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Physiological traits, crop growth, and grain quality of quinoa in response to deficit irrigation and planting methods

Sayyed Mohammad Mirsafi¹, Ali Reza Sepaskhah^{1,2*} and Seyed Hamid Ahmadi^{1,2}

Abstract

Climate change has become a concern, emphasizing the need for the development of crops tolerant to drought. Therefore, this study is designed to explore the physiological characteristics of quinoa that enable it to thrive under drought and other extreme stress conditions by investigating the combined effects of irrigation water levels (100%, 75%, and 50% of quinoa's water requirements, WR as I1, I2 and I3) and different planting methods (basin, on-ridge, and in-furrow as P1, P2 and P3) on quinoa's physiological traits and gas exchange. Results showed that quinoa's yield is lowest with on-ridge planting and highest in the in-furrow planting method. Notably, the seed protein concentrations in I2 and I3 did not significantly differ but they were 25% higher than those obtained in I1, which highlighted the possibility of using a more effective irrigation method without compromising the seed quality. On the other hand, protein yield (PY) was lowest in P2 (mean of I1 and I2 as 257 kg ha⁻¹) and highest in P3 (mean of I1 and I2 as 394 kg ha⁻¹, 53% higher). Interestingly, PY values were not significantly different in I1 and I2, but they were lower significantly in I3 by 28%, 27% and 20% in P1, P2, and P3, respectively. Essential plant characteristics including plant height, stem diameter, and panicle number were 6.1–16.7%, 6.4–24.5%, and 18.4–36.5% lower, respectively, in I2 and I3 than those in I1. The highest Leaf Area Index (LAI) value (5.34) was recorded in the in-furrow planting and I1, while the lowest value was observed in the on-ridge planting method and I3 (3.47). In I3, leaf temperature increased by an average of 2.5–3 °C, particularly during the anthesis stage. The results also showed that at a similar leaf water potential (LWP) higher yield and dry matter were obtained in the in-furrow planting compared to those obtained in the basin and on-ridge planting methods. The highest stomatal conductance (gs) value was observed within the in-furrow planting method and full irrigation (I1P3), while the lowest values were obtained in the on-ridge and 50%WR (I3P2). Finally, photosynthesis rate (An) reduction with diminishing LWP was mild, providing insights into quinoa's adaptability to drought. In conclusion, considering the thorough evaluation of all the measured parameters, the study suggests using the in-furrow planting method with a 75%WR as the best approach for growing quinoa in arid and semi-arid regions to enhance production and resource efficiency.

Keywords Drought tolerance, Leaf Area Index, Photosynthesis rate, Stomatal conductance

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Introduction

Plants are exposed to different environmental conditions such as different abiotic stresses including shortage of available water, salinity, and unfavorable temperature [1]. Climatic conditions in semiarid areas (limited precipitation and excessive evapotranspiration due to high temperatures) cause a negative water balance. Growing



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water demand from urban centers and industries, in addition to a more evaporative climate due to climate change, has reduced irrigation water availability for farmers [2]. Therefore, developing water-efficient cropping methods and adapting them to the impact of climate change is crucial. Different field management strategies have been reported to improve the performance of crops under extreme conditions, including appropriate planting methods [3–6], selecting appropriate planting density [7, 8], and deficit irrigation. Deficit irrigation is considered an approach to address water scarcity in arid and semi-arid areas [9–11].

Under climate change, crops that have been grown for decades are losing their potential for yield, and are unable to bridge the food supply–demand gap. This alarming situation necessitates the development of drought-tolerant crops. Plants have different approaches to cope with water stress such as morpho-anatomical, physiological, and biochemical adjustments which aim to preserve their hydric status [12]. Plants' tolerance to water stress mainly depends on plant genotype, stress intensity, and duration [13, 14]. The quinoa crop might be a suitable alternative to grain crops that are commercially grown to meet the food demand in inappropriate environments. Quinoa (*Chenopodium quinoa* Willd.) has gained increasing attention on a global scale since 2013 due to its greater protein content than other cereals and a better distribution of the necessary amino acids [15]. It is a C3 crop native to the Andean region, which is reported to be a potential crop for food security [16]. It is reported that quinoa has a low water requirement [17, 18], on the contrary, there are studies that indicate the evapotranspiration of quinoa varies between 1100 and 1600 mm in arid and semi-arid areas [7, 19].

Quinoa tolerance to water stress has been studied widely [20–25]. Quinoa deals with low water availability by tolerating water stress through a vigorous and deep root system [7, 26, 27], reducing transpiration, leaf area [27], and maintaining leaf turgor and closing of stomata [28].

The physiological indices including photosynthesis rate, stomatal conductance, intrinsic water use efficiency and transpiration reduced in response to a water shortage [29]. The most sensitive measure of water stress is the stomatal conductance, which is a common approach to plant studies in drought conditions that involves monitoring of gas exchange. Gas exchange estimates plant transpiration as a function of the leaf water status [30]. Leaf area index (LAI), the total one-sided area of photosynthetic tissue per unit horizontal ground surface area is one of the most important parameters as it regulates gas exchange processes such as photosynthesis [31] and evapotranspiration [32]. LAI

can be determined by direct methods, which are time-consuming. Light extinction coefficient (K) is used to estimate the irradiance into the canopy and is an indicator of light penetration through the crop canopy. LAI and K are the key indicators of vegetation canopy characteristics. Accurate quantification of these characteristics is essential as it plays a crucial role in ecosystem studies on productivity, carbon cycles, nutrient allocation, and biological diversity [33].

Water scarcity affects agricultural development and productivity, as well as food security [34]. Therefore, there is a need to introduce new crops which can be adapted to the arid and semi-arid areas, which are facing severe drought. To effectively understand the growth and yield of crops, a greater understanding of the variables, which are influencing biomass is necessary. This will make it possible to measure productivity in various situations, which will improve understanding of constraints brought on by stress, canopy design, and leaf area dynamics [34]. Quinoa's physiological adaptability, which enables it to thrive in drought and other extreme stress conditions, is an invaluable opportunity with enormous potential to cope with current and potential climate challenges [35]. However, it is necessary to investigate the effect of adverse environmental conditions on the growth and yield of quinoa, as a new crop, on a small scale before planting on a large scale.

Most of the cultivated areas in Iran are arid and semi-arid, that are short in water resources and groundwater depletion [36]. Therefore, appropriate irrigation water management such as deficit irrigation and in-furrow planting method should be used in field to reduce the irrigation water use and enhance its productivity [3, 11]. Quinoa cultivation area in Iran was about 300 ha in 2016 and is increasing recently, with mean yield of 1850 kg ha⁻¹ [37, 38]. In addition, to increase crop production, preserve water supplies, and establish sustainable agricultural practices in semi-arid regions like Iran, deficit irrigation and planting methods in relation to quinoa physiology must be investigated as they offer important insights into how quinoa reacts to water scarcity and how to effectively manage this crop in difficult environmental circumstances. Thus, investigating the variation in quinoa physiological parameters, gas exchange, morpho-physiological processes responsible for drought tolerance and light extinction coefficient is critical to cope with drought stress. So far, there are some reports on the physiological response of quinoa to drought in greenhouse experiments [29, 35] or in field [39, 40] but the variation of the effect of deficit irrigation combined with different planting method on quinoa has not been investigated. Thus, the aim of this study is to investigate the combined effects of irrigation water level and planting

method on the physiological growth and gas exchange of quinoa.

Methods and materials

Site description

This study was conducted at the Experimental Station, the School of Agriculture, Shiraz University, in a semi-arid region of the Bajgah area (29°56' N, 52°02' E and at 1810 m above the mean sea level) during 2017 and 2018 in south-western Iran. The physical and chemical characteristics of the field soil are listed in supplementary Table S1. Climatic data (including air temperature and humidity, wind speed, and hours of sunshine) were obtained from a standard weather station near the experimental field. Supplementary Figure S1 shows the average daily minimum and maximum temperature and average relative humidity during the first and second growing seasons. The daily vapor pressure deficit for each growing season is shown in Supplementary Fig. S2a. Total precipitation during the growing season was 15.5 and 60 mm in the first and second year, respectively (Supplementary Fig. S2b). The modified Penman–Monteith equation for semi-arid environments in the study area reported by [41] was used to calculate the potential reference evapotranspiration (ET_0) (Supplementary Fig. S2b).

Experimental design and treatments

A split plot arrangement in a randomized complete block design with three replicates was used with three irrigation water levels [100% (I1), 75% (I2), and 50% (I3) of quinoa water requirement (WR)] as the main plot, and three planting methods [basin planting method (P1), on-ridge planting (P2), and in-furrow planting (P3)] as the subplot with three replications. Quinoa water requirement was determined according to increasing soil water content to field capacity in the root zone in 100%WR (I1). The used irrigation water levels are similar to those applied in previous studies for other crops (i.e., wheat and saffron) in the same study area [10, 11]. Furthermore, the irrigation level of 100%WR (I1) was determined based on raising soil water content before irrigation event to soil field capacity; therefore, irrigation water level should not be less than 50%WR (I3) due to severe soil water stress. After deep plowing and leveling, plots of 1.5 m × 2.0 m were established. It might be claimed that the above- and below-ground growing conditions in this small plot would be interfered by its surrounding field, and any sampling during the growing season would also affect the crop growth. It should be mentioned that in this study, we have mainly focused on the non-destructive measurements obtained in the middle of plots. Furthermore, a buffer distance of 1.0 m was maintained between adjacent plots to prevent any adjacent plot interference. Also,

guard plots were established around the experimental site to avoid possible interference by the surrounding fields.

Triple superphosphate at a rate of 50 kg P ha⁻¹ was applied uniformly to all plots before planting. A schematic representation of the ridges and furrows for the basin, in-furrow, and on-ridge planting methods is shown in Supplementary Fig. S3.

Quinoa seeds (cv. Titicaca) were sown at 10–20 mm depth on May 5, 2017, and March 31, 2018. In the flat basin planting, the seed was sown at 30 cm row distances. For in-furrow planting, the seed was sown in rows 30 cm apart at the bottom of the furrows. For on-ridge planting, the seed was planted in rows 30 cm apart on top of the ridges. The seedlings were thinned to a planting density of 186,667 plants per hectare. During the growing seasons, urea was mixed with the topsoil layer at a rate of 75 kg N ha⁻¹ and applied to the plots at the beginning of the vegetative and reproductive (flowering) stages (total rate of 150 kg N ha⁻¹). Weeds were frequently removed manually.

Plots were irrigated regularly at 7-day intervals, increasing the water content of the soil to the soil field capacity in the root zone. The seven-day interval is consistent with the used irrigation schedule for quinoa experiments in the study region [42]. Soil water content was measured using the neutron scattering method before each irrigation event in three replicates at 10–30 cm, 30–60 cm, 60–90 cm, and 90–120 cm soil depth. Supplementary Figure S3 shows the location of the access tubes in each plot of the representative planting method. Soil water content in the first 10 cm of the soil layer was measured by gravimetric method. The following equation was used to determine the irrigation depth.

$$I = \sum_{i=1}^n [(\theta_{FCi} - \theta_i) \times Di] \quad (1)$$

where, I is the irrigation water depth (m), θ_{FCi} and θ_i are the volumetric soil water content in layer i at field capacity ($m^3 m^{-3}$) and soil water content in layer i before each irrigation event, respectively ($m^3 m^{-3}$), Di is the depth of each layer (m), and n is the number of soil layers within the rooting zone. The following equation was used to determine the rooting depth during the growing season [43]:

$$R_d = R_{dmin} + R_{dmax} \left(0.5 + 0.5 \sin \left(3.03 \frac{D_{ag}}{D_{tm}} - 1.47 \right) \right) \quad (2)$$

In which R_d , R_{dmax} , and R_{dmin} are the root depth (m), the maximum root depth (1.2 m) [7], and the seed sowing depth (0.05 m), respectively, D_{ag} is the number of days after sowing date in which the plants were supposed to

be irrigated. D_{tm} is the number of days after sowing that root reaches the maximum depth (96 days).

For most crops, the amount of time between planting and physiological maturity is often a function of accumulated heat and growing degree days (GDD). Each crop has a certain quantity of GDD needed to grow and mature [44]. The following equation is typically used to estimate daily GDD using the daily average air temperature:

$$\begin{aligned} \text{GDD} &= T_a - T_{c\text{-min}} & T_a < T_{c\text{max}} \\ \text{GDD} &= T_{c\text{max}} - T_{c\text{min}} & T_a > T_{c\text{max}} \\ \text{GDD} &= 0 & T_a < T_{c\text{min}} \end{aligned} \quad (3)$$

in which, T_a is the daily mean temperature, $T_{c\text{-min}}$ is the minimum required for growth and $T_{c\text{-max}}$ is the air temperature above which growth is limited. The corresponding values for quinoa are 4 °C and 35 °C, respectively.

The lengths of the entire growth cycle and each phenological stage of quinoa in the first and second growing seasons are shown in Supplementary Fig. S4 based on cumulative growing degree days (ΣGDD). Additionally, the growth stages are displayed using the Biologische Bundesanstalt, Bundessortenamt and Chemical industry (BBCH) system [45]. This scale system was developed to meet the need for basic biological knowledge and to identify the key life stages of a plant as well as the phenological events of plants that are important to agriculture [45]. The length of the growth cycle was 16 days longer in the second growing season. Mean daily maximum temperature and mean air temperature were 3.8 °C and 2.4 °C higher, respectively, in the first growing season than those in the second growing season which led to higher ET_o .

Growth and yield components

Quinoa crops were harvested on September 1, 2017 (first growing season) and August 13, 2018 (second growing season). The entire 3 m² plot was harvested for grain yield and shoot biomass. At the end of each growing season, grains were first cut from the stems to determine grain yield. To determine straw dry matter (leaves and stems), stems were cut from the soil surface and dried in an oven at 70 °C and weighed after 24 h. At the end of each growing season, the number of total productive branches per plant and the length of the main panicle (panicle placed at the top of the plant) were measured in 3 crops per plot, and the panicles were separated from the shoots. The quinoa grains were separated from the coatings by crushing and dried in an oven at 65 °C for 72 h to determine seed yield. Samples of the dried seeds were used to determine seed protein concentration (%) by multiplying the nitrogen concentration by 6.25. The nitrogen concentration of the seeds

was determined by the Kejdahl method [46]. Seed yield was multiplied by seed protein concentration to determine protein yield. Quinoa height, stem diameter, and leaf area index, the total one-sided area of photosynthetic tissue per unit horizontal ground surface (LAI), were measured on 3 crops per plot at 37, 65, 80, 95, 110 days after sowing (DAS) in the first growing season and at 43, 72, 88, 105, 115 (DAS) in the second growing season.

Partitioning coefficient (PC) is defined as the amount of dry matter required for seed production and it shows the ratio of the distribution of dry matter between foliage and seeds. To calculate PC, the intercept of the relationship between the grain yield and shoot dry matter (SDM), was deducted from the total dry matter, and divided by the seed weight.

Gas exchange measurements

A LCi analyzer (ADC BioScientific Ltd, UK.) was used to measure leaf surface temperature, net photosynthesis rate, stomata conductance, and transpiration rate under fair weather conditions at 11:00 a.m. 4 times in each growing season. These measurements were done during different phenology stages on 24, 52, 76, and 97 DAS in the first growing season and 32, 65, 89, and 110 DAS in the second growing season corresponding to early vegetative to seed filling growth stages. Leaf water potential was measured using a pressure chamber (Soil Moisture Equip. Corp. Mod. 5100A, Santa Barbara, CA, USA) on 24, 40, 52, 64, 76, 88, 106 and 113 days after sowing in the first growing seasons at 11 o'clock. The corresponding days for the second growing season were 30, 44, 60, 74, 90, 104 and 119.

Assuming that the air within the stomata is saturated, the saturated vapor pressure in the leaf was calculated by the following equation [47]:

$$e_s = 0.611 \exp\left(\frac{17.27T}{T + 237.3}\right) \quad (4)$$

In which, e_s is the saturated vapor pressure (kPa) and T is the leaf temperature (°C). The ambient vapor pressure (e_a) in the free air was calculated using saturated air vapor pressure (e_s):

$$e_a = RH \times e_s \quad (5)$$

In which, RH is the relative humidity of the outside air. The following equation was used to calculate the vapor pressure deficit between the leaf and the air:

$$VPD = e_s - e_a \quad (6)$$

In which, VPD is the vapor pressure deficit (kPa).

Photosynthesis active radiation (PAR) and extinction coefficient

In the absence of abiotic stress, biomass development only depends on incoming PAR (photosynthetically active radiation) which changes according to latitude, season, sowing date, and plant phenology [48]. Therefore, PAR was determined to understand how it would change under abiotic stress and how it would affect crop growth. The light extinction coefficient (K) is a key indicator of the efficiency of interception of light penetrating through the canopy because of the gradual decrease in light intensity due to repeated attenuation by leaf elements [49]. To calculate the extinction coefficient, instantaneous solar radiation was measured at the top of the canopy and bottom of the canopy with an instrument, simultaneously with leaf surface and dry matter sampling using Solari- meter LI-190R with quantum sensor (LI-COR Biosciences Ltd UK). The LI-190R measures the photosynthetically active radiation in μmol of photons $\text{m}^{-2} \text{s}^{-1}$.

Solar radiation was measured on each plot at 37, 65, 80, 95, and 110 days after planting in the first growing season and at 43, 72, 88, 105, and 115 days after planting in the second growing season between 11:00 and 13:00. For this purpose, two perpendicular measurements were taken on the top of the canopy and two measurements were taken on the bottom of the canopy (one measurement along the rows and one measurement perpendicular to the planting rows) on each plot. Knowing the leaf area index (LAI), the amount of PAR reaching the lower part of the canopy (PAR_c), and the amount of PAR reaching the upper part of the canopy (PAR_o), the light extinction coefficient (K) was determined based on the Beer-Lambert equation of light extinction [50] as:

$$\ln\left(\frac{\text{PAR}_c}{\text{PAR}_o}\right) = -K \times \text{LAI} \tag{7}$$

To calculate the daily absorbed light, first, the daily solar radiation (I_0) reaching the top of the canopy was calculated based on latitude, season, day length, atmospheric transmission coefficient and the solar hour of the area as follows.

$$I_0 = \left(a_s + b_s \left(\frac{n}{N}\right)\right) R_a \tag{8}$$

In which, R_a is the extraterrestrial radiation in $\text{MJ m}^{-2} \text{d}^{-1}$; n is the actual duration of sunshine in h; N is the maximum possible duration of sunshine in h and a_s and b_s are the coefficients of radiation function. Malek [51] found a_s and b_s equal to 0.31 and 0.55, respectively, in the study region with a latitude of $29^\circ 83' 50'' \text{ N}$; a longitude of $52^\circ 83' 50'' \text{ E}$ and an elevation of 1810 m above sea level.

$$\text{PAR}_a = I_0 \times 0.5 \times (1 - p)(1 - \exp(-K \times \text{LAI})) \tag{9}$$

where, PAR_a is the daily light absorbed by the canopy ($\text{MJ m}^{-2} \text{day}^{-1}$), I_0 is the daily solar radiation in $\text{MJ m}^{-2} \text{d}^{-1}$, p is the reflection coefficient, K is the extinction coefficient which is determined by Eq. (7).

Statistical analysis

MSTAT-C statistical software [52] was used for statistical analysis of interaction effects between irrigation water level and planting methods each year. Analysis of variance (ANOVA) was performed using Duncan’s method to detect statistically significant differences between means ($p \leq 0.05$). Also, the effect of the year on different parameters was analyzed. If the effect of year was not significant (p -value > 0.05), the data was pooled over the two growing seasons.

Results

Crop growth

Growth components

The variation of quinoa height during the growing seasons and at the end of the growing season under different irrigation water levels and planting methods are shown in Fig. 1 and Table 1, respectively. The interaction effect of irrigation water level and planting method on the height at the end of the season was not significant; however, irrigation water level significantly affected plant height only at 50%WR (Table 1). Plant height was reduced by 6.1% and 16.7% at 75%WR and 50%WR, respectively, compared to that in 100%WR. Although the plant height in 100%WR was not different in the different planting methods; in 75%WR it was, on average, 13.8% higher in the basin and in-furrow planting methods in comparison with on-ridge planting methods.

The planting method and irrigation water level affected the stem diameter significantly (p -value < 0.05). The stem diameter was 9% smaller in the on-ridge planting method in comparison with that obtained in the in-furrow. It was also significantly affected by irrigation water level as it was reduced by 6.4% and 24.5% at 75%WR and 50%WR compared to that obtained at 100% WR (Table 1, Fig. 2). Figures 1 and 2 show that the height and stem diameter of quinoa were not affected by irrigation water level during the first stages of crop growth as they had almost the same values in different treatments; however, after anthesis stage and in the beginning of seed filling stage both height and diameter were affected adversely.

Number of panicles (NP) and length of panicles (LP) in different treatments are presented in Table 1. The effect of year was not significant (p -value > 0.05); therefore, the data is pooled over two growing seasons. NP in the

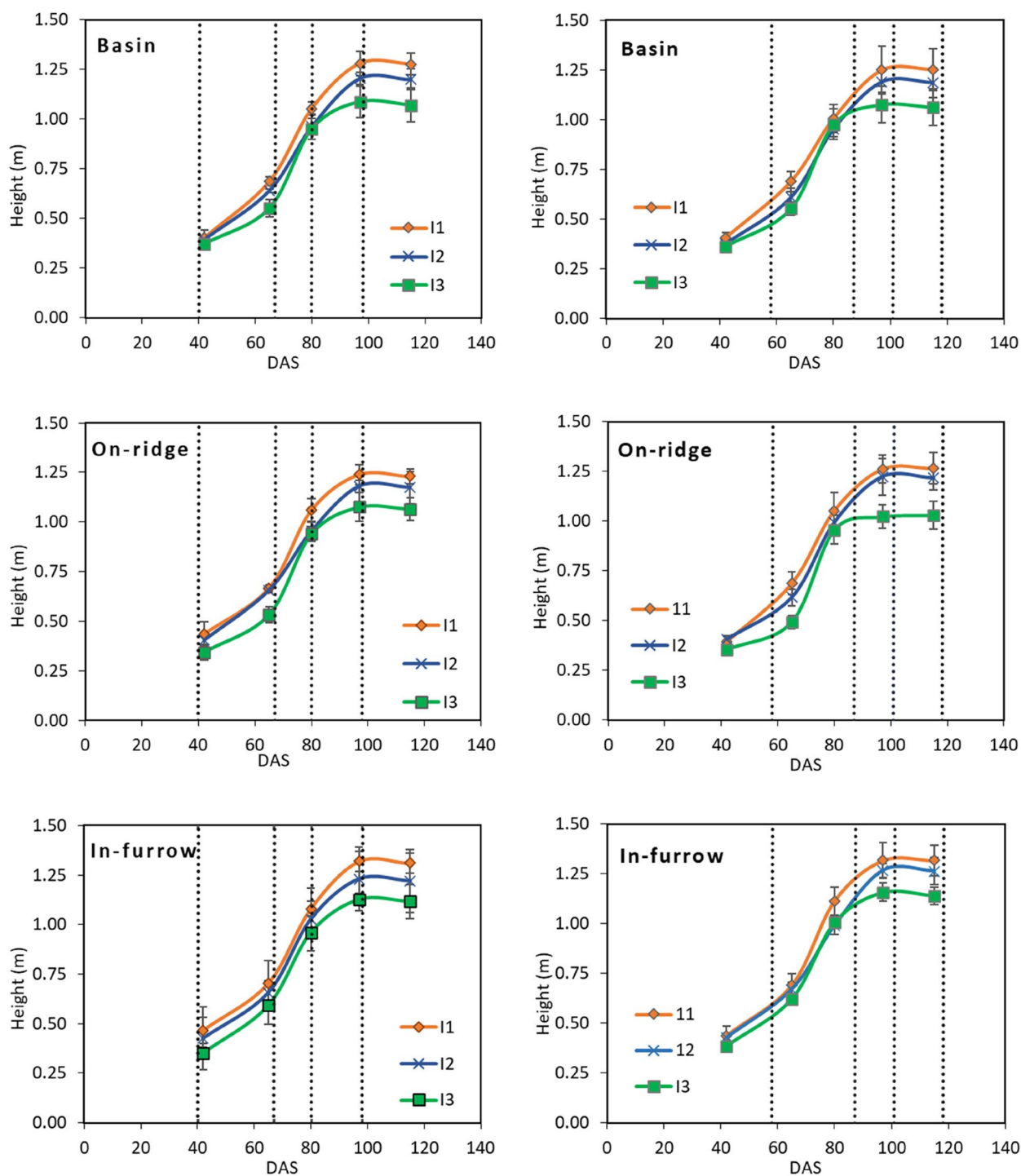


Fig. 1 Variation of quinoa height in different treatments (I1: 100%WR, I2: 75%WR and I3: 50%WR), and different planting methods in different days after sowing (DAS) (first column: 2017, second column: 2018). The dash lines indicate the growth stages as shown in Fig. S1

in-furrow was 15.4% higher than those obtained in basin and on-ridge planting methods. Irrigation water level affected the NP significantly (p -value < 0.05). Regardless of planting methods, 75%WR and 50%WR reduced NP

by 18.4% and 36.5%, respectively in comparison to those obtained in 100% WR. The same trend was observed in LP variation. LP in the in-furrow was 19.7% higher than those obtained in the basin and on-ridge in 100% WR.

Table 1 Plant height (m), maximum stem diameter (mm) and maximum LAI of quinoa, panicle number, main panicle length (cm), seed protein concentration (%) and seed protein yield (kg ha⁻¹) on average in two growing seasons

	P1 (Basin)	P2 (On-ridge)	P3 (In-furrow)
	Plant height (m)		
I1 (100%WR)	1.280 a ^a	1.240 a	1.320 a
I2 (75%WR)	1.207 ab	1.080 c	1.230 ab
I3 (50%WR)	1.087 c	1.077 c	1.127 bc
	Maximum stem diameter (mm)		
I1 (100%WR)	14.5 a	13.7 ab	14.45 a
I2 (75%WR)	13.4 b	12.9 b	13.8 ab
I3 (50%WR)	11.3c	10.6 c	12.3 bc
	Maximum LAI		
I1 (100%WR)	5.02 ab	4.88 b	5.34 a
I2 (75%WR)	4.62 b	4.18 c	4.83 b
I3 (50%WR)	3.64cd	3.47 d	3.87 cd
	Panicle number		
I1 (100%WR)	21.8ab	21.2ab	24.8a
I2 (75%WR)	19.3bc	17.3c	20.7b
I3 (50%WR)	15.8d	16.0cd	17.8c
	Main panicle length (cm)		
I1 (100%WR)	25.7b	26.0ab	30.9a
I2 (75%WR)	23.3b	22.2bc	23.9b
I3 (50%WR)	19.8c	19.8c	22.0bc
	Seed protein concentration (%)		
I1 (100%WR)	14.4cd	13.3d	16.1bc
I2 (75%WR)	16.7b	16.7b	19.5a
I3 (50%WR)	18.4ab	17.5b	20.5a
	Seed protein yield (kg ha⁻¹)		
I1 (100%WR)	320.9b	249.2c	376.0ab
I2 (75%WR)	328.3b	265.1c	412.4a
I3 (50%WR)	230.5cd	188.4d	313.2b

^a Means followed by the same letters in columns for each factor and each trait are not significantly different at 5% level of probability, using Duncan's multiple range test

The corresponding value for 50% WR was 10.9%. The main effect of irrigation water level was significant on LP (p -value < 0.05) as it was reduced by 18.6% and 33.6% in 75% WR and 50%WR, respectively, compared to that obtained in 100% WR.

Leaf area index

The interaction effect of irrigation water levels and planting methods on maximum leaf area index (LAI_{max}) was statistically significant (p -value < 0.05). The highest LAI (5.34) was observed in the in-furrow planting method under full irrigation (Table 1). Regardless of irrigation water level, LAI_{max} in the in-furrow planting method was 5.7% and 12.2% higher than those obtained in the basin and on-ridge planting methods, respectively. Deficit irrigation significantly reduced LAI_{max} in all planting methods (p -value < 0.05), as it was reduced by 11.9% and 24.1% in 75%WR and 50%WR, respectively in comparison with

that obtained in 100%WR. It should be noted that LAI_{max} in 75%WR treatment was not significantly different in the basin and in-furrow planting, whereas it was lower significantly in the on-ridge planting (ORP). However, its value was statistically similar to that obtained in 100% WR in the basin planting. (Table 1).

Seasonal variation of leaf area index of quinoa grown in different treatments during the first and second growing seasons are shown in Fig. 3. Maximum LAI occurred 80 days and 88 days after sowing in the seed filling growth stage, respectively in the first and second growing seasons. The difference in the obtained LAI in different planting methods is significant only in 100% WR treatment as the highest LAI values were obtained in the in-furrow planting method and the lowest values were observed in the on-ridge planting method. Deficit irrigation reduced the difference between LAI values in different planting methods.

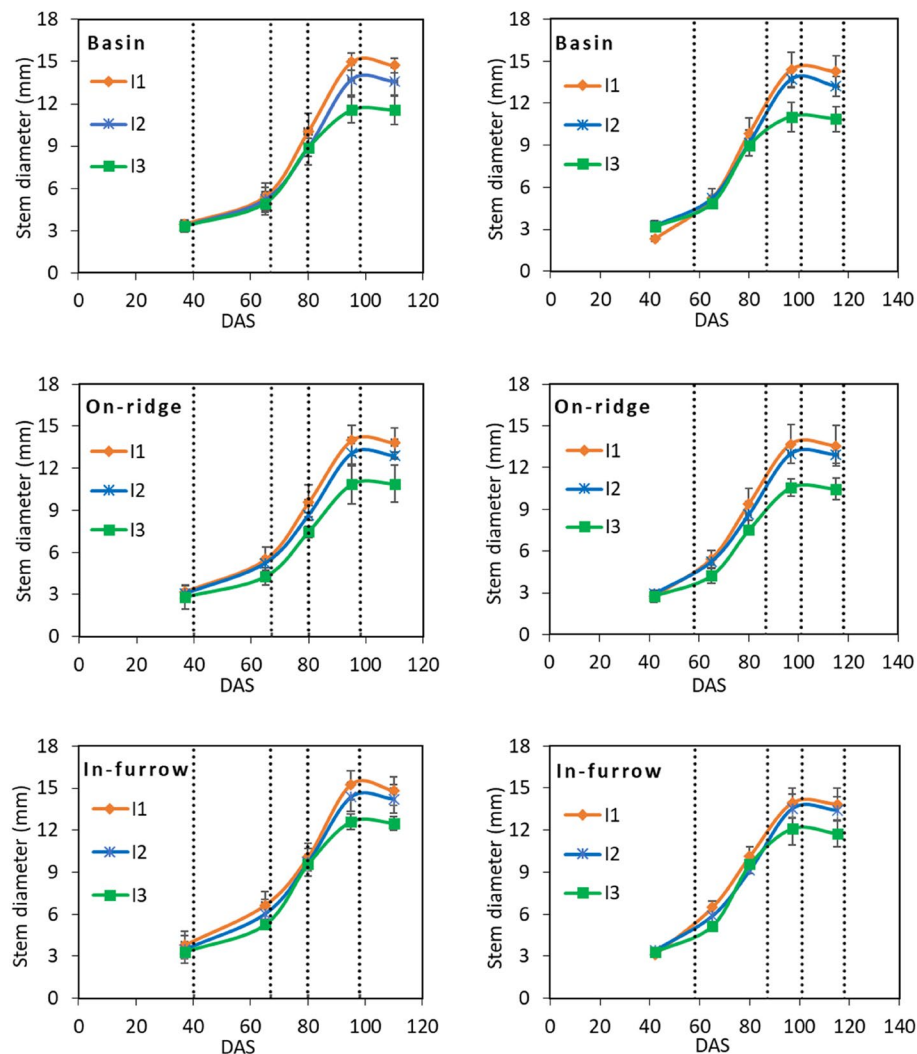


Fig. 2 Variation of quinoa stem diameter in different treatments in different days after sowing (DAS) on average in different treatments (I1: 100%WR, I2: 75%WR and I3: 50%WR), and different planting methods in different days after sowing (DAS) during two growing seasons (first column: 2017, Second column: 2018)..The dash lines indicate the growth stages as shown in Fig. 51

Dry matter, grain yield and protein yield of quinoa

The interaction effect of irrigation water levels and planting methods on total dry matter (sum of shoot and grain yield, TDM) and grain yield of quinoa was significant (p -value < 0.05). Results are shown in Fig. 4 and indicated that the irrigation regime of 75%WR reduced TDM by 3%, 11%, and 17% for the in-furrow, basin, and on-ridge planting methods, respectively, compared to 100% WR. The corresponding values for 50% WR were 11%, 21%, and 30%, respectively, which showed higher reduction.

The interaction effect of the planting methods and the irrigation water levels was significant for both protein yield and protein concentration (p -value < 0.05). The percentages of seed protein concentration and calculated protein yields are shown in Table 1. Statistical analysis showed that the interaction effect of the

planting methods and irrigation levels was significant (p -value < 0.05). The highest protein concentrations were obtained in 50%WR and in-furrow (20.5%), but the highest protein yield was observed at 75%WR and in-furrow (412.4 kg ha⁻¹). Deficit irrigation increased protein concentration, as it was 21% and 29% higher in 50%WR than those in 75% and 100%WR, regardless of planting methods, respectively. In addition, taking planting methods into consideration, protein concentration was 15% higher in the in-furrow planting compared to the other planting methods, on average, of different irrigation water levels. Although protein concentration was not significantly different in 75%WR and 50%WR in all planting methods, the protein yield was lower significantly in 50%WR. On the other hand,

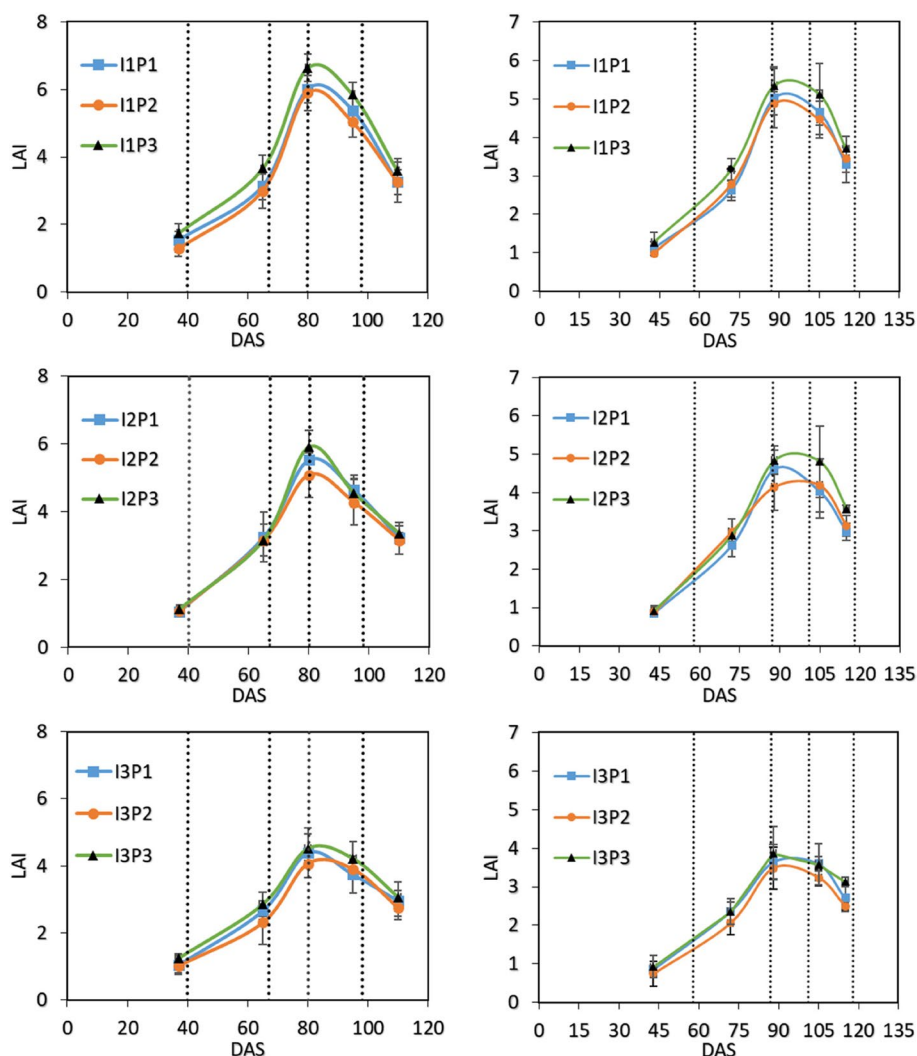


Fig. 3 Variation of quinoa leaf area index (LAI) in different treatments (I1: 100%WR, I2: 75%WR and I3: 50%WR), and different planting methods (P1: basin, P2: on-ridge, and P3: in-furrow) in different days after sowing (DAS) during two growing seasons (first column: 2017, Second column: 2018). The dash lines indicate the growth stages as shown in Fig. S1

protein yield in the in-furrow planting was 32% higher in 75%WR compared to 50%WR due to higher grain yield, indicating that the 75%WR in-furrow planting method is the optimal planting method.

Physiological traits

Leaf temperature

Leaf temperature (Tl) was measured four times during each growing season. The mean Tl in early vegetative, vegetative, anthesis and maturity was 32.3, 34.6, 35.7, and 36.7 °C in the first growing season, respectively. The corresponding values for the second growing season were 31.6, 33.2, 34.9, and 36.7 °C, respectively. In the anthesis and maturity stages, Tl was 10.5% and 14.8% higher than that obtained in the early vegetative stage, respectively. Tl

increased throughout the growing seasons regardless of different treatments (Fig. 5), which is mainly due to the increased air temperature (Fig. S1) especially in 75%WR and 50%WR treatments since the soil water content was not sufficient to support high transpiration rate. The quinoa seeds were sown earlier in the second growing season to avoid high air temperature during the anthesis and maturity stages; as a result, lower Tl in the second growing season was observed due to the lower air temperature (Fig. S1).

The main effect of irrigation water level was significant on Tl, and in 50%WR it was, on average, 1.7 and 1.0 °C higher than those obtained in 100%WR and 75%WR. In addition, Tl was 2.5–3 °C higher in the 50%WR in the anthesis stage in comparison to 100%WR and 75%WR

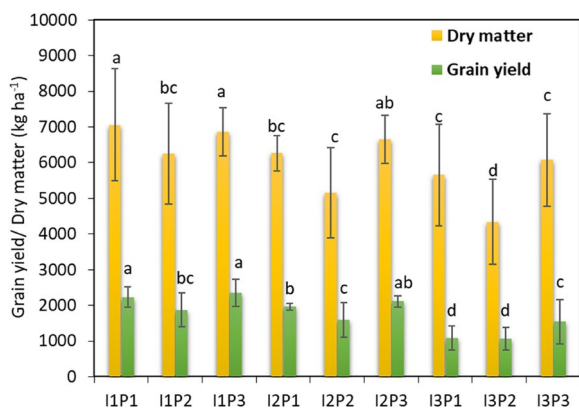


Fig. 4 Two years average of grain yield (kg ha⁻¹) and Biomass (kg ha⁻¹) in different treatments (I1: 100%WR, I2: 75%WR and I3: 50%WR), and different planting methods (P1: basin, P2: on-ridge, and P3: in-furrow)

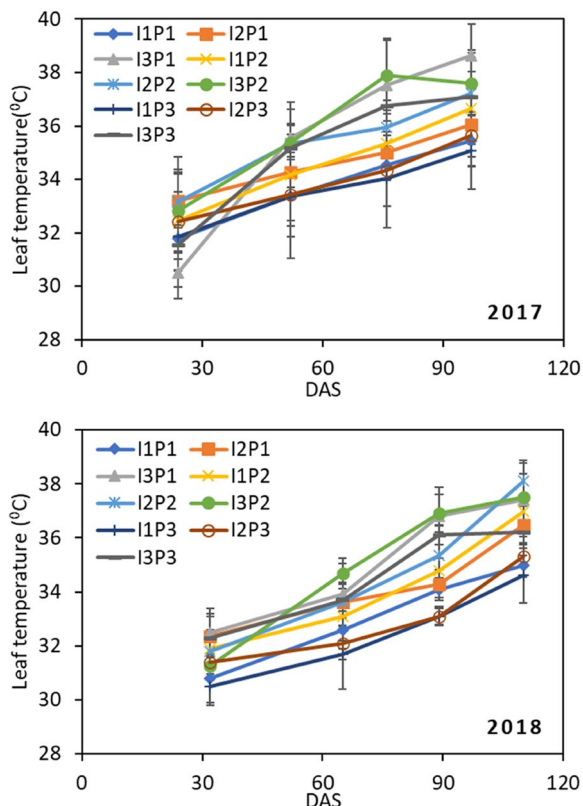


Fig. 5 Variation of the leaf temperature (°C) in different irrigation water levels (I1:100%WR, I2:75%WR and I3:50%WR) and planting methods (P1: basin, P2: on-ridge and P3: in-furrow) in different days after sowing (DAS) in the first (2017) and second (2018) growing seasons

irrigation levels. Also, higher TI was observed in on-ridge planting methods in comparison to those obtained in the basin and in-furrow planting methods. The TI values in the on-ridge planting were 1.3 and 0.8 °C higher in comparison to those obtained in the basin and in-furrow planting, respectively.

Leaf water potential

The leaf water potential (LWP) of quinoa was measured eight times during each growing season before each irrigation event (Fig. 6). LWP was the highest (-0.5 to -1.5 MPa) in the early growth stages and reduced gradually (-3.5 to -4.5 MPa) till late season. In both growing seasons, the highest reduction was observed in 50%WR especially during anthesis and seed filling stages (Fig. 6), which indicate the higher susceptibility of quinoa to extreme water stress during anthesis and seed filling. A decrease in yield was also reported when water stress was imposed at both the flowering and grain filling stages [27, 53, 54]. The mean value of LWP during the growing seasons is shown in Table 2. Results showed that 75%WR and 50%WR reduced LWP by 12.5% and 47.4% in comparison to that obtained in 100%WR, respectively. Also, the main effect of planting methods on LWP was significant as it was 15.8% and 9.9% lower in the on-ridge planting in comparison to those obtained in the in-furrow and basin planting, respectively.

Photosynthesis rate and stomatal conductance

The photosynthesis rate (An) of quinoa was measured four times during the first and second growing seasons. The variation of An during each growing season is shown in Fig. 7 and the mean values are shown in Table 2. The main effect of irrigation water level was significant on An as it was reduced, on average, by 7.1% and 18.3% in 75%WR and 50%WR in comparison with those obtained in 100%WR, respectively. In addition, the An values (pooled over the whole season, on average) were decreased by 8.1% in the on-ridge planting in two growing seasons.

The variation of stomatal conductance (gs) of quinoa was measured four times before the irrigation events during both growing seasons. As shown in Fig. 7, stomatal conductance was reduced from the highest values (0.5–0.8 mol m⁻² s⁻¹) in the early growing season to the minimum values (0.1–0.3 mol m⁻² s⁻¹) in the late season. The lower values of gs obtained in the late season may be due to the higher ambient temperature as both plant-specific characteristics, and the surrounding environment affect stomatal conductance. In the second growing season, quinoa was sown 35 days earlier than the first growing season to avoid very high air temperatures, especially in the mid-season. On average in two growing seasons,

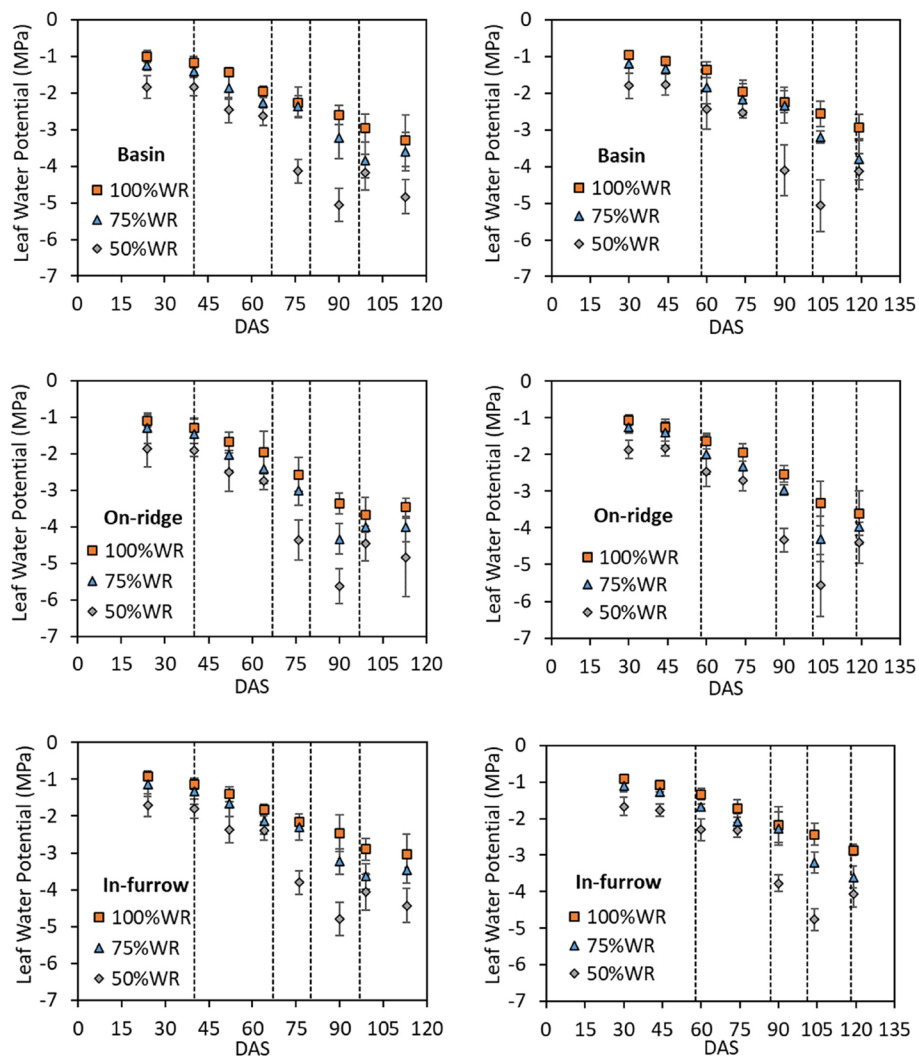


Fig. 6 Variation of mean water potential [LWP (MPa)] in different treatments (I1: 100%WR, I2: 75%WR and I3: 50%WR), and different planting methods in different days after sowing (DAS) during two growing seasons (first column: 2017, Second column: 2018). The dash lines indicate the growth stages as shown in Fig. 1

Table 2 Mean values of leaf water potential [LWP (MPa)], Leaf temperature (TI), photosynthesis rate [An ($\mu\text{mol m}^{-2} \text{s}^{-1}$)], stomatal conductance [gs ($\text{mol m}^{-2} \text{s}^{-1}$)], intrinsic water use efficiency [An/gs ($\mu\text{mol mol}^{-1}$)], transpiration rate [Tr ($\text{mol m}^{-2} \text{s}^{-1}$)] and transpiration efficiency (An/Tr (g kg^{-1})) at different irrigation water levels and planting methods on average in two growing seasons

Parameter	LWP (MPa)	TI (°C)	An ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	gs ($\text{mol m}^{-2} \text{s}^{-1}$)	An/gs ($\mu\text{mol mol}^{-1}$)	Tr ($\text{mmol m}^{-2} \text{s}^{-1}$)	An/Tr (g kg^{-1})
Irrigation level							
I1 (100%WR)	-2.08 ^a	33.6b	22.83a	0.46a	48.48b	4.67a	5.10a
I2 (75%WR)	-2.34b	34.3ab	20.71ab	0.40b	48.50b	4.46ab	4.64ab
I3 (50%WR)	-3.07c	35.7a	18.06b	0.32c	58.75a	3.97b	4.53b
Planting method							
P1 (Basin)	-2.46a	34.5a	21.02a	0.43a	51.7a	4.36a	4.82a
P2 (On-ridge)	-2.70b	35.1a	19.62a	0.38b	52.1a	4.19a	4.67a
P3 (In-furrow)	-2.30a	33.8a	20.98a	0.41ab	54.2a	4.55a	4.58a

^a Means followed by the same letters in columns for each factor and each trait are not significantly different at 5% level of probability, using Duncan's multiple range test

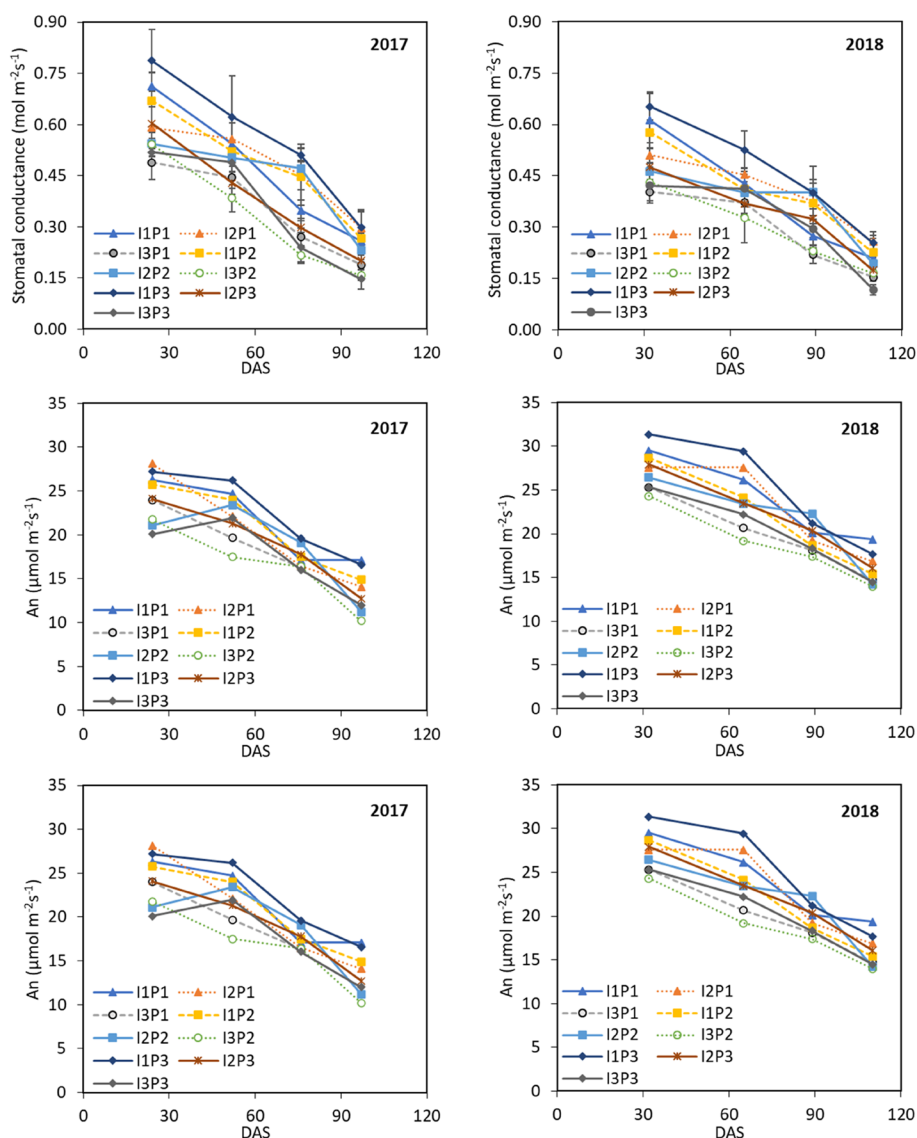


Fig. 7 Variation of photosynthesis rate [An (μmol m⁻² s⁻¹)] and stomatal conductance [gs (mol m⁻² s⁻¹)] and transpiration rate [Tr (mol m⁻² s⁻¹)] in different irrigation water levels (I1:100%WR, I2:75%WR and I3:50%WR) and planting methods (P1: basin, P2: on-ridge and P3: in-furrow) in the first(2017) and second growing seasons(2018)

the highest value of g_s ($0.72 \text{ mol m}^{-2} \text{ s}^{-1}$) was observed in the in-furrow planting when it was fully irrigated (I1P3), and the lowest value ($0.13 \text{ mol m}^{-2} \text{ s}^{-1}$) was obtained in the on-ridge planting and 50%WR (I3P2) as it was 21.6% and 29.3% lower than those obtained in 100%WR and 75%WR, respectively. Although the average g_s values were higher in the in-furrow planting method, the main effect of the planting method was not significant on average value of g_s . The main effect of irrigation water level on stomatal conductance was significant (p -value < 0.05) in 50%WR irrigation level (Table 2).

The main effect of irrigation water level and planting method on the intrinsic water use efficiency (An/ g_s) was investigated (Table 2). There was no significant difference in the An/ g_s values in different planting methods, however, 50%WR significantly increased the An/ g_s in both growing seasons. Leaf transpiration rates were also measured 4 times (on the same dates with An and g_s) during the growing seasons (Fig. 7). Leaf transpiration rate (Tr) was 17.6% higher in 100%WR in comparison to that obtained in 50%WR, respectively. Furthermore, Tr was 4.5% and 8.6% higher in the in-furrow in comparison

to basin and on-ridge planting methods, respectively (Table 2).

Light extinction coefficient

The fraction of transmitted radiation vs. leaf area index for quinoa, on average in two growing, is shown in Fig. 8, as the effect of year was not significant ($p\text{-value} > 0.05$) on K values. The slope of the fitted line to the logarithm of the ratio of transmitted light against the leaf area index (LAI) indicates the light extinction coefficient (K). The K values were higher in the in-furrow planting in comparison to the basin and on-ridge planting. On the other hand, irrigation water level significantly affected

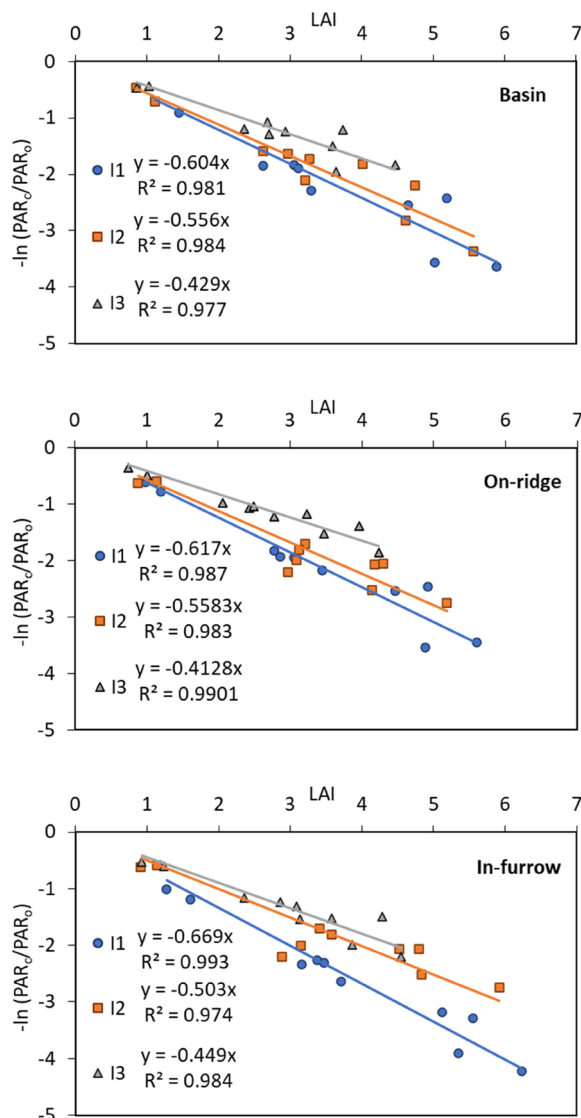


Fig. 8 Fraction of transmitted radiation vs. leaf area index in different Irrigation water levels (I1:100%WR, I2:75%WR and I3:50%WR) and planting methods in two growing seasons

Table 3 Extinction coefficient for different irrigation water levels and planting methods on average in two growing seasons

	P1 (Basin)	P2 (On-ridge)	P3 (In-furrow)
I1 (100%WR)	0.604	0.617	0.669
I2 (75%WR)	0.556	0.558	0.504
I3 (50%WR)	0.429	0.413	0.449

K values (Table 3). Pooled over planting method, K values were 0.63, 0.54 and 0.43 in 100%WR, 75%WR and 50%WR, respectively, which was 16.8% and 46.4% higher in 100%WR in comparison to those obtained in 75%WR and 50%WR, respectively. Also, the in-furrow planting increased the K by 8.4% and 10.8% in comparison to basin and on-ridge planting methods, respectively, when it was fully irrigated.

Discussion

Crop growth components and yield

Soil water stress is one of the abiotic stresses that plants encounter during their life cycle [55]. It poses a serious threat to various aspect of plant development including plant growth, yield, survival, and productivity [56–58]. In the current study, we observed a reduction of 11% in plant height of quinoa across the reduced water levels, while reduction in height ranged between 10 and 13% in basin, in-furrow and on-ridge planting, regardless of time. A reduction in growth parameters, grain yield and yield components as a result of limiting soil water content from complete irrigation to deficit irrigation and its effects on plant growth has been well established in the literature [59, 60]. Soil water stress negatively affect the plant physiological mechanisms that aid in water and nutrient uptake, thus severely affecting the cell growth and division [61, 62]. Also, the decrease in plant growth under deficit irrigation could be attributed to decrease in water and nutrient uptake as well as a decrease in stomatal conductance, which results in reduced photosynthesis [63].

Quinoa height, stem diameter and leaf area index were found to be significantly ($p\text{-value} < 0.05$) affected by deficit irrigation. This is consistent with previous research [64, 65], indicating that disruption in cell division and cell elongation processes is a direct effect of water stress leading to the reduction in plant height and leaf area of plants. Semerci et al. [66] observed a significant decline in total growth, including shoot height, biomass, and leaf number, during drought stress associated with reduced turgor pressure, which led to growth retardation in the plant. Also, it is reported that quinoa avoids water stress primarily by developing a longer root, intense root system, leaf dropping and reduced leaf area [67,

68]. Furthermore, the application of in-furrow planting treatments resulted in high leaf area index values, which may have contributed to lower evaporation from the soil surface.

Water scarcity disrupts the plants' water balance by lowering the soil's water potential, which seriously affects the plants' water potential. Consequently, the immediate reaction of all plants under drought stress is to reduce transpiration by closing the stomatal opening [69]. In response to the drought stress, the quinoa plant maintains its turgor by accumulating a variety of inorganic ions [70], which results in decreased leaf osmotic potential. In addition, drought escape, or tolerance is mainly achieved through low osmotic potential and tissue elasticity [35].

The relationship of the grain yield and the total dry matter with LWP in different planting methods is shown in Fig. 9a and b. The equations of the fitted lines are shown in Table 4,

in which, TDM is the total dry matter ($Mg\ ha^{-1}$), GY ($Mg\ ha^{-1}$) and LWP is the average leaf water potential

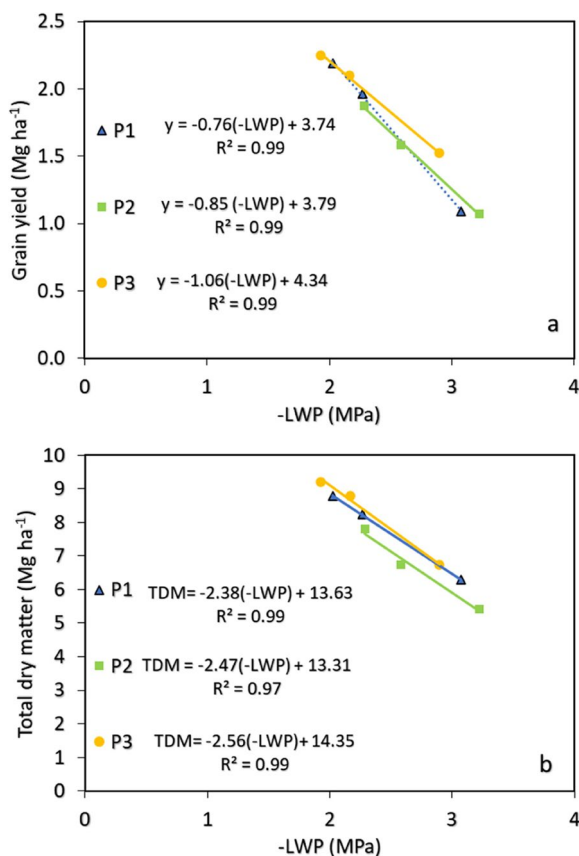


Fig. 9 The relation of total dry matter and grain yield with the average leaf water potential of quinoa in different planting methods (P1: basin, P2: on-ridge and P3: in-furrow) on average in two growing seasons

Table 4 Relationships between Total dry matter (TDM) and grain yield (GY) and leaf water potential (LWP)

Number	Planting	Equation	R^2	SE	p value
11	In-furrow	$TDM = -2.63(-LWP) + 14.35$	0.99	0.04	0.024
12	On-ridge	$TDM = -2.55(-LWP) + 13.58$	0.97	0.01	0.005
13	Basin	$TDM = -2.38(-LWP) + 13.63$	0.99	0.003	0.0015
14	In-furrow	$GY = -1.06(-LWP) + 4.34$	0.99	0.02	0.024
15	On-ridge	$GY = -0.85(-LWP) + 3.79$	0.99	0.02	0.005
16	Basin	$GY = -0.76(-LWP) + 3.74$	0.99	0.007	0.0015

^a R^2 is coefficient of determination, SE is standard error

(MPa). Our results provided further insights into how dry matter buildup interacts at a certain LWP threshold in different planting methods. The higher slope of the fitted line in the in-furrow planting showed that a higher amount of yield and dry matter was obtained in a specific LWP in comparison to those obtained in the basin and on-ridge planting indicating that less water stress was imposed to the crop in the in-furrow in comparison to on-ridge planting. The lower plant temperature in the in-furrow planting method can result in lower plant respiration which leads to higher grain and dry matter yield. Li et al. [71] reported that high respiration may be the primary contributor to yield losses in high temperatures. Also, Fig. 10 illustrates the relationship between leaf surface temperature and LWP. Results depict that as LWP decreased the leaf surface temperature increased owing to decreased transpiration or the loss of water vapor via the leaf stomata, that results in less cooling of the leaf surface.

We analyzed the combined effect of irrigation water level and planting methods on the yield and dry matter of quinoa. In this study, the grain yield varied within the

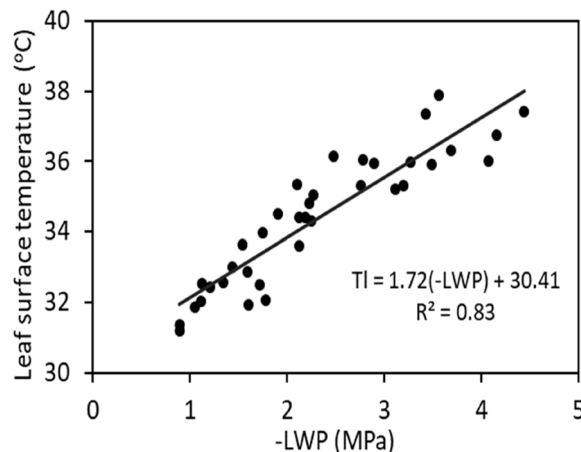


Fig. 10 The relationship between Leaf surface temperature and leaf water potential (LWP) of quinoa on average in two growing seasons

range of 1.05 Mg ha⁻¹ and 2.5 Mg ha⁻¹, which is consistent with the findings of Algosaiibi et al. [24] and Delgado et al. [72]. Yield reduction was mainly due to drought stress which was imposed on the crop. Our result showed that deficit irrigation can significantly reduce quinoa yield and dry matter especially in 50%WR, which is consistent with the results of Al-Naggar et al. [73] and in contrast with the results of Pulvento et al. [74] and Razzaghi et al. [75], which reported that deficit irrigation does not affect quinoa yield and growth significantly. The contrast may be due to different climate conditions (lower temperature) in their study region and the region of the current study. Bertero [76] also challenges the notion that quinoa reaches high yields with low water availability by analyzing several kinds of literatures on quinoa yield and reporting that the highest efficiency of quinoa is from temperate climates. Greater yield loss results from the interaction of the stresses of heat and drought than from either stress alone. Hinojosa [77] reported that quinoa is sensitive to the combination of heat and drought. Geerts et al. [54] reported that by applying 50% of the required irrigation water depth, the quinoa yield can be stabilized between the range of 1.2–2.0 Mg ha⁻¹. In addition, the TDM performance of quinoa under water stress in the in-furrow planting was better than the other two planting methods. Furthermore, TDM production of quinoa was not much affected under water stress conditions proportional to the imposed water stress. The relationship between quinoa grain yield and shoot dry matter was obtained as follows:

$$\begin{aligned} \text{GY} &= 0.37(\text{SDM}) - 423.0 \\ R^2 &= 0.79 \quad n = 72 \quad \text{SE} = 0.05 \quad p\text{-value} < 0.0001 \end{aligned} \quad (10)$$

In which, SY is the grain yield and SDM is the shoot dry matter (kg ha⁻¹). The intercept of the relationship between the grain yield and SDM showed that about 1143 kg ha⁻¹ of shoot dry matter is required before seed production begins. The process in which the assimilates move from source organs to sink organs (i.e., seeds) is called the partitioning of dry matter [78] that is an important variable to consider when assessing adaptability to abiotic stress [79]. In this study the dry matter partitioning coefficient (PC) for seed was 11.4%, 11.5% and 9.4% in 100%WR, 75%WR and 50%WR, respectively. Thus, 75%WR did not reduce PC for seed, however, it was reduced by 18.2% in 50%WR. Therefore, quinoa is susceptible to severe water stress.

Quinoa crop is drought resistant; nevertheless, their performance is reduced under water stress in deficit irrigation [80]. The effect of deficit irrigation on quinoa performance depends on the degree of water stress and it also influenced by other environmental factors [81].

Results revealed that deficit irrigation reduces quinoa growth and yield in the current investigation, and our results are in agreement with previous studies [81–85].

There are several methods to conserve the soil water and increase the crop growth [86], whereas in-furrow planting is one of these methods [59]. By in-furrow planting, where the canopy cover shades the soil surface in the furrow, it reduces the soil surface evaporation and increases the crop transpiration and crop growth [11]. Besides reduction in evaporation, in-furrow planting increases the soil temperature in winter and decreases it in summer, that enhances the soil environmental condition for root and crop growth [11]. The reduction of dry matter (Fig. 4) was more associated with a significant decrease in stem diameter rather than LAI (Table 1), which is in agreement with that reported by Hejnak et al. [87].

Physiological traits

Photosynthesis, which is regarded as an invariably important process, is extremely vulnerable to drought stress and is the first process that is affected by deficit irrigation [88]. Drought-induced decreases in photosynthetic capacity have been widely reported in the literature, because of reduced stomatal conductance and defective photosynthetic machinery [89]. In response to drought stress the plants lower their transpiration by closing stomatal openings. Stomatal openings regulate CO₂ and water in the plants. Stomatal closure reduces water loss; however, it lowers CO₂ absorption [90], which is an essential element of photosynthesis, resulting in carbon deficiency, which affects many other mechanisms [91]. There are many studies that reported that drought stress affects physiological parameters and gas exchange of plants. Ali et al. [92] reported a decline in photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO₂. Yang et al. [63] observed stomatal conductance reduction and enhanced leaf water potential in quinoa plants. They stated that the decrease in stomatal conductance can be attributable to the increasing ABA concentration in leaves as under abiotic stresses especially drought stress. It signals the plant to close its stomata to conserve water. The relationship between stomatal conductance and transpiration rate with leaf water potential are determined and shown in Fig. 11a and b and Table 5, in which, *g_s* is the stomatal conductance (mol m⁻² s⁻¹), *T_r* is the leaf transpiration rate (mmol m⁻² s⁻¹) and LWP is the leaf water potential (MPa). Comparing the slope of relationship between *g_s* and LWP (-0.133) and *T_r* and LWP (-0.69) showed that transpiration rate is more sensitive to the variation in LWP. The value of *g_s* at LWP equal to zero (0.69 mol m⁻² s⁻¹) is the highest *g_s* that can be obtained. The relationship between

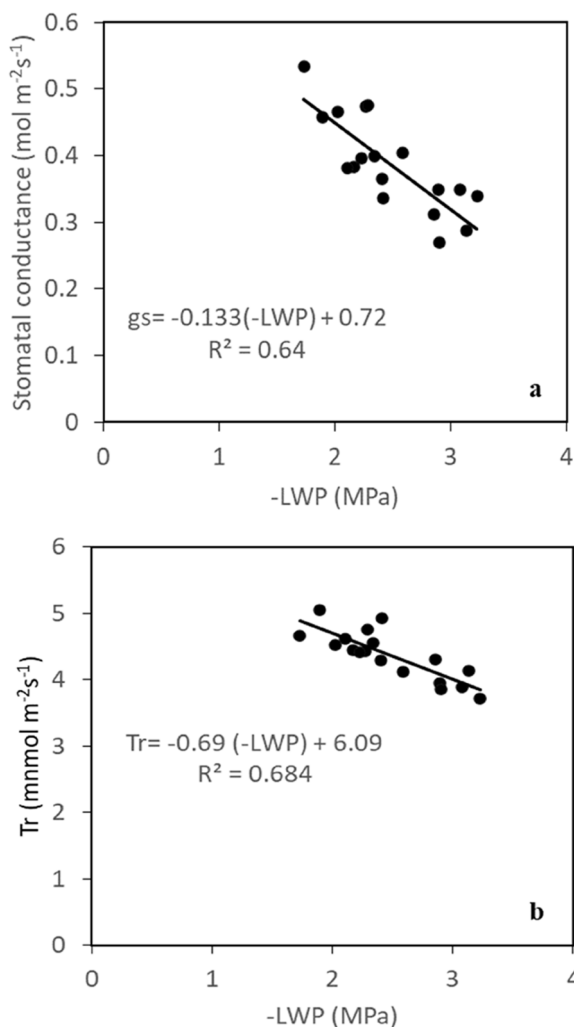


Fig.11 Relationship between **a:** stomatal conductance (g_s) and **b:** transpiration rate (Tr) with leaf water potential (LWP) measured during two growing seasons

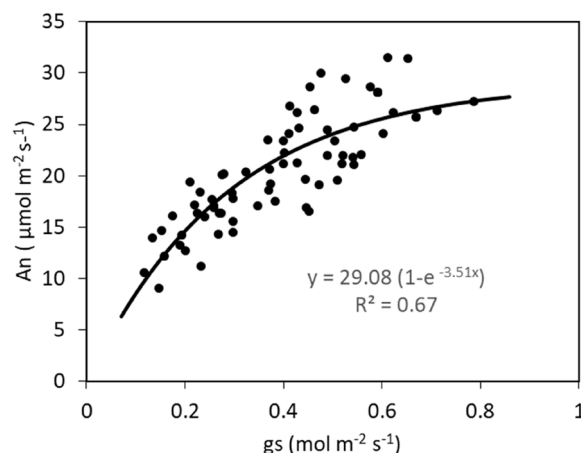


Fig.12 Relationship between stomatal conductance (g_s) and photosynthesis rate (A_n) measured during two growing seasons

photosynthesis rate and stomatal conductance was also determined (Fig. 12). In early growth stages of crops under water stress, reduced stomatal conductance, and lowered transpiration rate more than it does the intercellular CO_2 concentration, which is the driving force for photosynthesis [93]. Previous studies suggested nonlinear relationship between A_n and g_s [93, 94]; therefore, an exponential equation was fitted to the data and is shown in Table 5, in which, A_n is the photosynthesis rate ($\mu mol m^{-2} s^{-1}$) and g_s is the stomatal conductance ($mol m^{-2} s^{-1}$). In Fig. 12, $0.45 mol m^{-2} s^{-1}$ can be considered as the turning point of the fitted line, which indicated that water productivity can be increased at mild water stress because of the non-linear relationship between A_n and g_s and the fact that A_n is less sensitive to water stress than g_s [93]. For water-scarcity adaptation, the intrinsic water use efficiency (A_n/g_s) is regarded as a crucial factor [29]. In our study, no variations in A_n/g_s values amongst planting methods were found to be statistically significant; nevertheless, it was observed that A_n/g_s values in 50%WR were greater than those obtained in 100% and 75%WR. The A_n/g_s determination is based on gas exchange measurements made all at once which are unable to provide accurate variations in A_n/g_s [95].

Figure 12 shows the relationship between stomatal conductance and photosynthesis with the difference between air temperature (T_a) and leaf temperature (T_l). The negative $T_a - T_l$ is related to treatments exposed to severe water stress, where there was not enough water to help the plant to reduce the leaves temperature, and it was related to the mid and late season, when the air temperature exceeded $35^\circ C$ degrees. A reduction in stomatal conductance, an increase in photosynthesis, and a greater differential between air and leaf temperatures were related to high temperatures [96]. According to Fig. 13,

Table 5 Relationships between total dry matter (TDM) and photosynthesis rate (A_n), stomatal conductance (g_s) and leaf water potential (LWP), leaf transpiration (Tr) and LWP, A_n and g_s , and A_n and LWP

Number	Equation	^a R ²	^a SE	^a n	p value
17	$g_s = -0.133(-LWP) + 0.72$	0.68	0.0001	18	0.0001
18	$Tr = -0.69(-LWP) + 6.09$	0.68	0.0001	18	0.0001
19	$A_n = 29.08(1 - e^{-3.51g_s})$	0.66	-	-	-
20	$TDM = 367.3 A_n$	0.97	0.0001	18	0.0001
21	$A_n = -3.3451(-LWP) + 29.05$	0.91	0.0001	18	0.0001

^a R² is coefficient of determination, SE is standard error, n is number of data

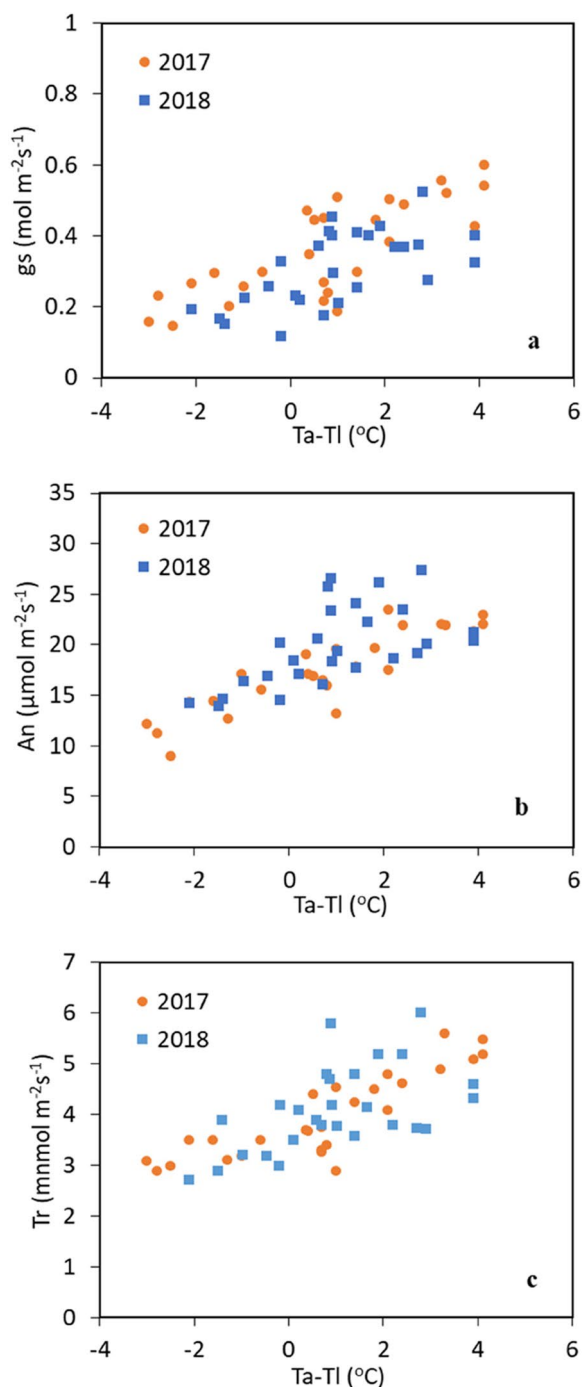


Fig. 13 The variation of **a**: stomatal conductance (g_s) and **b**: photosynthesis rate (A_n) and **c**: transpiration rate (T_r) with the difference between air temperature (T_a) and leaf temperature (T_l)

the highest A_n , g_s and T_r values occurred when the air temperature was 3–5°C higher than the leaf temperature. In addition, the relation between the difference between air and leaf temperature (ΔT) with leaf water potential

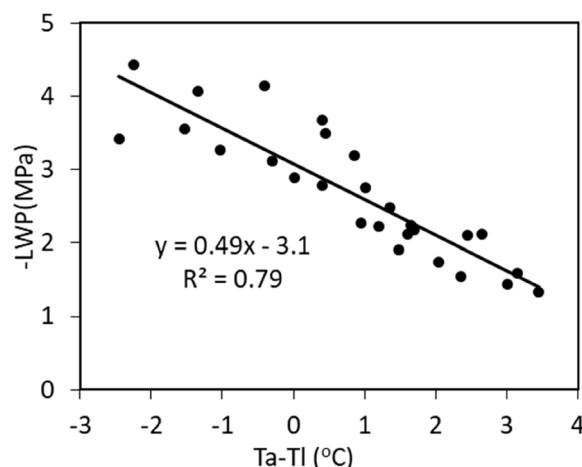


Fig. 14 The relationship of the difference between air and leaf temperature with leaf water potential ($-LWP$) on average during two growing seasons

(LWP) is shown in Fig. 14, which showed that ΔT is equal to zero when the LWP is -3.1 MPa. According to Fig. 14, when the LWP decreased to less than -3.1 MPa, the leaf temperature increased even to be higher than the air temperature as there was not enough water to help the crop cool down.

Also, the relationship between total dry matter and photosynthesis rate was determined and is shown in Table 5, in which, TDM is the total dry matter ($kg\ ha^{-1}$) and A_n is the photosynthesis rate ($\mu mol\ m^{-2}\ s^{-1}$). Results showed that there is a positive relationship between the seasonal mean photosynthesis rate and end-of-season dry matter. Thus, higher photosynthesis rates contributed to higher dry matter in both seasons. The relationship between the photosynthesis rate (A_n) and leaf water potential (LWP) was also determined and is shown in Table 5, in which, A_n is the photosynthesis rate ($\mu mol\ m^{-2}\ s^{-1}$) and LWP is the leaf water potential (MPa). Equation (21) in Table 5 shows that A_n was reduced with a decrease in leaf water potential; however, the rate of decline has not been very sharp. Also, the intercept of the equation shows that the highest photosynthesis rate at LWP equal to zero, is $29\ \mu mol\ m^{-2}\ s^{-1}$.

LAI regulates gas exchange processes such as photosynthesis [31], evapotranspiration [32]. LAI depends on species, developmental stage, prevailing site conditions, seasonality, and management practices [97]. Under water stress conditions, inhibiting leaf growth improves water balance and stress tolerance by reducing water loss to ensure plant survival [98]. LAI can be determined by direct methods which are time-consuming. The higher dry matter and leaf area index in the in-furrow is the result of higher photosynthesis rate. The value of A_n had

the highest amount at the beginning of the growing seasons and was reduced to the lowest in the late season. This may be due to the increase in air temperature at the end of the growing season.

Under high irrigation water level with high soil water condition the gas exchange parameters were higher, and this increase was in agreement with that reported by Hejnak et al. [87]. Furthermore, this increase in gas exchange parameters resulted in increase in crop yield. Lu and Zeiger [99] reported that the higher yield of cotton was associated with stomatal conductance (g_s), where Levi et al. [100] found no relation between cotton yield and g_s . Our results for quinoa were supported by the earlier findings under the well-watered conditions. However, it was not supported by the later finding due to different cultivars of cotton.

By decrease in irrigation level (100%WR to 50%WR) the reduction in An of quinoa was greater than g_s (Table 2); therefore, the An/ g_s was higher. However, decrease in irrigation level from 100%WR to 75%WR resulted no reduction in An/ g_s that is the reason for 75%WR and in-furrow planting to be optimal treatments. This also is supported by leaf water use efficiency (An/ T_r) in Table 3. Also, results of Hejnak et al. [87] for cotton indicated the enhanced tolerance to deficit irrigation was correlated with the g_s trait and efficiency of An. Furthermore, they showed that the most noticeable decrease in irrigation water level induced the gas exchange parameters, An, g_s and T_r .

Higher An in the in-furrow planting led to higher dry matter and LAI for saffron in comparison with that obtained in the basin planting [101, 102] due to appropriate soil water condition as a result of reduced soil surface evaporation. Furthermore, An is highly sensitive to severe deficit irrigation (soil water stress) [101, 103, 104]. However, in the current study on quinoa, 50%WR reduced the An by 21% in comparison with that obtained in 100%WR. This may be due to the fact that most of the quinoa water requirement is provided by irrigation water, which is reduced in 50%WR deficit irrigation. Also, results for quinoa showed higher An that led to higher leaf dry matter, that is in agreement with those reported by Echarte et al. [105]. The negative relationship between An and leaf water potential (LWP) [Eq. (21) in Table 5] was also determined. Similarly, Renau-Morata et al. [106] reported that high An was maintained by supplying water by root in higher LWP.

The value of g_s for quinoa was reduced in deficit irrigation compared to 100%WR similar as reported for saffron by Dastranj and Sepaskhah [101]. Its value was also higher in the in-furrow planting compared to the basin planting similar as reported for saffron by Dastranj and Sepaskhah [101]. Only deficit irrigation of 50%WR

reduced leaf transpiration (T_r) for quinoa (Table 2). Furthermore, the in-furrow planting increased T_r and leaf water use efficiency (An/ T_r) compared to the basin planting. These findings support the in-furrow planting and 75%WR irrigation as the optimal treatment for quinoa to be recommended in field irrigation management for quinoa.

At present, quinoa farmers in Iran do not use this field irrigation management. Common irrigation scheduling is four surface irrigation events with irrigation efficiency of 50% in semi-arid region in four different growth stages as: (i) Germination, (ii) Vegetative, (iii) flowering initiation, (iv) Grain filling [107]. Therefore, farmers can apply irrigation water depth as 75%WR at four different growth stages and save irrigation water.

Light extinction coefficient (K), which is a valuable metric for assessing light penetration through crop canopy, can be used to estimate LAI. It can also provide insights into quinoa's photosynthetic potential. The value of K is related to the leaf inclination angle, leaf arrangement and LAI. In the current study, K values varied between 0.41 to 0.67. This is consistent with the findings of Ruiz and Bertero [108], which reported that K varied between 0.52 and 0.74 for different planting densities. Comparatively, quinoa's extinction coefficients were moderate when comparing to other crops such as sunflower (0.82, [109], barley (0.4–0.46, [110], sorghum and corn (0.4, [111]). The decrease in K in the 75%WR and 50%WR treatments in comparison to 100%WR may be attributed to the change in leaf's angle because of the wilting and dropping of the leaves as a result of deficit irrigation and plant water stress. The negative correlation between K and LAI may be since the increase of LAI in the growing season is usually associated with the change in canopy architecture, such as foliage density, stem length, and clumping intensity. The amount of water needed to support normal plant development at any stage varies not only on the soil's water status but also on the environment around the plants as well as their individual characteristics [112]. The relation between the water stress coefficient (presented in [59]) and the extinction coefficient was determined (Fig. 15). Results showed that K increases as the Ks increases. Thus, water stress reduced leaf area growth resulting in decreased PAR interception, which in turn results in decreased K leading to decreased biomass production and yield.

Conclusion

A prominent abiotic stress that plants experience during their life cycle is drought stress, which poses a serious threat to plant productivity, yield, growth, and survival. To establish the optimal strategy for quinoa cultivation, we investigated how different planting techniques and

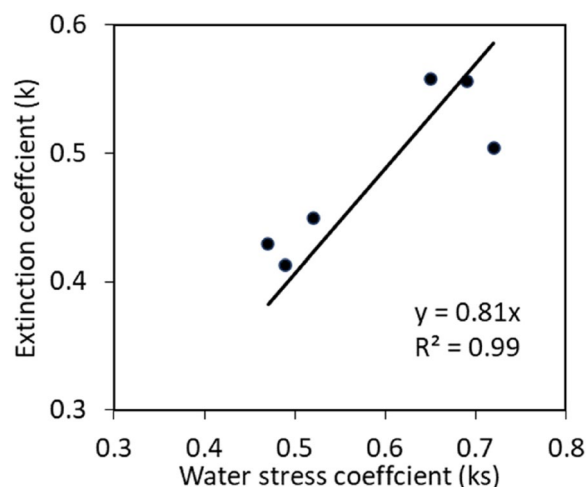


Fig. 15 The relationship between Extinction coefficient and water stress coefficient

irrigation water levels affected the production, physiological characteristics, and gas exchange of quinoa in a dry and semi-arid region.

Our research demonstrated that drought stress has a substantial effect on quinoa cultivation, emphasizing the need of using optimal planting procedures and irrigation strategies. The results revealed that the highest protein yield was obtained in 75%WR combined by in-furrow planting while the highest grain yield was observed in in-furrow planting method in 100%WR, which highlighted the possibility of using more effective irrigation method without compromising the seed quality. It is important to note that yield reduction can be primarily attributed to the imposed drought stress. Furthermore, the in-furrow planting exhibited higher leaf water potential, indicating better water availability for the crop compared to the other planting methods. On the other hand, the leaf temperature values in the on-ridge planting were higher in comparison to those obtained in the basin and in-furrow planting methods. Under water stress condition, the leaf growth was decreased to minimize the water loss to ensure plant survival; however, photosynthesis was the first process that was affected by deficit irrigation. However, photosynthesis rate (A_n) reduction with diminishing LWP was mild which provided insights to quinoa's adaptability to drought. The extinction coefficient for quinoa was found to be intermediate compared to other crops and it was decreased when exposed to the deficit irrigation. The order of grain yield and dry matter reduction in irrigation levels was 100%WR and 75%WR < 50%WR, and the order of planting methods

were in-furrow < basin < on-ridge planting; therefore, the in-furrow and 75%WR is preferable. Furthermore, the 75%WR and in-furrow planting is optimal for protein yield. To sum up, the on-ridge planting method is not suggested for quinoa cultivation and the in-furrow planting method with 75%WR proved to be the best treatment in terms of yield and physiological traits of quinoa in the study area.

Abbreviations

ABA	Abscisic acid
An	Photosynthesis rate
DAS	Days after sowing
ET _o	Potential reference evapotranspiration
ET _c	Standard crop evapotranspiration
GDD	Growing degree days
G _s	Stomatal conductance
GY	Grain yield
I1, I2, and I3	100% WR, 75%WR, and 50%WR
K	Light extinction coefficient
LAI	Leaf area index
LAI _{max}	Maximum leaf area index
LP	Length of leaf
LWP	Leaf water potential
NP	Number of panicles
P1, P2, and P3	Basin, on-ridge, and furrow planting
PAR	Photosynthetically active radiation
PC	Partitioning coefficient
PY	Protein yield
SDM	Shoot dry matter
T _a	Air temperature
TDM	Total dry matter
TI	Leaf temperature
Tr	Leaf transpiration rate
WR	Water requirement

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12870-024-05523-5>.

Supplementary Material 1.

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Authors' contributions

Conceptualization: A.R.S. Data curation: S.M. M. Formal analysis: S.M.M., and A.R. S. Funding acquisition: A.R.S. Investigation: S.M.M., and A.R. S. Methodology: S.M. M., and A.R.S. Project administration: A.R.S. Resources: A.R.S. Supervision: A.R.S. Validation: A.R.S., and S.H.A. Visualization: S.M.M., A.R.S., and S.H.A. Writing—original draft: S.M.M., and A.R.S. Writing – Review & editing: S.M.M., A.R.S., and S.H.A.

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Availability of data and materials

Data could be available by reasonable request.

Declarations

Ethics approval and consent to participate

The Quinoa seeds have been collected from the former experiments of the third author Seyed Hamid Ahmadi that had fulfilled and published the associated articles. The references to these experiments and articles are:

Razzaghi et al., (2011) Water Relations and Transpiration of Quinoa (*Chenopodium quinoa* Willd.) Under Salinity and Soil Drying, *Journal of Agronomy and Crop Science* 197(5): 348–360.

Razzaghi et al., (2012) Effects of Salinity and Soil–Drying on Radiation Use Efficiency, Water Productivity and Yield of Quinoa (*Chenopodium quinoa* Willd.), *Journal of Agronomy and Crop Science* 198(3): 173–184.

Consent for publication

Not applicable.

Competing interest

The authors declare no competing interests.

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