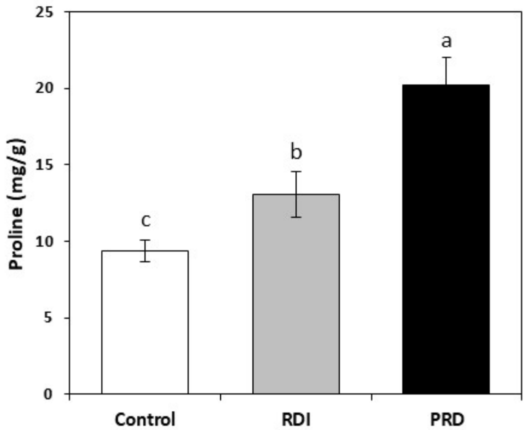

Figure 5. Change of proline concentration in three-month-old *C. annuum* plants under both RDI and PRD for 40 days

Means with different lowercase letters are significantly different according to Tukey's test ($p \leq 0.05$)

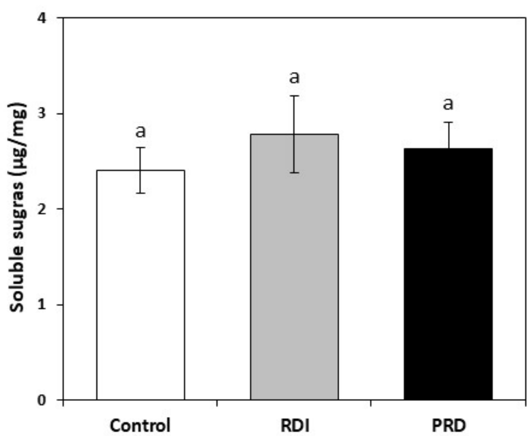

Figure 6. Change of soluble sugar concentration in three-month-old *C. annuum* plants under both RDI and PRD for 40 days

Means with different lowercase letters are significantly different according to Tukey's test ($p \leq 0.05$)

Based on PCA, we opted for the first two principal components, which account for the majority of the cumulative variance, totalling approximately 67.3% of the overall variance (PC1: 50.3% and PC2: 17.0%) (Figure 7). According to the component coefficient matrix and the bi-dimensional space (Figure 7a), PC1 exhibits strong correlations with LS (0.91), Chl a (0.91), Pro (0.87), Car (0.85), FBS (0.85), and DBS (0.84) in the positive side, while displaying correlation with Ψ_{pd} (0.71) and g_s (0.57) in the negative side. On the other hand, PC2 shows the highest correlations with IND (0.69), LA (0.69), and SS (0.49) in the positive side, and Pro (0.43), Car (0.37) and Chl b (0.35) in the negative side. PCA projection (Figure 7b) illustrates distinct separation between full irrigation regime (control) and both PRD and RDI by the PC1, whereas PRD and RDI were clearly distinguished by PC2. Corroborating the ANOVA findings, PCA revealed a clear and predominant separation between PRD and RDI, primarily attributed to higher levels of chlorophyll a and b, carotenoids, and proline in PRD.

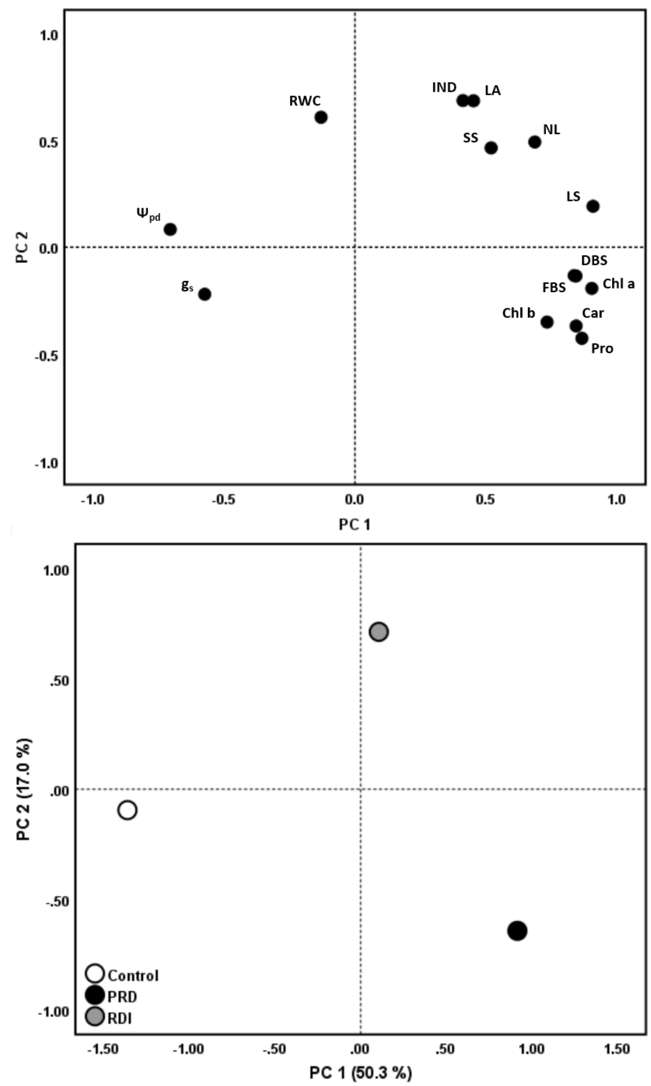

Figure 7. 2D scatter-plots showing the distribution of all studied parameters (a) and irrigation regimes (b) according to the two main principal components obtained by PCA in *C. annuum* plants

Discussion

The implementation of novel irrigation management methods is indeed a necessary practice to mitigate the impact of climate change, which exacerbates drought occurrence and diminishes crop yields and freshwater resources worldwide (Slamini *et al*., 2022). Furthermore, irrigation has been instrumental in facilitating rapid increases in agricultural yields and production over the past three decades, contributing to poverty reduction and lower food prices while enhancing health and nutrition outcomes (Rosegrant *et al*., 2009). Irrigated agriculture accounts for between 50 and 90% of all water resources in the Mediterranean basin, which is characterized by an arid to semi-arid climate (Tahi *et al*., 2007). PRD and RDI strategies are employed in the horticultural industry due to their ability to enhance the efficient use of irrigation water and often improve product quality (Slamini *et al*., 2022). According to our findings, both methods significantly enhanced stem length and leaf number in *C. annuum* plants compared to the control irrigation regime, without affecting the dry biomass of the aboveground portion. Lamaoui *et al*. (2018) reported that PRD and RDI improved the vegetative growth of two melon varieties, particularly in terms of leaf number, internode number, and stem length. This positive growth trend appeared to be variety-dependent, especially concerning stem length (Lamaoui *et al*., 2018). However, other studies have revealed that these two irrigation techniques significantly reduced shoot biomass compared to the control in beans (Wakrim *et al*., 2005), tomatoes (Tahi *et al*., 2007), and olive trees (Aganchich *et al*., 2007).

Although *C. annuum* plants under both PRD and RDI received 50% of the water supplied to the control, the different water distribution between the two soil compartments resulted in differences in stomatal conductance. Both irrigation methods reduced g_s without affecting RWC and leaf water potential in *C. annuum* plants. These methods have been proposed to stimulate physiological mechanisms that mitigate the relationship between g_s, an integrative parameter reflecting the intensity of plant water stress, and ambient evaporation conditions (Lamaoui *et al*., 2018; Slamini *et al*., 2022). Under mild water stress conditions, stomatal closure was highly effective in preventing water loss, given its relationship with unchanged leaf water potential and RWC under these deficit irrigation regimes (Lamaoui *et al*., 2018). Qualitative correlations among these three physiological parameters under the same irrigation regimes have been reported in different plant species (Wakrim *et al*., 2005; Tahi *et al*., 2007; Aganchich *et al*., 2007; Consoli *et al*., 2014). These two deficit irrigation regimes contribute to improving water use efficiency and productivity with minimal or insignificant impact on crop yield (Slamini et al., 2022). This is due, in part, to the long-distance signalling system (abscisic acid: ABA) of the plant as a physiological response, which results in reduced water loss through regulatory behaviors at the stomatal guard cell level, inducing reduced stomatal conductance and transpiration (Wakrim *et al*., 2005; Lamaoui *et al*., 2018). Similarly, it is due to the improvement of the photosynthesis-transpiration ratio (Iqbal *et al*., 2020); and on the other hand, by reducing the soil evaporation surface (Xie *et al*., 2012). Compared to our results, the significant reduction in stomatal conductance, especially under RDI, manifested by partial stomatal closure at the leaf level would increase water-use efficiency and productivity (Davies *et al*., 2002; Chakhchar *et al*., 2015). Under dry soil, roots synthesize higher levels of ABA compared to normal conditions. ABA serves as an anti-stress chemical signal, translocating from the roots to the shoots via transpiration and regulating stomatal conductance (Aslam *et al*., 2022). During moderate water stress, ABA exerts its effects before the hydraulic signal, which reflects alterations in xylem sap tension due to decreased soil water availability (Alemu and Llorens, 2020). When applying PRD to a crop, roots on the non-irrigated side stimulate ABA secretion, whereas fully hydrated roots sustain favorable water status in the aerial portion of the plant (Alemu and Llorens, 2020; Iqbal *et al*., 2020; Aslam *et al*., 2022).

Both deficit irrigation methods revealed significant differences between them in chlorophyll and carotenoids concentration. Unlike RDI, PRD induced a significant increase in the concentration of Chl a and carotenoids compared to the control. Contrary to our findings, Ghafari *et al*. (2020) reported a decrease in chlorophyll and carotenoid content in apple plants subjected to PRD, which could lead to a reduction in photosynthesis. Other studies have shown that PRD irrigation had a significant impact on photosynthesis, as observed in potatoes (Liu *et al*., 2006) and maize (Kirda *et al*., 2005). However, Tahi *et al*. (2007) reported that notwithstanding the reduced stomatal conductance observed under DRP and RDI, the photosynthetic activity of tomato plants remained significantly unaffected compared to the control irrigation regime.

The concentration of free proline significantly accumulated in *C. annuum* plants under both RDI and PRD compared to the control; however, total soluble sugars showed no significant difference. Due to its low molecular weight, proline acts as an osmoticum by facilitating water diffusion into cells and maintaining tissue turgor in plants. Under deficit irrigation conditions, proline accumulation can be associated with the regulation of osmotic potential in *C. annuum* plants according to the law of mass action to alleviate osmotic stress and improve water retention capacity (Chai *et al*., 2016). Osmotic adjustment mediated by proline in pepper plants appeared to be more pronounced under PRD than under RDI. Our findings align with previous studies showing that the accumulation of osmolytes, such as proline, drought-affected plants, promotes osmotic adjustment capacity, particularly when RDI (Chai *et al*., 2016; Aganchich *et al*., 2022) and PRD (Zhang *et al*., 2019; Aganchich *et al*., 2022) is applied early in growth. Considering all studied traits, PRD has shown greater efficacy in enhancing pepper resistance to drought stress compared to RDI.

Conclusions

Improving water use efficiency through the advancement of irrigation techniques shows promise for sustainable development. Even with a 50% decrease in water supply, pepper plants were able to maintain their growth. Our results obtained in this study have demonstrated that the implementation of RDI and PRD significantly reduced stomatal conductance in *C. annuum* plants without negatively affecting the dry biomass of the shoot. Particularly, PRD induced a significant accumulation of Chl a, carotenoids, and proline in pepper leaves compared to normal irrigation conditions. The adoption of PRD as a promising agricultural strategy for water-efficient management in pepper cultivation could prove effective and economically viable in terms of water resource conservation, sustainable development, and enhancing pepper resilience to climate change. However, further investigation is required to effectively apply this technique across various soil types, climates, and cultivars in field conditions.

Authors' Contributions

Conceptualization: A.C., A.F.M. and C.E.M.; Methodology: S.D. H.E. A.C.; Validation: A.C.; Writing—original draft preparation: A.C., S.D. and H.E.; Writing—review and editing: A.C.; Supervision: A.C., A.F.M. and C.E.M. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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