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Physiological basis to assess barley response to optimized regulated deficit irrigation for limited volumes of water (ORDIL)

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ABSTRACT

Agriculture must improve the productivity of irrigation water due to several factors, such as global warming, the increasing water demand of other sectors or the protection of the environment. The "optimized regulated deficit irrigation for limited volumes of water" (ORDIL) methodology may contribute to reach this objective by optimizing the allocation of irrigation water during the growing cycle, when the available volume is lower than the crop irrigation requirements. ORDIL was applied to a barley crop in a 3-year (2015–2017) field test under the semiarid conditions of Albacete (Spain). The main aim was to assess the influence of ORDIL on the physiological response of barley. The specific objectives were: 1) Identify if stomatal conductance (g_s), net assimilation rate (A_n), intrinsic water use efficiency (WUE_i) and total dry matter (TDM) evolution can be used as early and sensitive indicators of barley water status and crop performance; 2) Provide a mechanistic basis to understand barley physiological response to deficit irrigation at the most sensitive stages and; 3) Evaluate barley physiological response to ORDIL and its relation with yield. Thus, five irrigation treatments were performed. One without deficit (ND), and four with limited volumes of irrigation water (100%, 90%, 80% and 70% of typical irrigation needs). According to the results, g_s was a reliable variable to detect early water deficit in barley. Besides, critical thresholds for this variable were found to optimize irrigation and to avoid chronic physiological damages affecting the most sensitive and yield-related stages. In summary, the physiological approach applied in this study validates ORDIL methodology being useful for future irrigation scheduling and distribution improvements.

1. Introduction

The growing global demand for food makes irrigated agriculture essential (Singh and Panda, 2012). However, this food supply is threatened by the continuous reduction in the availability of water for agricultural use due to global warming and the competition with other sectors, such as manufacturing water use, public water supply or energy production (Flörke et al., 2018; Ringler et al., 2013; Rosegrant and Ringler, 2000). Besides, in semiarid regions, these water limitations can be especially important, even more in a climate change context (Elliott et al., 2014; Tian et al., 2015). For example, in important agricultural areas, such as Castilla-La Mancha (CLM) in Spain, reductions of irrigation water extraction are already a fact (Martínez-Romero et al., 2021). Hence, irrigation techniques under these circumstances should be reassessed to improve water productivity in these arid and semiarid regions with water limitations.

Moreover, the continued increase in energy costs require an improved efficiency in the use of agricultural water to become a sustainable activity (FAO, 2016; MINETUR, 2015). Regulated Deficit Irrigation techniques (RDI) are based on crops' different sensitivities to water deficit in their development stages and may allow water productivity to be increased without causing significant yield losses per unit of area (Chai et al., 2016; Marshall, 1990). If the availability of irrigable land is not a limitation, the lower yield per unit of area may be made up by cropping a larger area irrigated with the same volume of water. This way, RDI techniques may get a higher yield and profit in regions where water is a limitation but not the irrigable land (Georgiou and Papamichail, 2008; López-Mata et al., 2019; Marshall, 1990). The optimized regulated deficit irrigation (ORDI) methodology maximizes the yield of annual crops when the objective is to reach a certain deficit for the whole growing period (Domínguez et al., 2012a), or when the amount of available irrigation water is lower than the requirements of the crop

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(ORDIL) (Leite et al., 2015b). These methodologies were developed for the MOPECO model (Ortega et al., 2004), that was conceived for optimizing the gross margin (GM) of irrigated farms located in water scarce areas. This model has been calibrated for the main extensive annual crops in Castilla-La Mancha and others in different areas of the world (Carvalho et al., 2014; Domínguez et al., 2012a, 2012b, 2012c; Leite et al., 2015a; Léllis et al., 2017; López-Urrea et al., 2020; Martínez-Romero et al., 2019).

The analysis of functional traits can be used to address for the integrity, goodness and/or limitations of irrigation techniques under water limitation, allowing the improvement of water use productivity and efficiency of irrigation (Costa et al., 2007; Montoro et al., 2016). The interplay of different mechanisms of plant functioning (functional traits) ultimately determines overall performance of plants in terms of growth and crop yield. Thus, understanding the physiological responses to water availability can help to understand plant sensitivity to deficit irrigation (Álvarez et al., 2013; Parkash et al., 2021). This sensitivity will depend on the duration and intensity of the water deficit (Siopongco et al., 2006; Xu et al., 2010; Xu and Zhou, 2007) but also on the phenological stage in which the deficit is applied (Boonjung and Fukai, 1996; García-Tejero et al., 2010; Geerts and Raes, 2009). Hence, by an ecophysiological approach, crop management and irrigation scheduling, can be improved (de Oliveira et al., 2021; Jones, 2004, 2018). In this sense, ORDI methodology has already been evaluated in other herbaceous crops in terms of functional performance, being demonstrated that under water limitation, it is possible and advisable to save water in some crop stages to use it in specific crop phases which have greater impact on yield performance (Sánchez-Virosta et al., 2020). This approach reveals the underlying mechanisms of the plant in response to water availability at different crop stages. However, this ecophysiological assessment in relation to a deficit irrigation strategy has not been yet analyzed in barley.

Spain is the first country in area (24 %) and third in production (14 %) of barley in Europe (Anon, 2020). CLM region is the second largest barley producer in Spain with about 40 % of the total (MAPA, 2021). In this region, where farmers have limited irrigation water (varies between 2000 and 4500 m^3 ha^{-1} Anon, 2019), barley plays an important role in crop rotation due to its low irrigation needs (2500 m^3 ha^{-1}, Pardo et al., 2020) compared to other crops of higher profitability in the area such as onion, maize or alfalfa (5800, 6500 and 7500 m^3 ha^{-1}, respectively). Since it is a crop with one of the lowest water profitability in this region (0.10 € m^{-3}; Domínguez et al., 2017), farmers are demanding deficit irrigation techniques to save irrigation water in barley to use for other more profitable crops on their farms. In this sense, by following the ORDIL methodology, Pardo et al. (2020), have shown that with a volume of irrigation water lower than the crop needs, water use efficiency and economic water productivity can be greatly increased (48 % on average) obtaining high yields with malting quality (price of grain increases 15 % on average; Anon, 2017). However, the underlying functional mechanisms of this performance are unknown.

Thus, the main aim was to assess the influence of ORDIL on the physiological response of barley. The specific objectives were: 1) Identify if stomatal conductance (g_s), net assimilation rate (A_n), intrinsic water use efficiency (WUE_i) and total dry matter (TDM) evolution can be used as early and sensitive indicators of barley water status and crop performance; 2) Provide a mechanistic basis to understand barley physiological response to deficit irrigation at the most sensitive stages and; 3) Evaluate barley physiological response to ORDIL and its relation with yield.

2. Material and methods

2.1. Site description

The climate of the experimental area is characterized as semi-arid. The average annual precipitation is approximately 400 mm $year^{-1}$ (occurring mainly in spring and autumn), and the reference evapotranspiration values can exceed 1.100 mm $year^{-1}$ (Domínguez and de Juan, 2008). The soil of the experimental plots is classified as Calcixerrollic-Petrocalcic-Xerochrepts (USDA-NCRS, 2006). It has clay loam texture in the upper 50 cm of the soil profile. The effective depth of the root (40 cm) is limited by the development of petrocalcic horizons, which are partially fragmented (Camargo, 2013). The soil of the plots had a very basic pH (8.5) and slightly saline characteristics (electrical conductivity of saturated soil extract = 0.81 dS m^{-1}). The organic matter content is within the normal range (2.4%), but it decreases with depth. Fertilization was applied following the basic extraction rates of barley (Bellido, 1991).

Table 1
Mean temperature (T_{mean}); number of days above and below the threshold temperature for normal development (Days $T_{max(>28°C)}$ and Days $T_{min(<2°C)}$ respectively); vapour pressure deficit (VPD) and length of the stages in the three seasons. Data reported of T_{mean} and VPD are means ± standard errors based on daily records. Different letters indicate values significantly different at $P < 0.05$ according to a LSD Fisher test.

Year/ Stage	T_{mean} (°C)	Days T_{max} (>28°C)	Days T_{min} (<2°C)	VPD	Stage length (days)
Stage Ky (i')					
2015	5.30 ± 0.45a	0	42	0.26 ± 0.02a	57
2016	6.71 ± 0.45b	0	27	0.24 ± 0.02a	43
2017	6.18 ± 0.41ab	0	34	0.23 ± 0.01a	50
Stage Ky (i'')					
2015	10.73 ± 0.38d	0	13	0.39 ± 0.02 bc	51
2016	8.75 ± 0.38c	0	25	0.36 ± 0.02b	57
2017	10.54 ± 0.48d	0	26	0.42 ± 0.03 bc	48
Stage Ky (ii)					
2015	19.14 ± 0.77gh	10	0	1.15 ± 0.11fg	16
2016	13.22 ± 0.45e	0	5	0.50 ± 0.04 cd	30
2017	14.25 ± 0.63e	3	3	0.61 ± 0.05d	28
Stage Ky (iii)					
2015	16.64 ± 0.49 f	1	0	0.88 ± 0.04e	13
2016	18.78 ± 0.64 g	7	0	1.05 ± 0.07 f	18
\2017	19.67 ± 0.52ghi	11	0	1.09 ± 0.08 f	17
Stage Ky (iv)					
2015	19.27 ± 0.38ghi	9	0	1.02 ± 0.08ef	17
2016	21.12 ± 1.08hij	6	0	1.40 ± 0.11hi	10
2017	22.93 ± 0.94j	10	0	1.53 ± 0.15i	11

2.2. Experimental design

Three field trials were conducted during the seasons 2015, 2016 and 2017 in Centro Integral de Formación Profesional de Aguas Nuevas (Albacete, Spain), situated in UTM X: 595368, Y4311310, at 695 m.a.s.l. "Shakira" barley cultivar was sown with a density of 210 kg ha^{-1} in 2015, 2016 and 2017 seasons (January 12th, 13th and 13th, respectively). Five irrigation treatments with four randomly distributed repetitions were applied. One without deficit (ND), and the other four with different

Table 2
Number of irrigation events, amount of water received, global Eta/ETm and yield for each treatment and year during the whole crop cycle. Different letters in yield indicate values significantly different at< 0.05 according to a LSD Fisher test. Data reported of yield are means ± standard errors.

Year	Treatment	Irrigation events	Irrigation water (m^3 ha^{-1})	Total water (m^3 ha^{-1})	Yield (kg ha^{-1})
2015	**ND**	15	2856	3915	9199 ± 619.1**a**
	T100	15	2506	3565	8616 ± 457.5**a**
	T90	13	2251	3311	7620 ± 362.4**b**
	T80	13	2002	3061	7367 ± 169.4**b**
	T70	13	1753	2812	6404 ± 492.2**c**
2016	**ND**	18	3334	4373	8877 ± 295.6**a**
	T100	15	2584	3623	7985 ± 301.0**b**
	T90	15	2250	3290	7690 ± 443.7**bc**
	T80	13	2004	3043	7214 ± 215.0**c**
	T70	15	1755	2795	6331 ± 148.2**d**
2017	**ND**	22	3679	4718	9071 ± 510.7**a**
	T100	16	2500	3539	8032 ± 398.4**b**
	T90	15	2251	3291	7621 ± 250.3**bc**
	T80	16	2017	3057	7311 ± 231.5**c**
	T70	14	1748	2787	6283 ± 295.3**d**

Source:Adapted from Pardo et al. (2020).

irrigation water volumes, corresponding to 100% (T100), 90% (T90), 80% (T80) and 70% (T70) of net irrigation needs of barley for intermediate weather conditions of a typical meteorological year (TMY), established in 2500 m^3 ha^{-1} = T100 (Pardo et al., 2020). In the case of ND and T100, there were three plots instead of four. Both treatments were the same treatment up to the amount of water assigned to T100 was depleted (Table 2), so the differences could presumably occur in the last crop stage (ripening). In the case of T90, T80 and T70, the allocation of the amount of available irrigation water was optimized by using ORDIL (Pardo et al., 2020, 2022). A drip irrigation system (0.5 m between pipes and emitters) with self-compensating emitters (3.8 L h^{-1}) was used during the three seasons. The quality of irrigation water in the area is suitable for irrigation (pH = 7.66; electrical conductivity = 0.85 dS m^{-1}; total salt content = 0.6 mg L^{-1}; organic matter content = 0.93 mg L^{-1}). The climatic data (Table 1) were collected from the weather station "Albacete" placed in the experimental farm, which belongs to the national network of the agroclimatic information system for irrigation managed by the MAPAMA (https://eportal.mapa.gob.es//websiar/Inicio.aspx).

2.3. *Optimized regulated deficit irrigation for limited volumes of irrigation water*

During the field trials, daily irrigation scheduling was performed by using the simplified water balance methodology in the root zone (Allen et al., 1998), which is the one used by MOPECO (Domínguez et al., 2011). A more detailed description can be found in Pardo et al. (2020). To determine the irrigation scheduling of each treatment at each crop stage, the ORDIL methodology for limited volumes of available irrigation water was used (Leite et al., 2015b). This methodology determines the deficit target in terms of the ratio between actual and maximum evapotranspiration (ET_a/ET_m) at each crop yield response (Ky) stage. In the case of barley, these stages are divided in: Establishment = Ky(i'); Vegetative development = Ky(i''); Flowering = Ky(ii); Yield formation = Ky(iii); and Ripening = Ky(iv). Based on these crop yield response stages, the amount of irrigation water is assigned to be applied at each stage. During the real management of the crop, the ET_a/ET_m ratios proposed by the methodology must be updated in order to fit the real climatic conditions with the irrigation water available. In the case of ND there is not a deficit target and the ratio ET_a/ET_m is most of the time maintained in 1.0. A more complete explanation of this methodology and its application in this experiment can be found in Pardo et al. (2020).

2.4. *Physiological and growth parameters monitoring*

Data of physiological traits were collected from two plots of each treatment in two representative plants of the central part of each plot. Measurements of net assimilation rates (A_n) and stomatal conductance (g_s) were done under clear-sky conditions, on the third youngest and fully developed leaf without deformities or diseases.

Stomatal conductance (g_s) was measured at natural incident photosynthetic flux density (PPFD) between 10:00 a.m. and 2:00 p.m, with a dynamic diffusion type porometer (AP4 Leaf Porometer, Delta-T Devices Ltd., Cambridge, UK) with a measuring interval between 5 and 1200 mmol m^2 s^{-1}. Depending on the climatic conditions, g_s was measured with a frequency of 7–14 days throughout the three seasons and covering, at least, the flowering and yield formation stages.

Net assimilation rate (A_n) values were recorded by a portable photosynthesis system for gas exchange measurements (LI6400-TX model, LI-COR Bioscience, NE, USA). The parameters of the leaf chamber for data collection were determined according to the characteristics of the test area: 390 μmol mol^{-1} for CO_2 atmospheric concentration; 25 ± 0.5 °C for air temperature, 70 ± 5 % for air relative humidity; a flow rate of 650 μmol s^{-1} of air and a PPFD of 1500 μmol m^{-2} s^{-1}. Readings of A_n were made for each treatment at least once in every stage of 2016 and 2017 seasons. Concurrent with the A_n measurement, g_s values were recorded and the intrinsic water-use efficiency (WUE_i) was calculated for each plant as the ratio of leaf assimilation rate (A_n) to leaf stomatal conductance (g_s).

In addition to physiological measurements, samples of plant material were taken every 15 days to monitor total dry matter (TDM) evolution. In two plots of each treatment, biomass samples were collected from a 0.5 × 0.5 m area, located in the central part of the plot. Biomass sampling was initiated from the beginning of tillering. The last sampling was at harvest.

2.5. *Statistical analysis*

Analysis of variance (ANOVA) with three factors (Irrigation treatment, Stage and Year) was carried out to evaluate the effect of these factors on A_n, g_s, WUE_i and TDM, while Stage and Year were the factors analyzed on climatic variables. Afterwards, a post-hoc analysis (Fisher-LSD) was performed to identify homogeneous groups within each factor or combination of significant factors analyzed. Pearson's and logarithmic correlations were computed to explore the relationship between physiological variables and final yield. The software STATISTICA v.10 (Statsoft Inc., Tulsa, OK, USA) was used for data analysis and statistical significance.

3. Results and discussion

3.1. *Total dry matter responses to irrigation treatments and climatic conditions*

Water deficit can influence on barley phenology (McMaster and

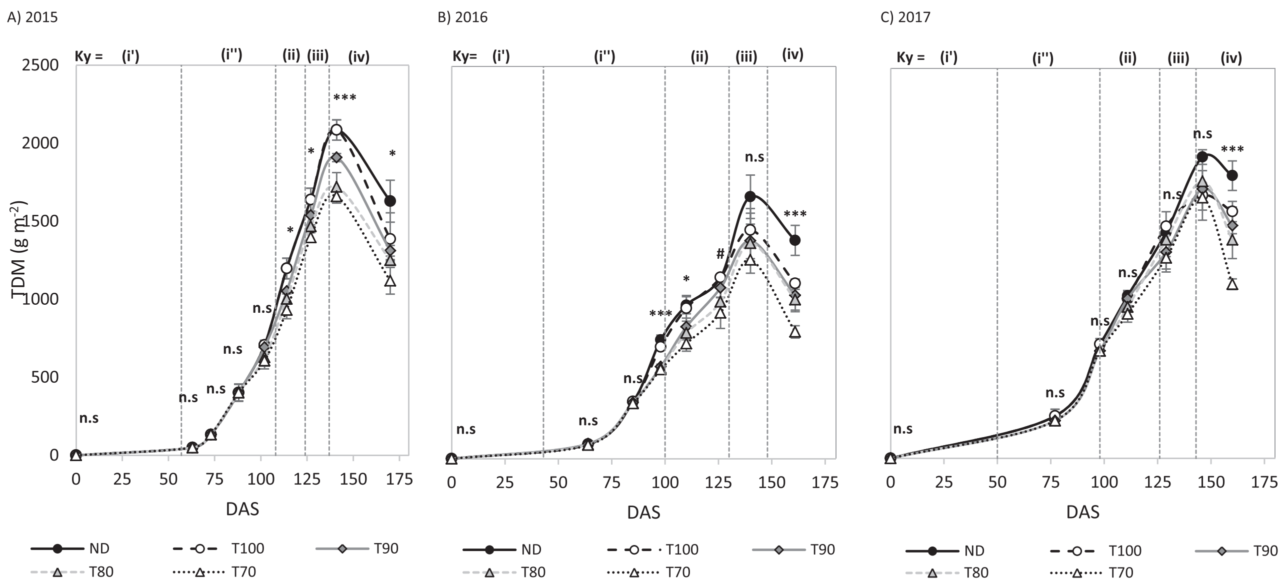

Fig. 1. Evolution of total dry matter content (TDM) of each treatment on A) 2015; B) 2016 and C) 2017 at: Establishment = Ky(i'); Vegetative development = Ky(i''); Flowering = Ky(ii); Yield formation = Ky(iii); and Ripening = Ky(iv). Each point represents the mean TDM of each treatment at a given day after sowing (DAS). Error bars represent standard error of the mean. Signification level of statistical differences:* =0.05 > p > 0.01; **= 0.01 > p > 0.005; ***p < 0.005; N.S=Not significant.

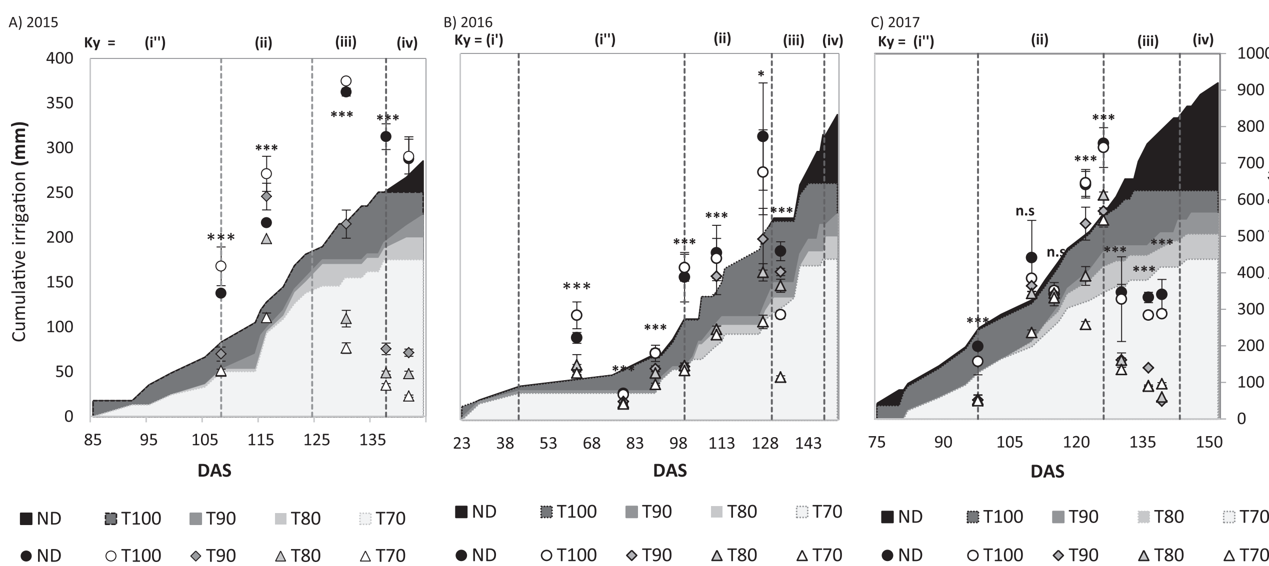

Fig. 2. Cumulative irrigation area and stomatal conductance (g_s) mean values of each treatment on A) 2015; B) 2016 and C) 2017 at: Establishment = Ky(i'); Vegetative development = Ky(i''); Flowering = Ky(ii); Yield formation = Ky(iii); and Ripening = Ky(iv). Each point represents the mean g_s of each treatment at a given day after sowing (DAS). Error bars represent standard error of the mean. Signification level of statistical differences:* =0.05 > p > 0.01; * *= 0.01 > p > 0.005; *** p < 0.005; n.s = Not significant.

Wilhelm, 2003) and total dry matter content (TDM) accumulation across the crop cycle (Goyne et al., 1993). In our study, phenological differences among treatments were not found (Fig. 1), with all the treatments following a regular growth pattern, similar to those found in other studies (Calera et al., 2004; Goyne et al., 1993). At the end of the crop cycle, the greater irrigated treatments accumulated higher biomass. These differences on TDM were not statistically shown until the middle of Ky (ii) or, as in the case of 2017 season, until the last stage. This can be because, at later growth stages of barley and under Mediterranean conditions, higher temperatures can exacerbate the water stress impact on TDM accumulation due to higher evaporative demand (Dreccer et al., 2018; McMaster and Wilhelm, 2003) which can increase the differences among treatments. In this sense, ORDIL distributed the highest amount of irrigation matching with the highest relative growth rate (see Ky (ii) and Ky (iii) in Figs. 1 and 2). This distribution aimed to optimize water use reducing the interaction between water deficit and high temperatures until maturation is reached and biomass gain is completed. Besides water availability, other environmental factors can directly influence on barley dry matter accumulation (Calera et al., 2004). For example, a lower TDM on 2016 was found, especially compared with 2015 season in all treatments (Fig. 1). Since there were not important differences of the irrigation treatments among seasons (Fig. 2), these differences can be explained by the significantly lower mean temperature observed during vegetative development in 2016 (see Ky(i'') in Table 1). High sensitivity to below-threshold temperature at this stage has already been observed (Sadras and Dreccer, 2015), which can induce low temperature injuries in barley, triggering growth declines (Muñoz-Amatriaín et al., 2020) as that observed in this study in 2016. In summary, biomass

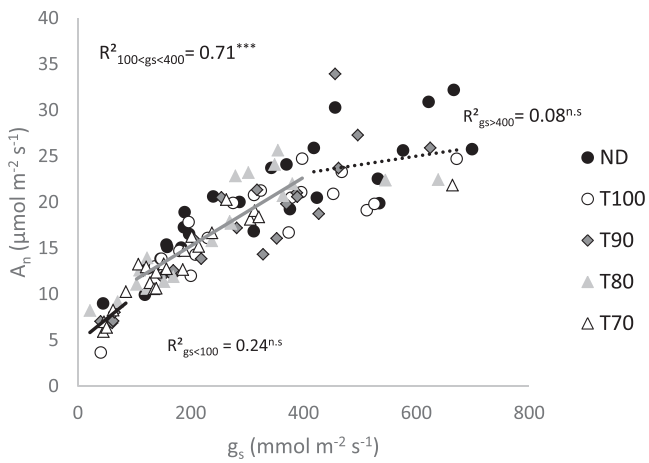

Fig. 3. Scatterplot of A_n respect g_s for ND (black dot); T100 (white dot); T90 (grey diamond); T80 (grey triangle) and T70 (white triangle). Linear adjustment and R^2 values were obtained for mean g_s values at each time point measurement on $g_{s>400}$ (black dotted line); $_{100<}g_{s<400}$ (grey line) and $g_{s<100}$ (black line). Statistical significance of the correlations:* =0.05 > p > 0.01; **= 0.01 > p > 0.005; *** p < 0.005; n.s = Not significant.

monitoring was a valuable tool to describe growth patterns under different climatic conditions, yet, as shown here, it was difficult to predict water stress with TDM data until latter stages.

3.2. Stomatal conductance (g_s) sensitivity to deficit irrigation

Stomatal closure is a rapid response to water deficit (Chaves et al., 2002; Murata and Mori, 2014) and g_s can be considered a valuable reference parameter in plants response to drought (Medrano et al., 2002). Nonetheless, g_s has also been discussed as a useful water-status related trait depending on the isohydric or anisohydric behaviour of each species and/or variety (Villalobos-González et al., 2019). Although barley has been claimed as an anisohydric behaviour species (Tardieu and Simonneau, 1998), in our study, the stomatal response of barley cv. "Shakira" was very sensitive to the irrigation amount applied at each treatment and stage (Fig. 2), as found in other studies with several barley genotypes (Munns et al., 2010). In this study, the non-deficit treatments presented clearly higher values of g_s compared to the deficit treatments across the stages. These differences were greatest at Ky (ii), which indicates a high sensitivity to water availability at this stage, as found by other authors (Cossani et al., 2009; Qureshi and Neibling, 2009). However, it should also be noted that those deficit irrigation treatments distributed by ORDIL (i.e. T90, T80 and T70), presented their relative highest g_s values also at Ky (ii), a critical stage for yield, especially if water deficit occur under the limiting climatic conditions of Mediterranean areas (Dreccer et al., 2018; Sánchez-Díaz et al., 2002). This highest amount of irrigation distributed by ORDIL along with the highest g_s values at Ky (ii) indicates: i) non-chronic physiological damages at previous stages (Lichtenthaler, 1996; Sánchez-Virosta et al., 2020) and ii) an efficient use of the available water at this critical stage (Araus et al., 2008; Blum, 2009; Mateos and Araus, 2016).

3.3. Physiological gas exchange responses across ORDIL treatments

Net CO_2 assimilation rate (A_n) is highly dependent on the stomatal aperture (Chaves et al., 2016; Collatz et al., 1991; Lawlor and Cornic, 2002). In Fig. 3, a robust linear correlation (R^2 = 0.84) between g_s and A_n when g_s values were in the range between 100 and 400 mmol m^{-2} s^{-1} ($_{100<}g_{s<400}$) can be observed. This indicates that, in this range of g_s values, the degree of stomatal aperture was the main factor influencing A_n, as previously found in other studies in barley (Lopes et al., 2004). Interestingly, in this study we found no statistical correlations between

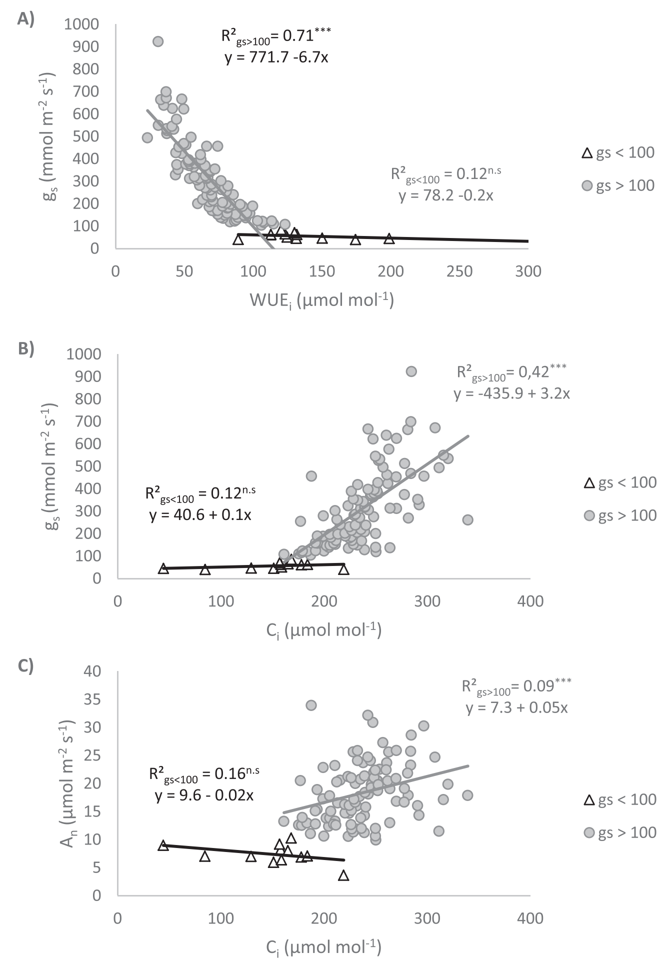

Fig. 4. Scatterplot of: A) g_s respect WUE_i; B) g_s respect C_i; C) A_n respect C_i. White triangles = $g_{s<100}$; grey circles = $g_{s>100}$. Linear adjustment and R^2 were obtained for $g_{s<100}$ (black line) and $g_{s>100}$ (grey line). Statistical significance of the correlations:* =0.05 > p > 0.01; **= 0.01 > p > 0.005; *** p < 0.005; n.s = Not significant.

g_s below 100 ($g_{s<100}$) or above 400 ($g_{s>400}$) mmol m^{-2} s^{-1} (Fig. 3). The A_n response to stomatal aperture is not always linear and depends on the degree of stress (Chaves et al., 2011; Flexas and Medrano, 2002) and other inherent factors influencing photosynthetic efficiency, such as leaf chlorophyll content, leaf morphology, stomatal density, growth stage, etc. (Lawrence et al., 2021; Nikolopoulos et al., 2002; Poorter and Evans, 1998). The absence of correlation of $g_{s>400}$ with A_n means that water supply to overcome this threshold was not directly reflected on higher assimilation rate. This matter can provide an insight on ORDIL irrigation scheduling efficiency. In this sense, 64 % of the $g_{s>400}$ values corresponded to ND and T100 treatments, which were not optimized by ORDIL. The rest (36 %) of $g_{s>400}$ values corresponded to T90, T80 and T70 treatments. These results imply that, these irrigation treatments distributed by ORDIL were overwatered at some point and should be considered for future improvements. Besides, the absence of statistical correlation of $g_{s<100}$ with A_n, indicate that non-stomatal limitations could have happened, due to the deficit irrigation itself or, since this low g_s values were also found on ND treatment, because other environmental factors besides water deficit. This matter is further discussed in the following section.

3.4. Photosynthesis performance in response to stomatal conductance thresholds

Significant and robust correlations were generally found between gas

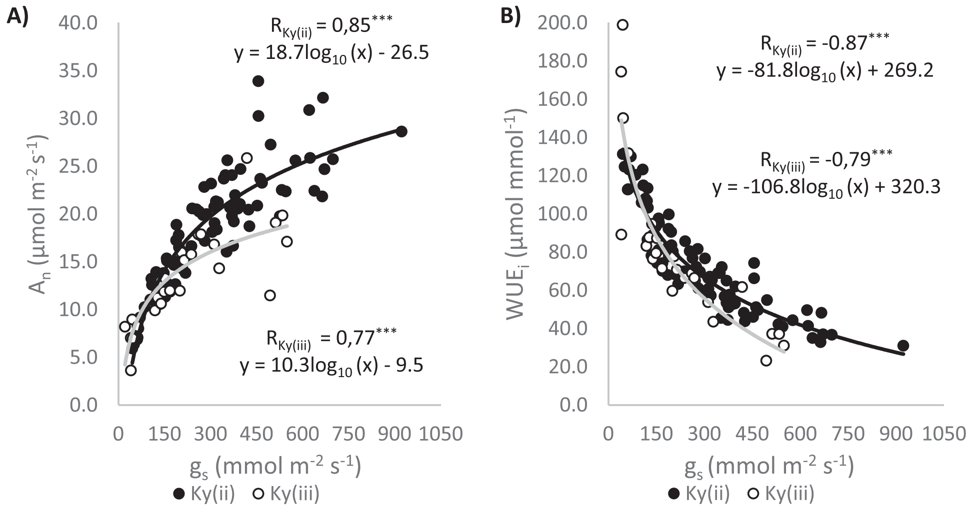

Fig. 5. Scatterplot of: A) A_n respect g_s and B) WUE_i respect g_s. Black circles= data obtained at Ky(ii); White circles = Data obtained at Ky (iii). R values of logarithmic adjustment were obtained for Ky (ii) (black line) and Ky (iii) (grey line). Statistical significance of the adjustment:* =0.05 > p > 0.01; **= 0.01 > p > 0.005; *** p < 0.005; n.s = Not significant.

exchange variables except on $g_{s<100}$ (Fig. 4). In general, g_s was negatively related to the WUE_i (Fig. 4A). The increase of WUE_i under low or moderate water deficit due to stomatal closure it is a well-known pattern in plants, since the decline on g_s is greater than in A_n (Larcher, 2003; Sinclair et al., 2009). Interestingly, in our study, the pattern of WUE_i response was erratic once g_s values dropped to $g_{s<100}$ and the intrinsic water use efficiency did not necessarily increase with stomatal closure below this threshold. In fact, irregular patterns were also found when $g_{s<100}$ on the response of stomatal conductance and net assimilation rate respect the intercellular CO_2 (C_i) (Fig. 4B and C). These results, along with that showed in Fig. 3 for $g_{s<100,}$ can be explained since, under severe stress, non-stomatal limitations can affect photosynthesis performance (Flexas et al., 2002; Flexas and Medrano, 2002; Marino et al., 2018). Contrary to the results obtained by Robredo et al. (2007) in an experiment in barley under elevated CO_2 environment, in this field study, stomatal closure did not trigger an increase on C_i (Fig. 4B). In fact, we found an exponential increase of C_i with the increase of g_s (Fig. 4B) and an irregular pattern of A_n respect C_i, especially when $g_{s<100}$ (Fig. 4C). Based on this, we can assume that once g_s values dropped to $g_{s<100}$ net assimilation rate no longer depended only on the stomatal aperture or C_i concentration (Ahumada-Orellana et al., 2019; Marino et al., 2018). Hence, it can be expected that metabolic impairments (Flexas et al., 2004; Marino et al., 2018; Medrano et al., 2002) and/or senescence (Chaves et al., 2012) did not allow a regular photosynthesis performance under very low stomatal conductance values. These results, along with those shown in the previous section, can be very valuable to determine the optimal (i.e. around 400 mmol m^{-2} s^{-1}) and minimum (i.e. $g_{s<100}$) stomatal conductance thresholds in barley for a proper deficit irrigation strategy.

3.5. Gas-exchange variability responses across phenological stages

Variability in the response of gas-exchange variables was also found at different yield stages (Fig. 5). In general, net assimilation rate was more efficient per unit of g_s in Ky (ii) than in Ky (iii) (Fig. 5A). In previous studies, the influence of growth stage on photosynthetic performance (Lawrence et al., 2021) and how A_n and g_s on barley decreases with leaf age (Robredo et al., 2007) have been shown. At Ky (iii) the WUE_i was generally lower compared to Ky (ii) (Fig. 5B). In fact, the highest absorbed photosynthetically active radiation happens when the vegetative growth peak is reached (Gower et al., 1999), which permits the greatest conversion of photo-assimilates to biomass gain in barley (Calera et al., 2004; Gower et al., 1999). With these differences between Ky (ii) and Ky (iii) stages, it can be inferred that irrigation was properly optimized by ORDIL, since the highest amount of water was distributed at Ky (ii), before seasonal higher temperatures increased evapotranspiration and senescence. In fact, under limiting climatic conditions, such as high temperatures or high vapour pressure deficit, available water for the plant became scarcer (Chaouche et al., 2010; González et al., 2008; Tognetti et al., 2006). All these circumstances together can be crucial in terms of irrigation management and efficiency (Bhattacharya, 2019; Kirda, 2002).

In our experiment all the $g_{s<100}$ values corresponded to two measurements dates in 2016 season, specifically, to May 3rd, in the middle of Ky (ii) and in June 7th, at the end of Ky (iii). On May 3rd, the minimum temperatures of the three nights before measurement were below the non-stressful threshold temperature for barley (2ºC). These prolonged cold temperatures could damage the root zone and leaves resulting in stomatal conductance and photosynthesis constrains (Allen and Ort, 2001; Melkonian et al., 2004; Vernieri et al., 1991). On the other hand, on June 7th, five days of above the threshold temperature for development (28ºC) took place prior to the measurement. These high temperatures can induce premature senescence and are related with stomatal conductance damages and physiological impairments (Hlaváčová et al., 2018) impacting yield.

In summary, at Ky (iii), seasonal higher temperatures and evapotranspiration along with the starting of leaf senescence led to lower g_s and gas-exchange performance despite of the irrigation treatment, while more efficient use of water at Ky(ii) in terms of physiological performance was found at this stage.

3.6. Yield response to physiological performance and inter-annual climatic variability

Although barley is one of the best adapted cereals to moderate water deficit (Robredo et al., 2007; Sánchez-Díaz et al., 2002; Teulat et al., 1998), water stress reduces barley yield (Lopes et al., 2004). This is in agreement with our findings. In this study, barley yield declined in parallel with irrigation amount (Table 2). Besides, inter-annual yield varied under the same irrigation treatments. For example, yields were higher in 2015 compared to the other two seasons. Under the same water supply, differences in yield for barley and other cereal crops have been observed due to factors other than water availability, such as VPD, temperature or radiation (Dreccer et al., 2018; Sadras and Rodriguez, 2007; Van Ittersum et al., 2013). Temperature effect is especially accentuated when several days of extreme temperatures occurred

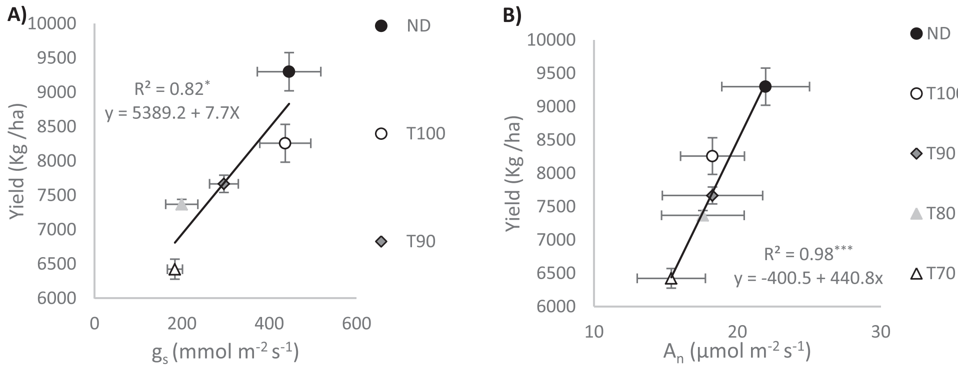

Fig. 6. Scatterplot of: A) Yield respect g_s for the three years of the study and B) Yield respect A_n at Ky(ii) for 2016 and 2017. Data provided are mean values and standard error bars of each treatment and year. R^2 values of linear adjustment are provided. Statistical significance of the correlations: * =0.05 > p > 0.01; **= 0.01 > p > 0.005; *** p < 0.005; n.s = Not significant.

(Dreccer et al., 2018; Ugarte et al., 2007). Very high temperatures, as those observed in 2016 and 2017 during grain filling (Table 1), results in resource caption constrains, grain abortion and yield declines on cereal crops (Dreccer et al., 2018; Ferris et al., 1998; Wheeler et al., 1996). Besides, very low temperatures at vegetative growth in barley, as those observed at Ky (i'') in 2016 and 2017 (Table 1), can notably affect vegetative growth and decrease final yield (Dreccer et al., 2018; Muñoz-Amatriaín et al., 2020).

The impact of factors other than water supply can be also detected through gas-exchange variables, as already reported for barley (Sánchez-Díaz et al., 2002) which are related with yield. In fact, when all years were pooled at the same treatment to buffer the inter-annual variability, we found very robust correlations of barley yield with mean g_s during the whole cycle (Fig. 6A) and with A_n at Ky(ii) (Fig. 6B). The correlation between gas-exchange variables with biomass and/or yield parameters has been previously reported in barley (Jiang et al., 2006; Sánchez-Díaz et al., 2002) and other cereal crops (Lu et al., 1998). The robustness of the correlations in this study supports the significant contribution of g_s and A_n on final barley yield. It should be considered that gas-exchange variables were mainly monitored during the most yield-related phenological stages. Moreover, all the years were pooled for one single treatment, diminishing the multi-year noise introduced by interannual climatic variability (Ehrlich and Lambin, 1996).

These results together reinforce the fact that eco-physiological variables can be valuable performance indicators of deficit irrigation techniques (Álvarez et al., 2013a; Costa et al., 2007; Matese et al., 2018), since they responded to water-related factors, as well as other environmental variability that influence crop production, especially at the most sensitive and yield-related phenological stages.

3.7. *Future prospects for ORDIL improvements*

Based on these results, ORDIL correctly optimized irrigation in terms of physiological performance. Threshold values of g_s have been previously proposed for deficit irrigation strategies in other crops (Ahumada-Orellana et al., 2019; Cifre et al., 2005; Marino et al., 2018), yet this is the first reported result for barley. However, this study also shows that there is still room for improvement. It would be ideal to find an optimized distribution that maintains stomatal conductance above 100 mmol m^{-2} s^{-1} trying to maintain values close to 400 mmol m^{-2} s^{-1}. At that level, the net assimilation rate in relation to stomatal aperture was optimal. However, gas-exchange monitoring for field phenotyping is laborious and time-consuming (Carvalho et al., 2021; Costa et al., 2013). New remote-sensing tools are becoming important to predict yield potential and stress adaptation (Araus et al., 2008). For future improvements, thermography appears as a valuable tool for phenotyping (Araus et al., 2008; Costa et al., 2019; Lima et al., 2016) and as a predictor of biomass gain (Sánchez-Virosta and Sánchez-Gómez, 2020). In fact, it has been already proposed for barley monitoring (Munns et al., 2010) and can be managed with unmanned aerial vehicles (Deery et al., 2016; Sullivan et al., 2007) in high throughput manner (Melandri et al., 2020; Prashar et al., 2013).

4. Conclusions

The findings of this study indicate that ecophysiological based studies can be very valuable for an accurate estimation of barley irrigation requirements. In this study, optimum g_s values (ca. 400 mmol m^{-2} s^{-1}) for physiological performance and yield potential, and minimum g_s values (not below 100 mmol m^{-2} s^{-1}) to avoid chronic physiological damages have been proposed for barley cv. "Shakira", which can be used in barley irrigation management and distribution. Besides, the high correlations found between physiological parameters (i.e. g_s and A_n), at different phenological stages, Ky(ii) and Ky(iii), with yield, validate the irrigation distribution made by ORDIL under limited volumes or irrigation. Finally, advances in ecophysiological monitoring and the understanding of the influence of other climatic factor can be crucial for future optimizations of deficit irrigation techniques as ORDIL.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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