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Genotypic differences in leaf gas exchange and growth responses to deficit irrigation in *reticulatus* and *inodorus* melons (*Cucumis melo* L.)

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Abstract

Leaf gas exchange and growth responses of three melon cultivars, *i.e.,* Mission, Da Vinci (var. *reticulatus*), and Super Nectar (var. *inodorus*) to two irrigation regimes, 50 and 100% crop evapotranspiration (ETc) were investigated under water-limited conditions of southwest Texas. In 2012, deficit irrigation (50% ETc) significantly decreased above-ground biomass, leaf area, leaf number, and specific leaf area, while leaf gas exchange, relative water content, water potential, chlorophyll fluorescence (F_v/F_m), and chlorophyll content (SPAD index) were not affected. However, in the drier year 2011, deficit irrigation significantly reduced net photosynthetic rate (P_N) and stomatal conductance (g_s). Further, the responses to water deficit varied with cultivars. At 50% ETc, P_N and g_s were maintained in cv. Da Vinci while decreased in Mission and Super Nectar. Thus, the late maturing cv. Super Nectar appeared to be more sensitive to drought stress, possibly due to the decrease in leaf area and P_N.

Additional key words: chlorophyll fluorescence; muskmelon; photosynthesis; specific leaf area; stomatal conductance; transpiration.

Introduction

The increased frequency and intensity of drought events and severe restrictions on groundwater use for irrigated crops are likely to affect melon cultivation in semiarid regions of Texas (Leskovar *et al.* 2001, Leskovar and Piccinni 2005) and worldwide. Thus, to sustain melon production in the region, the implementation of the '*more crop per drop'* irrigation strategy is urgently needed (Blum 2011). Under sustained deficit irrigation plants are supplied with water below their ETc demands throughout the growing season (Fereres and Soriano 2007) and thus, are deliberately exposed to a gradual moisture stress which, depending upon the crop and/or cultivar sensitivity, may have deleterious effects on crop physiology, growth, and yield.

Plants can avoid losses associated with drought stress through morphological and physiological adaptations (Blum 2005), but these responses may vary with crops/cultivars, growth stages, environments and timing, severity and duration of water stress (Cattivelli *et al.* 2008). Some examples include improved root growth in melons (Sharma *et al.* 2014, 2018), decrease in leaf dry mass ratio in wheat (*Triticum aestivum* L) (Boogaard *et al.* 1996), reduction in specific leaf area in *Amaranthus* spp. and in *Arundo donax* L (Liu and Stützel 2004, Romero-Munar *et al.* 2018), decrease in chlorophyll (Chl) content (Mafakheri *et al.* 2010), and restricted shoot growth with unchanged root growth in maize (*Zea mays* L.) (Sharp and Davies 1979). Most of these growth traits are rapidly affected by very mild stress, while, prolonged water deficit can adversely affect leaf gas-exchange characteristics (Huck *et al.* 1983) due to stomatal closure and related low C_i (Raschke and Hedrich 1985) and certain other nonstomatal factors (Janoudi *et al.* 1993). Under greenhouse conditions, water stress decreased net CO_2 assimilation rate (P_N), g_s, C_i, and transpiration rate (E) of melon seedlings (Huang *et al.* 2010, Agehara and Leskovar 2012). Most of these studies have been conducted under controlled conditions, while field experiments designed to assess the impact of water deficit on growth and leaf gas exchange of melons are lacking.

Plant morphological and physiological processes differ in their sensitivity to water stress. Subbarao *et al.* (1995) reported that leaf area expansion is more sensitive to

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Abbreviations: ABM – aboveground biomass; C_a – ambient CO_2 concentration; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; ETc – crop evapotranspiration; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; K_c – crop coefficients; L_s – stomatal limitations; LA – leaf area per plant; LN – number of leaves per plant; P_N – net photosynthetic rate; RWC – relative water content; SLA – specific leaf area; SPAD – chlorophyll index; TFY – total fruit yield; WUE – water-use efficiency (P_N/E).

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water stress than photosynthesis and transpiration in grain legumes. Further, Karimi *et al.* (2015) emphasized that ability to preserve relative water content was involved in drought-tolerance mechanism in almond. While Ashraf *et al.* (2002) argued that the decreased P_N is the most common physiological response to moisture stress, due to stomata closure and inhibition of Calvin cycle enzymes like Rubisco, particularly when plants are exposed to gradual water stress under field conditions (Medrano *et al.* 1997). Indeed, it is the total crop photosynthesis, not the $P_{N,}$ that contributed in the past to improvement in yield of grain crops, thus the maintenance of leaf area is more important than P_N (Richards 2000). Within this context, identifying traits useful for selecting melon cultivars tolerant to soil moisture deficit has become a priority in this study.

Melons are highly productive under well-watered conditions (Sharma *et al.* 2014) and are considered to be sensitive to water stress. Under water-deficit conditions, melon crop exhibited significant reductions in fruit yield (Fabeiro *et al.* 2002, Cabello *et al.* 2009) and quality (Lester *et al.* 1994, Long *et al.* 2006). The high stomatal density on both upper and lower surface of melon leaves (Abdulraham *et al.* 2011), may result in high stomatal conductance and hence enhanced sensitivity to mesophyll or parenchymatous outer cortical tissue dehydration. Genetic adaptive responses to water deficit have been reported in several crops, such as *Amaranthus* spp. (Liu and Stützel 2004), chickpea (*Cicer arietinum* L.) (Mafakheri *et al.* 2010), cotton (*Gossypium hirsutum* L. r. *latifolium* Hutch) (de Brito *et al.* 2011), okra (*Abelmoschus esculentus* (L.) Moench) (Razavi *et al.* 2008) and *Prunus dulcis* Mill. (Karimi *et al.* 2015), and tomato (Fullana-Pericàs *et al.* 2017). Melon has shown a positive association between P_N and fruit yield (Kitroongruang *et al.* 1992) possessing a wide genetic variability for leaf gas-exchange traits (De *et al.* 2008). However, morphological and physiological adaptation responses to water deficit of melon cultivars from diverse horticultural groups have not been investigated.

The objective of this study was to determine the effect of deficit irrigation (50% ETc) on growth adaptation and physiological traits of three diverse melon cultivars belonging to the muskmelon, Tuscan, and honeydew group. The selected cultivars differ in their fruit shape, size, color, ripening behavior, and maturity. It was hypothesized that differences in fruit characteristics between these cultivars would also be exhibited in morphological and photosynthetic adaptation responses to deficit soil moisture. We expect, this information will be useful in melon breeding for screening cultivars with specific traits linked to drought adaptation.

Materials and methods

Plant material and treatments: Three melon cultivars, *i.e.*, Mission (var. *reticulatus*; muskmelon type), Da Vinci (var. *reticulatus*; Tuscan type), and Super Nectar (var. *inodorus*; honeydew type) were grown under field conditions at the Texas A&M AgrilLife Research and Extension Center at Uvalde, TX (29°13”N, 99°45”W), on a clay soil (Hyperthermic Aridic Calciustolls) during 2011 and 2012 seasons. These cultivars were chosen because they are the representative and highly productive varieties representing important commercial horticultural melon groups. Further, no previous study has investigated their growth and photosynthetic responses to water deficit under field conditions.

The experimental site has a semiarid climate with average annual high/low temperatures of 27.4/13.6°C and a mean annual precipitation of 663 mm. The mean annual evapotranspiration (ET) is 1522 mm, which is more than twice the mean annual rainfall. Average minimum and maximum temperatures are given in Fig. 1S (*supplement*) while, Fig. 1 depicts the vapor pressure deficit and rainfall events of the experimental site.

Irrigation rates (50% ETc and 100% ETc) and cultivars

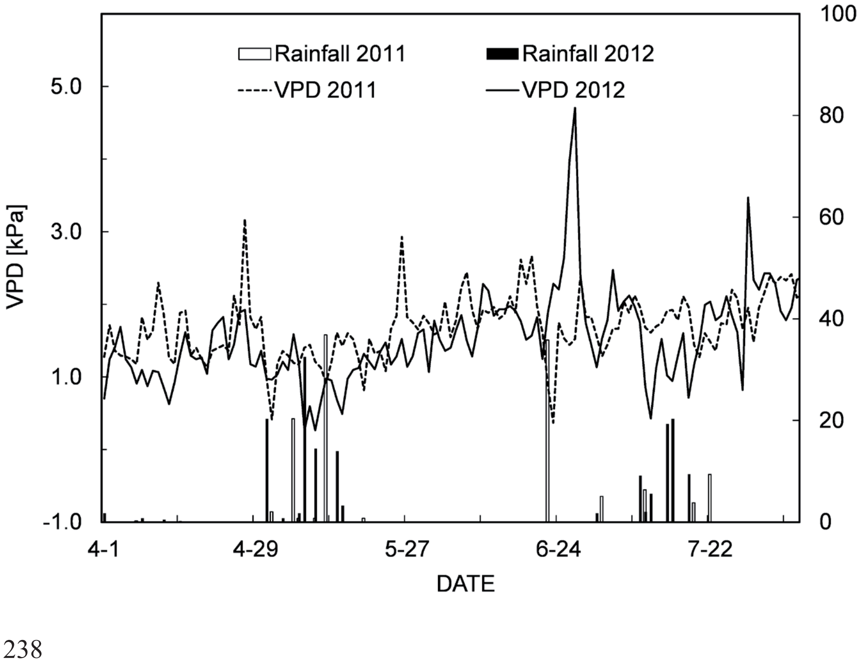

Fig. 1. Daily vapor pressure deficit (VPD) (*lines*) and rainfall (RF) events (*bars*) at Uvalde, TX in 2011 and 2012 seasons.

were arranged in a split plot design, with three replicates. Seeds were planted on raised beds (2.03 m row to row, 0.30 m plant to plant spacing) covered with black plastic mulch thickness of 0.02 mm on 1 April 2011 and 15 April 2012. The irrigation was applied as subsurface drip based on the daily crop evapotranspiration (ETc) which was calculated as a product of the reference evapotranspiration (ET_0) obtained from the lysimeter facility located at the Texas A&M Center (Ko *et al.* 2009) and the stage specific K_c. K_c values were used as; $K_{c\ ini}$ = 0.5, $K_{c\ mid}$ = 0.85, and $K_{c\ end}$ = 0.60 (Allen *et al.* 1998). The irrigation requirement was calculated with adjustments for effective rainfall (50%), black plastic mulch (bare soil K_c = 0.2) (Shinohara *et al.* 2011, Sharma *et al.* 2017), effective irrigation wetting bed width (estimated at 70%) and canopy growth. Irrigation was triggered twice a week when cumulative irrigation requirement reached at 10 mm approximately. The drip tape (*T-Tape*, *John Deere*, Moline, IL, USA) with 1.02 L h^{-1} flow rate at 55 kPa was buried in the middle of each bed at a 15-cm depth with drippers spaced at 30.48 cm. Irrigation amount applied was calculated from drip tape flow rate, duration of irrigation applied (hours) and the linear length irrigated. Total fertilizers 90N-42P-30K kg ha^{-1} and 73N-30P-36K kg ha^{-1} were applied through fertigation during 2011 and 2012 seasons, respectively.

During the first 34 d after transplantation (DAP) in 2011 and 38 DAP in 2012, both irrigation rate treatments received full irrigation (*i.e.*, equivalent 100% ETc, 78 mm and 27 mm, respectively) water to ensure good germination and seedling establishment. Since the objective of the study was to expose the cultivars to a mild gradual stress, the differential irrigation of melon cultivars began on 5 May 2011 and 23 May 2012, with 50% and 100% ETc treatments receiving 184 and 335 mm water for 27 irrigation events in 2011, respectively. In 2012, 32 applications after May 23 applied 200 and 382 mm for 50% and 100% ETc, respectively. Therefore, the deficit irrigation (50% ETc) actually received 63% (261 *vs*. 413 mm) and 55% (227 *vs*. 409 mm) of irrigation water applied in 2011 and 2012, respectively.

Gas exchange and Chl fluorescence: Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) were measured at 53, 67, 95, and 110 DAP in 2011 and 36, 50, 64, 81, and 95 DAP in 2012. Two random plants were selected in each plot and fully expanded mature leaves (4th or 5th from the main growing vine tip) were used for measurements. A portable photosynthesis system *LI-6400XT* (*LI-COR Inc*., Lincoln, NE, USA) equipped with an open-flow infrared gas analyzer was used at a steady state (PAR of 2,000 μmol $m^{-2}\ s^{-1}$, reference CO_2 concentration of 400 μmol mol^{-1}, air flow rate of 500 μmol s^{-1}, and block temperature of 30°C) for all measurements (Agehara and Leskovar 2012). The stomatal limitations (L_s) to photosynthesis were computed by using the formula, $L_s = 1 - C_i/C_a$ (Jones 1985).

To measure the efficiency of light absorption, Chl fluorescence was determined using a portable pulse modulated Chl fluorometer *OS-30P* (*OPTISCIENCES*, USA) with 1-s excitation pulse (660 nm) and saturation intensity of 3,500 μmol(photon) $m^{-2}\ s^{-1}$ after 30-min dark adaptation of the same leaves used for gas-exchange measurements by fixing dark-adaptation clips on each leaf. The sensor of the fluorometer was inserted in the cuvette on the leaf clip and F_v/F_m values were recorded. Since, F_v/F_m gives the measure of efficiency of excitation energy captured by the open PSII reaction centers (Oyetunji *et al.* 2007), it provides an indication of the photo-/thermo-stability of the photosynthetic machinery. Chl fluorescence was recorded at 36, 64, and 81 DAP in 2012 season. Leaf Chl index was also measured immediately on the same leaves using a Chl *SPAD-502* meter (*Konica Minolta Sensing*, Tokyo, Japan). Five readings were taken per leaf on two plants per plot, around 1 cm away from the margin avoiding major leaf veins. All measurements were done between 11:00 to 15:00 h (Hamidou *et al.* 2007).

Plant water status: Midday leaf water potential (Ψ_l) was measured between 12:00 and 14:00 h as described in Agehara and Leskovar (2012), using a pressure chamber (*Model 3005*; *Soil moisture Equipment*, Santa Barbara, CA). For measuring relative water content (RWC), one entire leaf from two plants per plot was collected. After fresh mass (FM) was recorded, leaves were floated on deionized water in a petri dish and hydrated in darkness for 4 h. Thereafter, the turgid mass (TM) was recorded, and samples were subsequently dried to a constant mass at 85°C to determine the dry mass (DM) (Goreta *et al.* 2007). Relative water content expressed as a percentage was calculated as follows:

$$RWC = [(FM - DM)/(TM - DM)] \times 100$$

Growth and yield: Total leaf area and dry matter content of leaves, stems, and fruit were determined twice, at 37 (*i.e*., before starting differential irrigation) and 68 DAP (*i.e*., 30 d after applying deficit irrigation). Six plants per treatment were sampled by cutting them at ground level and separated into leaf, stem, and fruits. At each sampling total leaf area per plant (LA) was measured using a portable leaf area meter (*LI 3100*, *Licor*, Lincoln, Nebraska, USA). Leaf, stem, and fruit fresh mass was recorded and all three plant components were dried to a constant mass at 85°C to determine their respective dry masses to calculate the above ground biomass (ABM). Specific leaf area (SLA) was calculated as the total plant leaf area divided by leaf dry mass.

Fruits were harvested at half to full slip stage between 18 June (78 DAP) to 5 August 2011 (126 DAP), and between 25 June (71 DAP) and 24 July 2012 (100 DAP), and total fruit yield (TFY) [t ha^{-1}] was recorded.

Statistical analysis: Data for each variable were subjected to the analysis of variance (*ANOVA*) with a split plot design using generalized linear model procedures (*SAS 9.1*, *SAS Inst*., Cary, N.C., USA). Irrigation regime (50% and 100% ETc) was the main plot, cultivar (Mission, Da Vinci, and Super Nectar) the subplot, and sampling dates (DAP) the sub-sub plot factor (McIntosh 1983). Where significant main effects were found, means were separated by *Duncan*'s multiple-range test. Relationships among P_N,

g_s, *E*, F_v/F_m, SPAD, LA, SLA, leaf number (LN), TFY, WUE, and ABM were determined by correlation analysis.

Results

Overall, deficit irrigation (50% ETc) resulted in significant decrease in P_N and g_s in the 2011 season (Table 1). Data for 2012 showed no statistically significant trend (Table 2). The melon cultivars also exhibited significant differences for P_N and *E* parameters in both seasons, with Da Vinci having the lowest values for both traits as compared to cv. Mission and Super Nectar. The lowest g_s was also recorded in Da Vinci in both years, but the difference was only significant in 2012 (Tables 1, 2). Sampling dates also had significant effect on all the leaf gas-exchange parameters in 2011 and 2012 seasons (Tables 1, 2), indicating that leaf gas exchange varied with the phenological stages and weather conditions. In 2011, leaf gas-exchange parameters, *i.e.,* g_s, *E*, and C_i followed a gradual decrease over the sampling dates; however, both P_N and water-use efficiency (WUE; P_N/E) increased at 67 DAP though P_N decreased thereafter, while WUE remained unchanged at 95 DAP, and then increased at 110 DAP. Similarly, in 2012, P_N and WUE significantly increased up to 64 DAP and decreased thereafter. While, g_s increased at 50 DAP and decreased during rest of the season. Further, *E* and C_i followed the decreasing trend, except a significant increase at 95 DAP. Stomatal limitations (L_s) significantly increased between 64 and 81 DAP and again declined at 95 DAP.

In 2011, cultivar × sampling date interactions were significant for P_N, g_s, *E*, and C_i (Table 1), indicating that leaf gas-exchange responses to deficit irrigation varied among the cultivars and sampling dates (Fig. 2). P_N increased up to 67 DAP in Mission, 95 DAP in cv. Da Vinci, while started to decrease in cv. Super Nectar after 53 DAP (Fig. 2). Similar trends were observed for g_s and *E*. C_i decreased in all the cultivars at 67 DAP, it remained unchanged in cv. Mission and Da Vinci up to 95 DAP, but decreased in cv. Super Nectar at 95 DAP. Thus, the decrease in gas exchange was more rapid in Mission, while the decrease was consistent in Da Vinci, and it was more variable in Super Nectar. WUE showed an increasing trend over time for all cultivars. Fig. 3 shows the irrigation rate and cultivar interactions for P_N and g_s between 53 and 110 DAP in 2011. Deficit irrigation did not reduce P_N and g_s in cv. Da Vinci, rather it was improved at 67 DAP.

Similarly, in 2012, cultivar × sampling date interactions were significant for P_N, g_s, *E*, C_i, and L_s (Table 2). In general, P_N and L_s increased up to 64 DAP, however, g_s decreased significantly at 64 DAP and remained lesser thereafter. WUE showed a similar trend in all the cultivars and increased up to 64 DAP and decreased thereafter (Fig. 4).

Deficit irrigation did not affect water potential (Ψ_l) and relative water content (RWC) of melon cultivars when measured at 81 DAP (data not shown). However, under 50% ETc, a numerical increase in Ψ_l was recorded for cv. Mission and Super Nectar. RWC of all the three cultivars remained similar at both irrigation rates.

Chl fluorescence (F_v/F_m) in melons was not affected by deficit irrigation (data not shown). Similarly, 50% ETc did not cause any leaf chlorosis in all the cultivars as indicated by no significant differences in Chl index (data not shown). Deficit irrigation caused a significant increase in stomatal density of in cv. Mission as compared to 100% ETc (Fig. 2S, *supplement*). The increase in stomatal density was similar in Da Vinci and Super Nectar, but not significant.

No differences in LA, ABM and SLA were observed between the irrigations rates at 37 DAP (*i.e.*, before starting the differential irrigation). However, at 68 DAP (*i.e.*, 30 d of differential irrigation), 50% ETc significantly reduced leaf number per plant (LN) by 43%, leaf area per plant (LA) by 50%, aboveground biomass per plant (ABM) by 37%, and specific leaf area (SLA) by 14% as compared to 100% ETc (Table 3). These reductions varied in extent with cultivars. Leaf area and specific area decreased in all the cultivars while, LN and ABM decreased in Mission and Da Vinci. The trend was similar in Super Nectar, but not significant.

Deficit irrigation caused a significant reduction in leaf (LDM), stem (SDM), and fruit (FDM) dry masses in cv. Mission and Da Vinci as compared to 100% ETc (Fig. 3S, *supplement*). In cv. Super Nectar, the reduction was statistically significant only for stem dry mass. Overall, deficit irrigation reduced LDM by 49, 53, and 18%, SDM by 54, 53, and 21% and FDM by 40, 43, and 3% in cv. Mission, Da Vinci, and Super Nectar, respectively.

Under 50% ETc, the ABM had a strong correlation with leaf area (LA) ($r = 0.920$) and number of leaves per plant (LN) ($r = 0.888$) (Table 1S, *supplement*). Similarly, TFY had a significant correlation with LA ($r = 0.736$), LN ($r = 0.873$) and SLA ($r = 0.786$) which indicates that under water deficit a decrease in TFY and ABM was associated with decrease in leaf area per plant. Moreover, under 100% ETc, ABM was positively correlated with LA. TFY had no correlation with ABM, LA and LN. This indicates that under optimum moisture conditions an increase in LA can result in enhanced ABM but not necessarily a corresponding increase in fruit yield.

There were significant interactions between irrigation rates and cultivars for total fruit yield in both seasons (Fig. 4S, *supplement*). Deficit irrigation significantly reduced total fruit yield in all the cultivars in 2012, and a similar trend was observed in 2011 though the reduction in yield was significant only in cv. Super Nectar. The highest yield reduction was measured in cv. Super Nectar, 38% in 2011 and 33% in 2012 in response to deficit irrigation. Similarly, cv. Mission and Da Vinci recorded a 26% and 31% reduction in TFY in 2012, and 11% and 14% in 2011, respectively.

Discussion

Melons are usually cultivated in arid to semiarid conditions during hot and dry summers and thus, are often subjected to extreme droughts and high temperatures. These weather extremes adversely affect growth and photosynthetic capacity of plants which in turn reduces their yield potentials (Kusvuran 2010, Sharma *et al.* 2014). Thus, adjustments in morphological, physiological, and biochemical traits in response to changes in the environment of a crop

Table 1. Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), intercellular CO_2 concentration (C_i), and water-use efficiency (P_N/E) of melon cultivars as influenced by irrigation rates over sampling dates (DAP) in 2011. Means in a column followed by *the same letter* are not significantly different at $P \leq 0.05$ according to the *Duncan*'s multiple range test. ET_c – crop evapotranspiration, DAP – days after planting. †, ** – significant difference at $P \leq 0.1$, and 0.01, respectively. NS – not significant at $P \leq 0.1$.

Treatment		P_N [μmol m^{-2} s^{-1}]	g_s [mmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	C_i [μmol mol^{-1}]	WUE [μmol mmol^{-1}]
Irrigation (ETc)						
	50%	18.6^{b}	0.21^{b}	6.5	153.7	3.2
	100%	21.7^{a}	0.28^{a}	7.3	169.5	3.1
Cultivar						
	Mission	21.4^{a}	0.25	7.12^{a}	287.8	3.2
	Da Vinci	19.6^{b}	0.22	6.69^{b}	287.7	3.2
	Super Nectar	19.4^{a}	0.27	6.90^{a}	286.2	3.1
Sampling date						
	53	23.8^{a}	0.50^{a}	10.1^{a}	235.9^{a}	2.4^{b}
	67	25.0^{a}	0.29^{b}	8.28^{b}	171.5^{b}	3.1^{a}
	95	18.2^{b}	0.20^{c}	6.38^{c}	162.6^{c}	3.1^{a}
	110	14.8^{c}	0.09^{d}	3.89^{d}	89.2^{d}	3.7^{a}
Interaction						
IR×DAP		NS	**	NS	NS	NS
IR×C		NS	NS	†	NS	NS
C×DAP		**	**	**	†	NS
IR×C×DAP		NS	NS	NS	NS	NS

Table 2. Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), intercellular CO_2 concentration (C_i), water-use efficiency (P_N/E), and stomatal limitations (L_s) of melon cultivars as influenced by irrigation rates over sampling dates (DAP) in 2012. Means in a column followed by *the same letter* are not significantly different at $P \leq 0.05$ according to the *Duncan*'s multiple range test. ET_c – crop evapotranspiration, DAP – days after planting. †, ** – significant difference at $P \leq 0.1$, and 0.01, respectively. NS – not significant at $P \leq 0.1$.

Treatment		P_N [μmol m^{-2} s^{-1}]	g_s [mmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	C_i [μmol mol^{-1}]	WUE [μmol mmol^{-1}]	L_s
Irrigation (ETc)							
	50%	20.1	0.75	11.9	284.4	1.84	0.23
	100%	20.5	0.77	12.2	290.1	1.79	0.21
Cultivar							
	Mission	21.1^a	0.75^{ab}	12.4^a	287.8	1.83	0.22
	Da Vinci	19.1^b	0.65^b	11.6^b	287.7	1.79	0.23
	Super Nectar	20.7^a	0.79^a	12.3^a	286.2	1.83	0.23
Sampling date							
	36	14.6^e	1.13^b	17.0^a	333.5^a	0.85^d	0.11^c
	50	24.3^b	1.44^a	13.0^b	316.2^b	1.88^b	0.13^c
	64	26.3^a	0.52^c	9.30^d	250.8^d	2.85^a	0.31^a
	81	19.5^c	0.30^c	9.74^d	248.3^d	2.02^b	0.33^a
	95	16.8^d	0.47^c	11.18^c	287.5^c	1.48^c	0.23^b
Interaction							
IR×DAP		NS	NS	NS	NS	NS	NS
IR×C		NS	NS	NS	NS	NS	NS
C×DAP		**	*	*	*	NS	**
IR×C×DAP		NS	NS	NS	*	NS	†

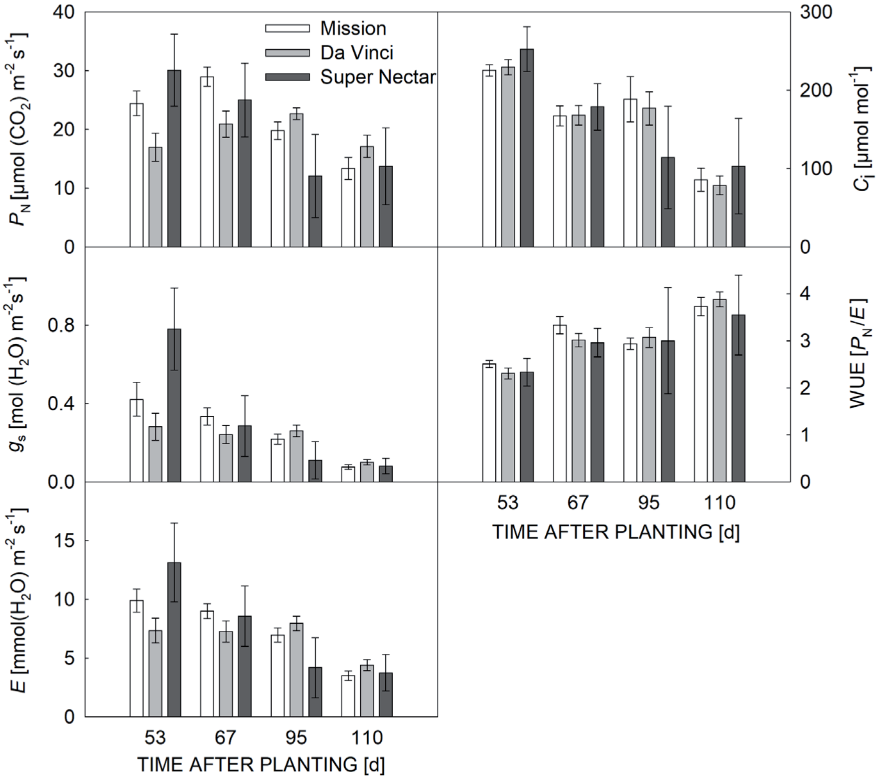

Fig. 2. Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E); intercellular CO$_2$ concentration (C_i), and water-use efficiency (WUE, P_N/E) of melon cultivars between 53 and 110 days after planting in 2011.Vertical bars represent 95% confidence intervals.

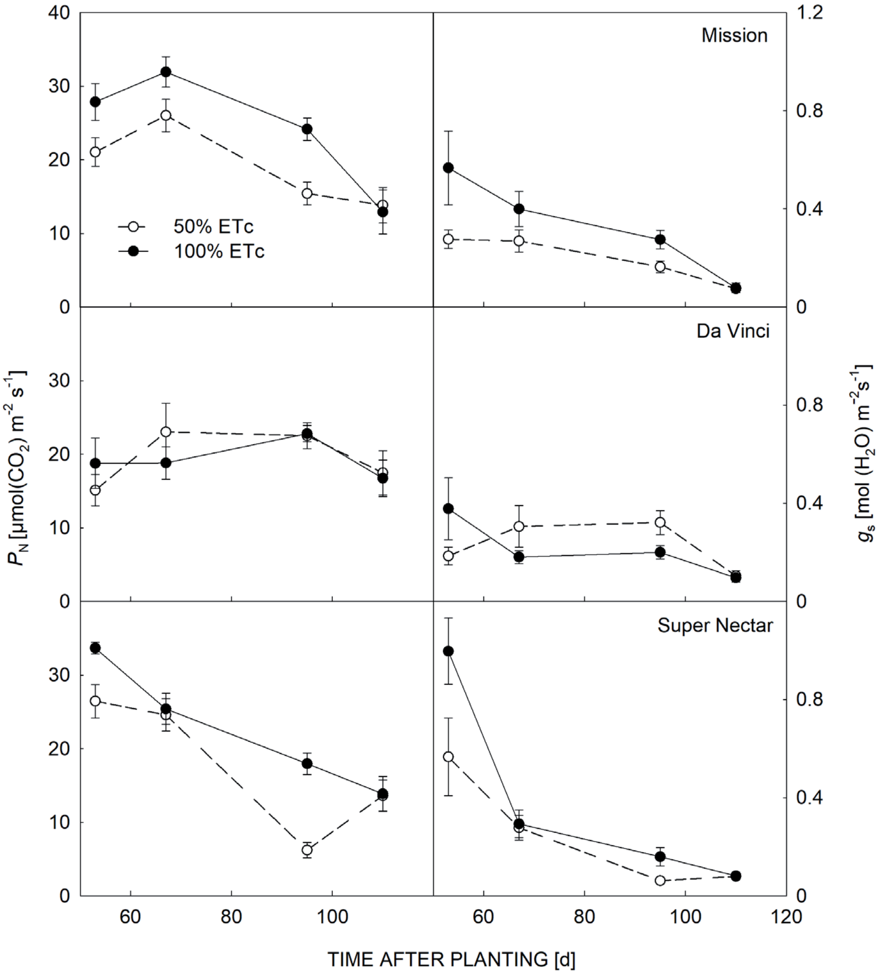

Fig. 3. Net photosynthetic rate (P_N) and stomatal conductance (g_s) of melon cultivars in response to irrigation rates over days after planting in 2011. Values are represented as mean ± SE.

or cultivar determine its adaptability to water deficit conditions. Kusvuran (2010) mentioned that the potential for drought tolerance exists in melon genotypes, which was further corroborated by a significant genotypic variability for leaf gas-exchange traits in this crop (De *et al.* 2008). Thus, further information on growth and leaf gas exchange of melon cultivars will enhance understanding of their adaptation mechanisms to water deficit conditions, which can be then applied to implement water saving strategies (*e.g.*, deficit irrigation) with minimum yield losses.

Deficit irrigation (50% ETc) reduced the leaf gas-exchange parameters in melon in both seasons, but significant differences were only recorded in 2011 (Table 1) and not in 2012 (Table 2). The year to year variation for photosynthetic traits is not unusual in drought-prone environments where stress events vary in timing, duration, and severity (Cattivelli *et al.* 2008). During this study period, the experimental site experienced the most severe drought since 1950's, with varied drought events in timing and severity in both years (Fig. 1). Overall 2011 was a drier year with a higher VPD (Fig. 1) as compared to 2012, which resulted in significant reduction in P_N and g_s in 2011. Janoudi *et al.* (1993) also reported that increased VPD induced stomatal closure in cucumber (*Cucumis sativus* L.) plants, which limited CO_2 availability and ultimately resulted in reduced photosynthesis.

Plants under deficit irrigation had a decrease in P_N and g_s (Table 1), suggesting that under water stress stomatal closure prevented water loss at the expense of CO_2 for photosynthesis (Agehara and Leskovar 2012). Even though with deficit irrigation, WUE may increase (Sun *et al.* 2013) but it can be at the expense of reduced leaf gas exchange. The results of this study did not show significant improvement in WUE. However, WUE had a negative correlation with g_s under 50% ETc in comparison to 100% ETc (–0.390 *vs.* –0.149) to (–0.621 *vs.* –0.180) (Table 1S), indicating that decrease in g_s increased WUE under water-deficit conditions (Figs. 2, 4; Table 1S).

Leaf gas exchange of melons varied with growth stages and climatic conditions. P_N increased significantly up to the fruit development stage (67 DAP in 2011 and 64 DAP in 2012). Further, a decrease in stomatal conductance (42–63%) at this stage resulted in a significant increase in WUE (Tables 1, 2). In *Malus* spp., Sun *et al.* (2013) also reported a negative correlation between WUE and g_s. During fruit ripening (95 DAP in 2011), the combination of the cumulative water deficit and high VPD (Fig. 1), resulted in a further decrease in g_s, causing a significant reduction in $P_{N,}$ which can be attributed to a reduced C_i. Janoudi *et al.* (1993) also reported that CO_2 limitation reduced P_N in cucumber plants.

Under 50% ETc, g_s, and P_N decreased in cv. Mission and Super Nectar while these were maintained in cv. Da Vinci (Fig. 3). The later cultivar was also more stable for all gas-exchange traits over the sampling dates as compared to cv. Mission and Super Nectar (Figs. 2, 4). Thus, lower g_s (Fig. 3, Table 1) and the ability to sustain P_N under 50% ETc in cv. Da Vinci indicates the potential of this cultivar for physiological adaptation to water deficit conditions. These results together with the positive association of P_N

Table 3. Leaf area per plant (m^2; LA), total aboveground biomass (g of dry mass; ABM), specific leaf area [$cm^2\ g^{-1}$(dry mass)]; SLA), number of leaves per plant (LN) of melon cultivars as influenced by irrigation rates at 37 and 68 DAP in 2012. Means in a column followed by *the same letter* are not significantly different at $P \leq 0.05$ according to the *Duncan*'s multiple range test. ET_c – crop evapotranspiration, DAP – days after planting.

		37 DAP*			68 DAP			
Main factor	Subfactor	LA	ABM	SLA	LN	LA	ABM	SLA
Irrigation rate (IR, ET_c)								
	50%	0.40^a	26.4^a	235.7^a	260.5^b	1.92^b	539.7^b	117.0^b
	100%	0.38^a	27.4^a	220.5^a	455.8^a	3.82^a	853.6^a	136.3^a
Cultivar (CV)								
	Mission	0.38^a	26.3^a	230.3^a	372.0^a	2.74^a	625.9^a	124.8^b
	Da Vinci	0.41^a	28.2^a	218.5^a	336.8^a	2.97^a	710.8^a	124.4^b
	Super Nectar	0.37^a	25.8^a	238.5^a	365.8^a	2.91^a	753.4^a	130.8^a
Interaction (IR × CV)†								
Mission	50%	0.37^a	24.5^a	243.0^a	241.0^b	1.66^b	434.0^b	114.7^b
	100%	0.39^a	28.1^a	217.7^a	503.0^a	3.82^a	817.7^a	134.9^a
Da Vinci	50%	0.42^a	26.8^a	214.5^a	210.0^b	1.61^b	479.9^b	110.8^b
	100%	0.41^a	29.6^a	222.5^a	463.5^a	4.32^a	941.6^a	137.9^a
Super Nectar	50%	0.40^a	27.8^a	249.6^a	330.5^a	2.50^b	705.3^a	125.3^b
	100%	0.33^a	23.0^a	221.8^a	401.0^a	3.32^a	801.6^a	136.2^a

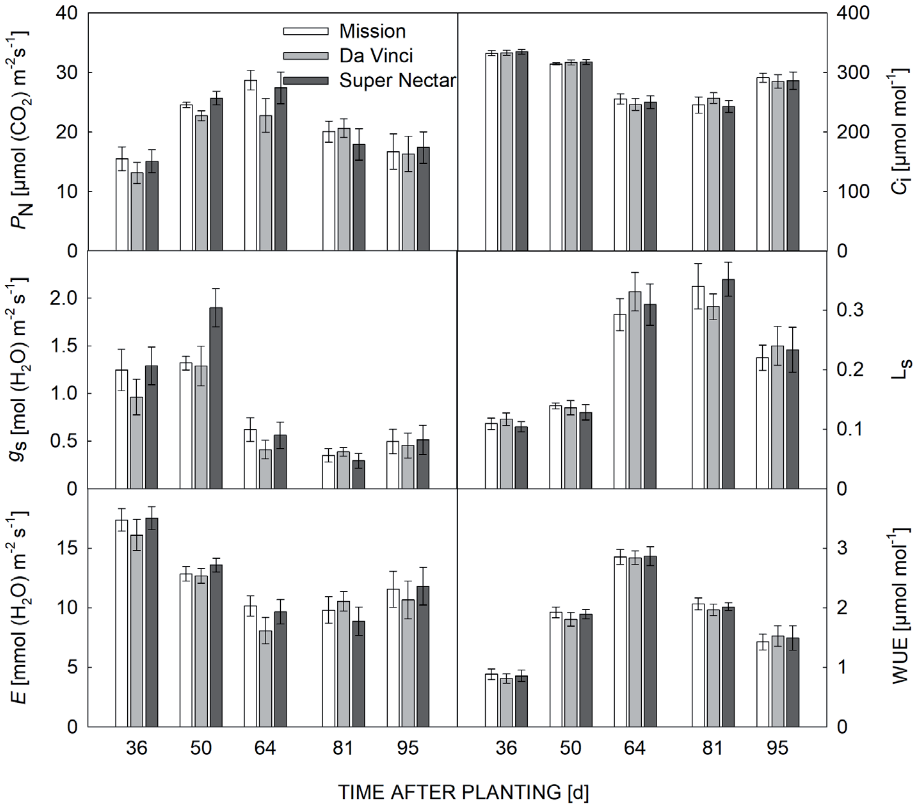

Fig. 4. Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), intercellular CO$_2$ concentration (C_i), nonstomatal limitation value (L$_s$), and water-use efficiency (WUE, P_N/E) of melon cultivars over days after planting in 2012. Vertical bars represent 95% confidence intervals.

with a total fruit yield, though not statistically significant, (Table 1S) also indicates the possibility of using the leaf photosynthetic capacity as a selection criteria for drought tolerance in melons (Ashraf and Harris 2013). Conversely, the cultivar Super Nectar had a higher g_s during initial growth stages (53 DAP in 2011 and 50 DAP in 2012) (Figs. 2, 3, 4), indicating the possibility for honeydew melons to have higher transpiration requirements as compared to Tuscan and muskmelon types.

The insignificant differences between irrigation treatments for the maximum photochemical efficiency of PSII (F_v/F_m) revealed that the photochemical apparatus was not damaged by the intensity of the water deficit imposed through the application of 50% ETc, indicating that PSII in melon was stable under water-deficit conditions. In cotton, de Brito *et al.* (2011) also reported no differences for quantum yield between stressed and watered conditions, despite genotypic differences for other physiological parameters, for example membrane leakage and carbon isotope composition. These results suggested that quantum yield (F_v/F_m) may not be a useful trait in differentiating melon cultivars for their responses to water deficit.

No significant interactions between irrigation rate and cultivars were observed for RWC and leaf water potential (Ψ_l) (data not shown). However, deficit irrigation caused a numerical decrease (<0.3 MPa) in Ψ_l in cv. Mission, and Super Nectar, while it was maintained in cv. Da Vinci. According to Hsiao (1973), water stress can be termed as mild, moderate, and severe if Ψ_l is lowered by less than 0.8, 1.2–1.5, and >1.5 MPa, respectively, under water-deficit conditions. Thus, these results indicated cv. Mission and Super Nectar experienced a mild level of water stress. The maintenance of Ψ_l in Da Vinci can be attributed to lower g_s and E in this cultivar, while a less reduction in Ψ_l in cv. Mission can be attributed to the enhanced root length intensity (mm cm^{-2}) under deficit irrigation (Sharma *et al.* 2014), which might have increased water uptake potential in this cultivar (Table 2, Fig. 3).

Leaf area expansion is more sensitive to water stress than photosynthesis and transpiration (Subbarao *et al.* 1995). Under slow and gradual water deficit development, plants adjust their transpiring surface by reducing leaf growth to balance the transpiration demand with reduced water uptake (Hsiao 1982). Crop transpiration is reduced linearly with a reduction in leaf area under soil water deficit conditions (Ritchie 1985). Therefore, adjustment and maintenance of optimum leaf area under water deficit conditions is the major plant process in determining crop productivity (Subbarao *et al.* 1995). In our study, although the photosynthetic traits were not affected by deficit irrigation in 2012, a significant reduction in total leaf area (50%), leaf number (43%), and SLA (14%) was recorded under deficit irrigation as compared to 100% ETc (Table 3). Under water deficit, reduction in leaf number and leaf area have also been reported in strawberry (Razavi *et al.* 2008), and SLA in *Amaranthus* spp. (Liu and Stützel 2004).

The ability of melons to adjust leaf area in response to deficit irrigation appears to be cultivar dependent as cv. Mission, Da Vinci, and Super Nectar decreased LA by 50, 50, and 20% and LN by 60, 60, and 20%, respectively. Genotypic differences for leaf area expansion under water stress have also been reported in *Amaranthus* spp. (Liu and Stützel 2004) and groundnut (Muchow 1985, Subbarao *et* *al.* 1995). However, SLA reduction under 50% ETc was 10% more in Da Vinci than in Mission and Super Nectar, indicating a decreased transpiring area and an increased leaf thickness in Da Vinci. Further, Liu and Stützel (2004) also reported that *Amaranthus* genotypes differed in their water conserving strategies, cv. WS80-192 exhibited reduction in SLA to control water loss. They also argued that drought tolerance is determined by a conservative balance between the water transpiring and absorbing plant organs. Thus, plants try to control water loss by decreasing leaf area. Further, the thicker leaves have higher Chl density and exhibit more photosynthetic capacity than thinner leaves. Thus, under water deficit, the maintenance of higher P_N in Da Vinci could be attributed to greater reduction in SLA in comparison to Mission and Super Nectar.

Despite the benefit of water deficit tolerance for survival, it can have an adverse impact on yield potential. Yield responses to deficit irrigation varied among cultivars. In both years, cv. Super Nectar recorded the highest yield reductions in response to deficit irrigation, while Mission and Da Vinci had significant reductions in 2012 which can be attributed to the significant drought experienced during the fruit setting stage in 2012. The drought induced water deficit caused a reduction in leaf area and there by total crop photosynthesis decreasing crop productivity. Richards (2000) reviewed that the maintenance of total crop photosynthesis is more important than the increase in the rate of photosynthesis per unit leaf area. Reduction in leaf area and fruit yield has also been reported in strawberry under field conditions during severe deficit irrigation (Liu *et al.* 2007).

Generally, honeydew melon (cv. Super Nectar) takes longer time from planting to fruit ripening as compared to cantaloupe (cv. Mission) and Tuscan type melons (cv. Da Vinci). Deficit irrigation caused the lowest aboveground biomass (ABM) reduction in cv. Super Nectar (10%) than that in cv. Mission (50%) and Da Vinci (50%) (Table 3). Conversely, the highest reduction in total yield was recorded in Super Nectar (Fig. 4S). These contradictory results can be attributed to late maturity and longer cropping season of cv. Super Nectar, which was exposed to drought for longer period before the final harvest. This was also evident from the significant reduction in root length density in this cultivar at final harvest stage (Sharma *et al.* 2014), which might have resulted in an imbalance between water losing and absorbing surfaces. Similarly, Cattivelli *et al.* (2008) reviewed that earliness is an effective breeding strategy for improving yield in environments where the crops are exposed to terminal droughts.

Conclusion: The total fruit yield and biomass production of the three melon cultivars investigated in the present study were positively correlated with leaf gas-exchange parameters, leaf area, leaf number, and specific leaf area under water deficit conditions. Thus it appears that adaptation responses to water-deficit conditions in melons are related to the maintenance of gas-exchange capacity along with adequate leaf area and thus, to the total crop photosynthesis. The early maturing cultivars Mission and Da Vinci escaped the cumulative stress developed through gradual water deficit over the growing season and also exhibited water loss limiting adaptations such as a decrease in leaf area and leaf gas exchange adaptations, respectively; however, cv. Super Nectar due to late maturity and longer duration had higher yield penalties. Thus, early maturing and short duration melon cultivars that have the capacity to maintain leaf area development under water deficit conditions, can better sustain productivity in drought prone semiarid growing regions.

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