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Alternate furrow irrigation of four fresh-market tomato cultivars under semi-arid condition of Ethiopia – Part II: Physiological response

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Abstract

Understanding the variation in physiological response to deficit irrigation together with better knowledge on physiological characteristics of different genotypes that contribute to drought adaptation mechanisms would be helpful in transferring different irrigation technologies to farmers. A field experiment was carried to investigate the physiological response of four tomato cultivars (*Fetan*, *Chali*, *Cochoro* and *ARP Tomato d2*) to moderate water deficit induced by alternate furrow irrigation (AFI) and deficit irrigation (DI) under semi-arid condition of Ethiopia during 2013 and 2014. The study also aimed at identifying physiological attributes to the fruit yield of tomato under different deficit irrigation techniques. A factorial combination of irrigation treatments and cultivar were arranged in a complete randomized design with three replicates. Results showed that stomatal conductance (g_s) was significantly reduced while photosynthetic performance measured as chlorophyll fluorescence (Fv'/ Fm'), relative water content (RWC) and leaf ash content remained unaffected under deficit irrigations. Significant differences among cultivars were found for water use efficiency (WUE), g_s, chlorophyll content (Chl_{SPAD}), normal difference vegetation index (NDVI), leaf ash content and fruit growth rate. However, cultivar differences in WUE were more accounted for by the regulation of g_s, therefore, g_s could be useful for breeders for screening large numbers of genotypes with higher WUE under deficit irrigation condition. The study result also demonstrated that cultivar with traits that contribute to achieve higher yields under deficit irrigation strategies has the potential to increase WUE.

Keywords: alternate furrow irrigation, chlorophyll content, fruit growth rate, relative leaf water content, stomatal conductance, tomato

1 Introduction

Scarcity of freshwater and recurrent drought is one of the major bottlenecks that limit agricultural production in most arid and semi-arid regions of Ethiopia (Amede, 2015). Though Ethiopia has large water reserves that could be used for a wide range of irrigation development, statistical figures show that from estimated 5.3 Mio. ha irrigable land, less than 5 % is currently equipped for irrigation (Awulachew *et al.*, 2010).

It was shown that out of four of the most widespread tomato cultivars in Ethiopia, two, namely *Cochoro* and *Fetan*, performed well under alternate furrow irrigation (AFI), while *Chali* and *ARP Tomato d2* performed relatively better under full irrigation (FI). This data is an important baseline both for breeders to im-

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prove drought resistance in tomatoes and also for producers to choose the optimal variety dependent on water availability. However, it is also of crucial importance to understand the underlying physiological functions of tomato subjected to AFI. In general, it is assumed that in AFI, as in as in partial root-zone drying irrigation (PRD), deliberately irrigates only part of the root-zone, while the remainder is allowed to dry and alternating subsequently these wet and dry zones in the next irrigation events, an increase of WUE comes through tight regulation of stomatal aperture as plants open their stomata for CO_2 uptake and at the same time lose water (Kang & Zhang, 2004). Consequently, biomass production may be reduced as gas exchange is restricted due to stomatal closure causing water savings. One of the options for the potential adaptation to such a situation is the use of genotypes with higher WUE.

Different response of cultivars to deficit irrigation treatments has been reported in tomatoes (Mahadeen *et al.*, 2011; Patanè *et al.*, 2014), which have been described in terms of total yield and WUE. The study carried out by Patanè *et al.* (2014) indicated that the cv. 'Season' exhibited nearly twice greater efficiency in the use of total water available compared to 'Solerosso' with an equal amount of water savings. Barrios-Masias & Jackson (2016) also reported that 'CXD255' had a 10 % greater WUE than 'AB2'. The differences among cultivars may be related to water economy through regulating their stomata aperture and maintaining their leaf water status (Riccardi *et al.*, 2016). Understanding physiological responses to irrigation associated within different climate and soil conditions is helpful in transferring different irrigation technologies to farmers and optimize regional water management (Morison *et al.*, 2008). Studies have shown that stomatal conductance was reduced while the photosynthetic rate was not greatly impaired under PRD treated plants (Campos *et al.*, 2009; Yang *et al.*, 2012). Substantial reduction in stomatal conductance coupled with little effect on photosynthesis, including photosystem efficiency (PSII), could lead to improved crop WUE (Dry & Loveys, 1998). Nevertheless, there is no evidence that a characteristic decrease of stomatal conductance under mild stress condition as deliberately induced in deficit irrigation is associated with a characteristic decrease in Fv/Fm values.

Water deficit also often results in premature induction of leaf senescence and consequently leads to inefficient conversion of resources and finally to yield losses (Ramírez *et al.*, 2014). Leaf chlorophyll concentration and a variation in normalized difference vegetation index (NDVI) are used as integrative method to assess the canopy senescence rates (Rolando *et al.*, 2015). Maintenance of green leaf (a low rate of leaf senescence) under low water availability is a desirable trait because it may reflect the photosynthetic activity and capacity for light harvesting during the fruit development and ripening period leading to larger fruit size.

The final fruit size of horticultural crops determines the quality, profitability and customers' acceptance (Wubs *et al.*, 2012). Studies have shown that deficit irrigation strategies can save substantial irrigation water but caused small fruit size (Favati *et al.*, 2009; Patanè & Cosentino, 2010). Water deficit during the linear fruit growth can often induce a reduction in total final yield due to smaller fruit sizes (Savić *et al.*, 2008). Different genotypes may have different mechanisms to cope with water deficit induced by deliberate deficit irrigations; adoption of drought tolerant genotypes will sustain crop production under low water availability. Therefore, the study was conducted to identify cultivars to be used under water shortage conditions employing different deficit irrigation strategies. The study was also carried out to investigate physiological responses and variation in fruit growth patterns of different cultivars under deficit irrigation techniques. The study will facilitate an evaluation of water saving deficit irrigation strategies with neither compromising fruit yield nor fruit sizes. This second part of the study presents the physiological response of tomato, which allows additional insight to explain the agronomic responses presented in part I.

2 Materials and methods

2.1 Location and experimental setup

The experiment at Melkassa Agricultural Research Center was setup as a randomized complete block design comprising a factorial combination of four cultivars (*Fetan*, *Chali*, *Cochoro* and *ARP Tomato d2*) and three irrigation treatments with three replications. Irrigation treatments were (1) full irrigation, FI (crop water requirements applied uniformly to all furrows), (2) deficit irrigation, DI (50 % of crop water requirement applied uniformly to all furrows) and (3) alternate furrow irrigation, AFI (50 % of crop water requirement applied to every other furrow and alternating the furrows at each irrigation event). Total crop water requirement was estimated based on soil-water deficit as the difference between measured volumetric soil water content (θAC) and soil water content at field capacity (θFC) multiplied by plot area and rooting depth of 0.60 m. A detailed description of the location, varieties used and agronomic details can be found in part I of the study.

2.2 Plant growth parameters

Data on fruit growth was collected from three tagged plants per plot. Three fully opened flowers on the third truss were tagged for measuring the fruit diameter (FD) at a six days interval using a digital calliper (Harbor Freight Tools, USA) starting from 60 days after transplanting (DAT). Development of standardized fruit diameter (SFD) was calculated between 60 and 102 DAT as:

$$SFD(t) = \frac{FD(t) - FD60}{FD102 - FD60}$$

Fruit-growth duration (FGD) was taken as the time between anthesis and the final harvest. Absolute fruit growth rate (AGR) was also quantified by dividing the fruit diameter at harvest by FGD. Plant height was measured before commencement of deficit irrigation (39 DAT) and at harvest. Stem diameter (girth) of the main stem 5 cm above soil surface was measured using a calliper at ten day intervals starting at 60 DAT.

2.3 Relative leaf water content

Relative leaf water content (RWC) was measured at two occasions from the fully expanded leaves from each plot at 45 and 65 DAT in 2013 and 55 and 65 DAT in 2014. Immediately after cutting at the base of lamina, leaves were sealed within a plastic bag and transferred to the laboratory. Fresh weight (FW) was measured after excision and the full turgid weight (TW) after hydration of the leaves by placing them in a plastic flask containing 100 ml distilled water for 24 h at room temperature (about 21 °C). Dry weight (DW) was measured after oven drying at 70 °C for 72 hrs.

$$RWC = \frac{FW - DW}{TW - DW} * 100$$

2.4 Stomatal conductance (g_s) and chlorophyll fluorescence

Stomatal conductance (g_s) was measured on five fully expanded leaves per plot on the abaxial leaf surface with a steady state diffusion porometer SC-1 (Decagon, USA) on five occasions at ten days interval from 45 through 85 DAT in 2013 and on four occasions in 2014. The measurements were conducted from 12:00 to 14:00. Chlorophyll fluorescence emission kinetics was also measured on three occasions in 2013 and 2014 using a portable fluorometer FluorPen FP 100 (Photon Systems Instruments, Czech Republic) from four most recently fully expanded leaves per plot. Continuous fluorescence yield in non-actinic light adapted initial fluorescence (Ft) and Photosystem II quantum yield efficiency (Fv’/ Fm’) were used to assess the photosynthetic performance of the four tomato cultivars under different irrigation treatments.

2.5 Chlorophyll contents (Chl_{SPAD}) and normalized difference vegetation index (NDVI)

Chlorophyll content ($\mathrm{Chl}_{\mathrm{SPAD}}$) was measured with a portable chlorophyll meter SPAD-502 (Konica Minolta, Japan). The mean values of ten readings per plot were used for analysis. Measurement was done once at fruit development stage (65 DAT) in 2013 and six readings of $\mathrm{Chl}_{\mathrm{SPAD}}$ were used to assess stay-greenness (senescence rate) at a five days interval starting from 90 through 110 DAT in 2014. Normalized difference vegetation index (NDVI) used to assess the maintenance of green foliage growth under deficit irrigation treatments was also undertaken using a commercial GreenSeeker® portable spectroradiometer (Trimble Navigation, USA) in 2014. Means of five readings of NDVI from the central four rows of each plot at distance of one meter above the canopy were used for analysis. NDVI and SPAD measurements were carried out on the same day.

2.6 Leaf ash content

Ash content, expressed on dry weight basis (%), was determined from leaves after complete combustion of the samples. Samples were collected from each plot, oven-dried for 48 h at 72 °C and grounded to a fine powder. Approximately 3.0 g of the samples were incinerated at 575 °C for 16 h in an electric muffle furnace.

2.7 Data analysis

Analysis of variance (ANOVA) was applied to examine the effects of cultivars and irrigation treatments on different physiological variables using SAS Proc MIXED procedure (SAS 8.02 Cary, NC, USA). Physiological attributes that were measured on two or more occasions during the growing season were also subjected to ANOVA with repeated measurement over time using SAS Proc GLM procedure. Means were compared by LSD ($P < 0.05$). Linear functions were employed and the slopes were used to compare the temporal trends of each physiological attribute among irrigation treatments. Each pair of slopes was compared using Student‘s t-test. Pearson correlation index was also employed to define the relative predictors of physiological attributes to marketable fruit yield and WUE.

3 Results

3.1 Fruit growth patterns

The dynamics of fruit diameter increase of four cultivars were similar under FI (Fig. 1). However, differences in relative growth pattern among cultivars under deficit irrigation treatments were visible during the time of rapid fruit development (66–84 DAT). Higher relative fruit growth was observed in *Fetan* and *ARP Tomato d2* whereas it was reduced in *Chali* and *Cochoro* under DI and AFI. On the other hand, irrigation treatments did not significantly affect FGD (Table 1). Nevertheless, cultivars differ in both FGD and AGR. The highest AGR recorded in *Fetan* followed by *ARP Tomato d2* whereas the lowest was recorded in *Chali* (Table 1). Thus *Fetan* and *ARP Tomato d2* maintained relatively higher fruit size under deficit irrigation. *Chali* had shorter FGD and lower fruit size. *Cochoro* maintained a prolonged FGD and relatively higher AGR, resulting in larger fruit under DI and AFI.

3.2 Relative leaf water content (RWC)

RWC was not significantly affected by irrigation treatments, time factors and treatment by time interaction (Table 2 and 3), but cultivars articulated different responses of leaf tissue water status to different irrigation treatments (Table 2 and 3). Only *Chali* exposed lower leaf RWC while no distinct variation was observed among the other three cultivars. RWC was reduced in *Chali* under DI and AFI by 7.4 % and 3.7 % relative to FI, respectively.

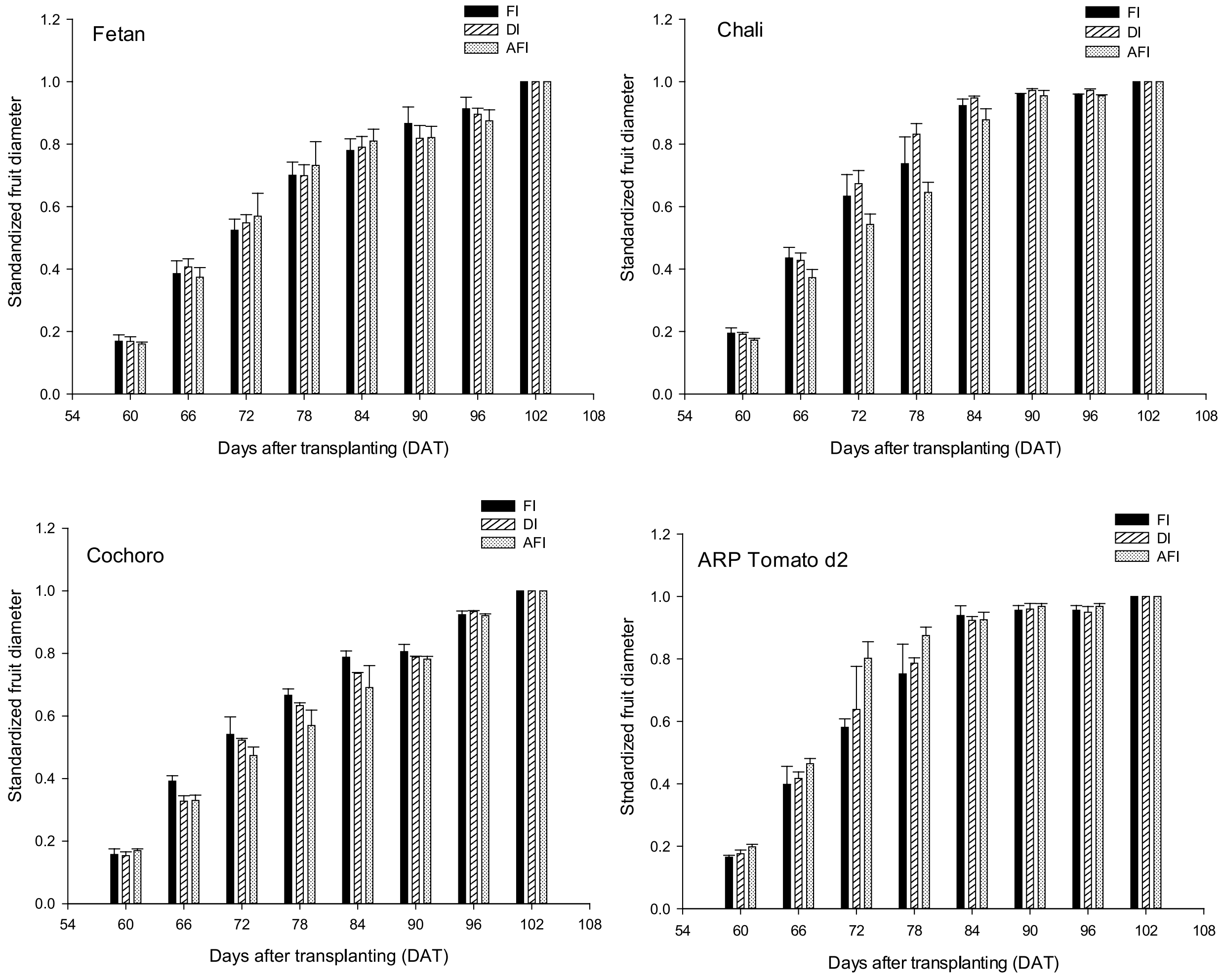

Fig. 1: *Standardized fruit diameter (SFD) between 60 and 102 days after transplanting (DAT) of four tomato cultivars under full irrigation (FI), deficit irrigation (DI) and alternate furrow irrigation (AFI) in 2014.*

Table 1: *Fruit growth duration (FGD) and absolute fruit growth rate (AGR) of four cultivars under full irrigation (FI), regulated deficit irrigation (DI) and alternate furrow irrigation (AFI) in 2014.*

Cultivar	*Fruit growth duration* (days after anthesis)				*Absolute fruit growth rate* (mm day^{-1})			
	FI	*DI*	*AFI*	*Mean*	*FI*	*DI*	*AFI*	*Mean*
Fetan	$^{A}46^{a}$	$^{A}47^{a}$	$^{B}48^{a}$	47	$^{A}1.24^{b}$	$^{AB}1.14^{b}$	$^{A}1.45^{a}$	1.28
Chali	$^{B}39^{a}$	$^{B}38^{a}$	$^{C}38^{a}$	39	$^{A}1.14^{a}$	$^{B}1.04^{a}$	$^{C}1.17^{a}$	1.12
Cochoro	$^{A}50^{a}$	$^{A}51^{a}$	$^{A}50^{a}$	50	$^{A}1.18^{a}$	$^{A}1.19^{a}$	$^{C}1.21^{a}$	1.19
ARP Tomato d2	$^{AB}42^{a}$	$^{A}43^{a}$	$^{B}48^{a}$	48	$^{A}1.23^{a}$	$^{A}1.23^{a}$	$^{B}1.32^{a}$	1.26

Means within column preceded by different capital letters or means within rows followed by different lower-case letters indicate significant differences among cultivars and irrigation treatments, respectively ($P < 0.05$).

Table 2: *Analysis of variance (ANOVA) showing F-value of relative leaf water content (RWC), stomatal conductance (g_s), chlorophyll content (Chl_{SPAD}), initial fluorescence (Ft) and quantum yield efficiency (Fv'/Fm') among four cultivars and three irrigation treatments in 2013.*

Physiological Parameter	*Cultivar*	*Irrigation treatments (IT)*	*Time*	*IT*Time*	*Mean Value*		
					FI	*DI*	*AFI*
RWC	*Fetan*	0.04 ^{NS}	1.66 ^{NS}	7.76 ***	$^{A}0.89^{a}$	$^{A}0.90^{a}$	$^{A}0.89^{a}$
	Chali	2.17 ^{NS}	1.57 ^{NS}	0.41 ^{NS}	$^{B}0.75^{a}$	$^{B}0.78^{a}$	$^{B}0.80^{a}$
	Cochoro	0.94 ^{NS}	2.94 ^{NS}	0.55 ^{NS}	$^{A}0.88^{a}$	$^{A}0.87^{a}$	$^{B}0.82^{a}$
	ARP Tomato d2	3.22 ^{NS}	0.16 ^{NS}	0.26 ^{NS}	$^{A}0.89^{a}$	$^{A}0.87^{a}$	$^{A}0.93^{a}$
g_s	*Fetan*	5.89 **	21.83 ***	1.06 ^{NS}	$^{B}136.9^{a}$	$^{A}125.9^{b}$	$^{B}112.3^{b}$
	Chali	23.4 ***	42.39 ***	2.85 *	$^{A}164.0^{a}$	$^{A}127.9^{b}$	$^{A}125.9^{b}$
	Cochoro	24.27 ***	51.61 ***	1.66 ^{NS}	$^{B}136.6^{a}$	$^{B}114.8^{b}$	$^{B}109.6^{b}$
	ARP Tomato d2	5.91 *	49.72 ***	1.88 ^{NS}	$^{B}139.2^{a}$	$^{B}118.5^{b}$	$^{A}124.5^{b}$
Chl_{SPAD}†	*Fetan*	5.13 *	–	–	$^{A}44.1^{b}$	$^{A}42.9^{b}$	$^{AB}48.4^{a}$
	Chali	8.40 **	–	–	$^{A}42.3^{b}$	$^{A}44.5^{b}$	$^{AB}48.3^{a}$
	Cochoro	104.86 ***	–	–	$^{A}41.9^{b}$	$^{AB}41.5^{b}$	$^{A}50.0^{a}$
	ARP Tomato d2	28.98 ***	–	–	$^{B}38.1^{b}$	$^{B}39.1^{b}$	$^{B}46.0^{a}$
Ft	*Fetan*	1.19 ^{NS}	21.99 ***	0.89 ^{NS}	$^{A}247.5^{a}$	$^{B}258.0^{a}$	$^{B}259.8^{a}$
	Chali	3.78 *	5.19 *	1.26 ^{NS}	$^{A}261.7^{b}$	$^{A}286.4^{ab}$	$^{A}300.4^{a}$
	Cochoro	3.75 *	2.86 ^{NS}	1.74 ^{NS}	$^{A}259.8^{b}$	$^{A}277.5^{a}$	$^{B}269.7^{ab}$
	ARP Tomato d2	1.21 ^{NS}	32.05 ***	4.09 **	$^{A}259.8^{a}$	$^{B}256.7^{a}$	$^{B}274.2^{a}$
Fv'/Fm'	*Fetan*	3.42 ^{NS}	16.60 ***	2.45 ^{NS}	$^{A}0.57^{a}$	$^{A}0.56^{a}$	$^{A}0.54^{a}$
	Chali	0.10 ^{NS}	4.19 *	0.80 ^{NS}	$^{A}0.56^{a}$	$^{A}0.56^{a}$	$^{A}0.56^{a}$
	Cochoro	2.66 ^{NS}	6.18 **	2.14 ^{NS}	$^{A}0.57^{a}$	$^{A}0.56^{a}$	$^{A}0.54^{a}$
	ARP Tomato d2	0.54 ^{NS}	8.20 ***	0.30 ^{NS}	$^{A}0.56^{a}$	$^{A}0.55^{a}$	$^{A}0.56^{a}$
Leaf ash content†	*Fetan*	1.36 ^{NS}	–	–	$^{A}0.30^{a}$	$^{A}0.30^{a}$	$^{A}0.31^{a}$
	Chali	1.26 ^{NS}	–	–	$^{A}0.31^{a}$	$^{B}0.29^{a}$	$^{A}0.30^{a}$
	Cochoro	9.76 **	–	–	$^{A}0.30^{b}$	$^{A}0.32^{a}$	$^{B}0.28^{c}$
	ARP Tomato d2	9.96 *	–	–	$^{A}0.31^{a}$	$^{B}0.29^{b}$	$^{AB}0.29^{b}$

(NS) non significant, *, **, *** significantly different at 5 %, 1 %, 0.1 % probability level, respectively. Means within column preceded by different capital letters or means within rows followed by different lower-case letters indicate significant differences among cultivars and irrigation treatments, respectively ($P < 0.05$). † sampled once during the experimental year.

Table 3: *Analysis of variance (ANOVA) showing F-value of relative leaf water content (RWC), stomatal conductance (g_s), chlorophyll content (Chl_{SPAD}), normalized difference vegetation index (NDVI), initial fluorescence (Ft) and quantum yield efficiency (Fv'/Fm') among four cultivars and three irrigation treatments in 2014.*

Physiological Parameter	*Cultivar*	*Irrigation treatments (IT)*	*Time*	*IT*Time*	*Mean Value*		
					FI	*DI*	*AFI*
RWC	*Fetan*	0.04 ^{NS}	0.78 ^{NS}	0.17 ^{NS}	^{A} 0.89 ^{a}	^{A} 0.90 ^{a}	^{A} 0.90 ^{a}
	Chali	2.79 ^{NS}	0.02 ^{NS}	0.32 ^{NS}	^{B} 0.81 ^{a}	^{B} 0.75 ^{a}	^{B} 0.78 ^{a}
	Cochoro	0.08 ^{NS}	1.08 ^{NS}	1.05 ^{NS}	^{A} 0.89 ^{a}	^{A} 0.91 ^{a}	^{A} 0.92 ^{a}
	ARP Tomato d2	1.43 ^{NS}	2.30 ^{NS}	2.36 ^{NS}	^{AB} 0.86 ^{a}	^{A} 0.92 ^{a}	^{A} 0.92 ^{a}
g_s	*Fetan*	64.9 **	98.54 ***	8.79 ***	^{A} 196.1 ^{a}	^{B} 137.8 ^{b}	^{B} 115.3 ^{c}
	Chali	4251.5 ***	61.45 ***	2.92 ^{NS}	^{A} 199.2 ^{a}	^{A} 160.8 ^{b}	^{A} 134.7 ^{c}
	Cochoro	110.7 *	67.37 ***	5.25 ^{NS}	^{B} 158.5 ^{a}	^{C} 123.4 ^{b}	^{A} 130.6 ^{b}
	ARP Tomato d2	188.1 ***	135.66 ***	8.15 ***	^{A} 192.8 ^{a}	^{C} 126.9 ^{b}	^{A} 138.3 ^{b}
Chl_{SPAD}	*Fetan*	3.52 ^{NS}	57.4 ***	1.15 ^{NS}	^{A} 43.0 ^{a}	^{B} 42.3 ^{a}	^{B} 42.9 ^{a}
	Chali	17.1 ***	76.9 ***	1.13 ^{NS}	^{B} 33.5 ^{b}	^{C} 31.4 ^{b}	^{B} 39.7 ^{a}
	Cochoro	12.0 ***	64.3 ***	5.14 ***	^{A} 42.4 ^{b}	^{A} 47.7 ^{a}	^{A} 46.5 ^{a}
	ARP Tomato d2	7.15 ***	127.7 ***	2.37 *	^{A} 41.5 ^{a}	^{B} C35.6 ^{b}	^{B} 37.2 ^{b}
NDVI	*Fetan*	0.11 ^{NS}	0.24 ^{NS}	51.3 ***	^{B} 0.46 ^{a}	^{B} 0.45 ^{a}	^{A} 0.45 ^{a}
	Chali	1.79 ^{NS}	0.43 ^{NS}	82.1 ***	^{B} 0.43 ^{a}	^{C} 0.41 ^{a}	^{B} 0.40 ^{a}
	Cochoro	3.15 ^{NS}	2.63 ^{NS}	68.9 ***	^{A} 0.51 ^{a}	^{A} 0.53 ^{a}	^{A} 0.47 ^{a}
	ARP Tomato d2	2.92 ^{NS}	2.03 ^{NS}	128.9 ***	^{B} 0.48 ^{a}	^{BC} 0.43 ^{a}	^{A} 0.45 ^{a}
Ft	*Fetan*	0.80 ^{NS}	43.85 ***	0.80	^{C} 259.8 ^{a}	^{A} 264.1 ^{a}	^{B} 260.4 ^{a}
	Chali	2.07 ^{NS}	63.49 ***	10.80 ***	^{B} 270.8 ^{a}	^{A} 264.8 ^{a}	^{B} 262.4 ^{a}
	Cochoro	22.10 ***	25.19 ***	0.63 ^{NS}	^{A} 295.6 ^{a}	^{A} 271.9 ^{b}	^{A} 283.3 ^{ab}
	ARP Tomato d2	16.55 ***	82.05 ***	3.65 **	^{D} 247.1 ^{b}	^{A} 262.9 ^{a}	^{A} 275.6 ^{a}
Fv'/Fm'	*Fetan*	1.03 ^{NS}	50.96 ***	11.87 ***	^{A} 0.55 ^{a}	^{A} 0.57 ^{a}	^{B} 0.56 ^{a}
	Chali	0.10 ^{NS}	45.26 ***	3.73 **	^{A} 0.57 ^{a}	^{A} 0.55 ^{a}	^{B} 0.55 ^{a}
	Cochoro	1.15 ^{NS}	6.78 **	3.91 ^{NS}	^{A} 0.57 ^{a}	^{A} 0.57 ^{a}	^{A} 0.58 ^{a}
	ARP Tomato d2	0.04 ^{NS}	38.04 ***	4.29 ***	^{A} 0.56 ^{a}	^{A} 0.56 ^{a}	^{B} 0.56 ^{a}
Leaf ash content †	*Fetan*	14.81 **	–	–	^{A} 0.21 ^{b}	^{A} 0.27 ^{a}	^{A} 0.23 ^{b}
	Chali	1.29 ^{NS}	–	–	^{A} 0.24 ^{a}	^{A} 0.26 ^{a}	^{A} 0.22 ^{a}
	Cochoro	1.69 ^{NS}	–	–	^{A} 0.20 ^{a}	^{B} 0.18 ^{a}	^{B} 0.18 ^{a}
	ARP Tomato d2	3.81 *	–	–	^{A} 0.22 ^{ab}	^{B} 0.20 ^{b}	^{A} 0.25 ^{a}
Stem diameter	*Fetan*	0.24 ^{NS}	27.88 ***	0.73 ^{NS}	^{A} 12.8 ^{a}	^{A} 12.9 ^{a}	^{A} 13.5 ^{a}
	Chali	0.25 ^{NS}	140.52 ***	2.91 **	^{A} 12.2 ^{a}	^{A} 13.2 ^{a}	^{A} 12.4 ^{a}
	Cochoro	1.92 ^{NS}	28.51 ***	0.13 ^{NS}	^{A} 13.0 ^{a}	^{A} 12.1 ^{a}	^{A} 13.8 ^{a}
	ARP Tomato d2	1.84 ^{NS}	49.92 ***	0.43 ^{NS}	^{A} 12.3 ^{a}	^{A} 13.5 ^{a}	^{A} 13.2 ^{a}

NS is non-significant, *, **, *** significantly different at 5 %, 1 %, 0.1 % probability level, respectively. Means within columns preceded by different capital or means within rows followed by different lower-case letters indicate significant differences among cultivars and irrigation treatments, respectively ($P < 0.05$). † ash content sampled once.

3.3 Stomatal conductance (g_s)

Marked temporal variations were observed for g_s (mmol m^{-2} s^{-1}) among the different irrigation treatments and cultivars in both years (Fig. 2). g_s progressively declined over the course of sampling date (Fig. 2) with maximum and minimum values observed at 45 and 75 DAT, respectively. g_s was significantly reduced by deficit irrigation treatments relative to FI, and the trends of reduction were similar for both DI and AFI (Table 2 and 3). In some cases, however, slightly lower g_s was observed under AFI (Fig. 2a and b), resulting in reduction of 16.7 % and 20.4 % g_s compared to FI under DI and AFI, respectively (Table 2). In 2014, on average, FI plants had g_s values of 186.7 mmol m^{-2} s^{-1} while the corresponding g_s values for DI and AFI plants were 26.5 % and 30.5 % lower (Table 3). Statistically significant differences were found among cultivars with respect to g_s. *Chali* had the highest values of g_s under DI (Table 2 and 3) and *Cochoro* had the lowest. *Fetan* also showed significantly lower values of g_s under AFI. Generally, cultivars with higher g_s under deficit irrigation treatments had lower WUE compared to other cultivars.

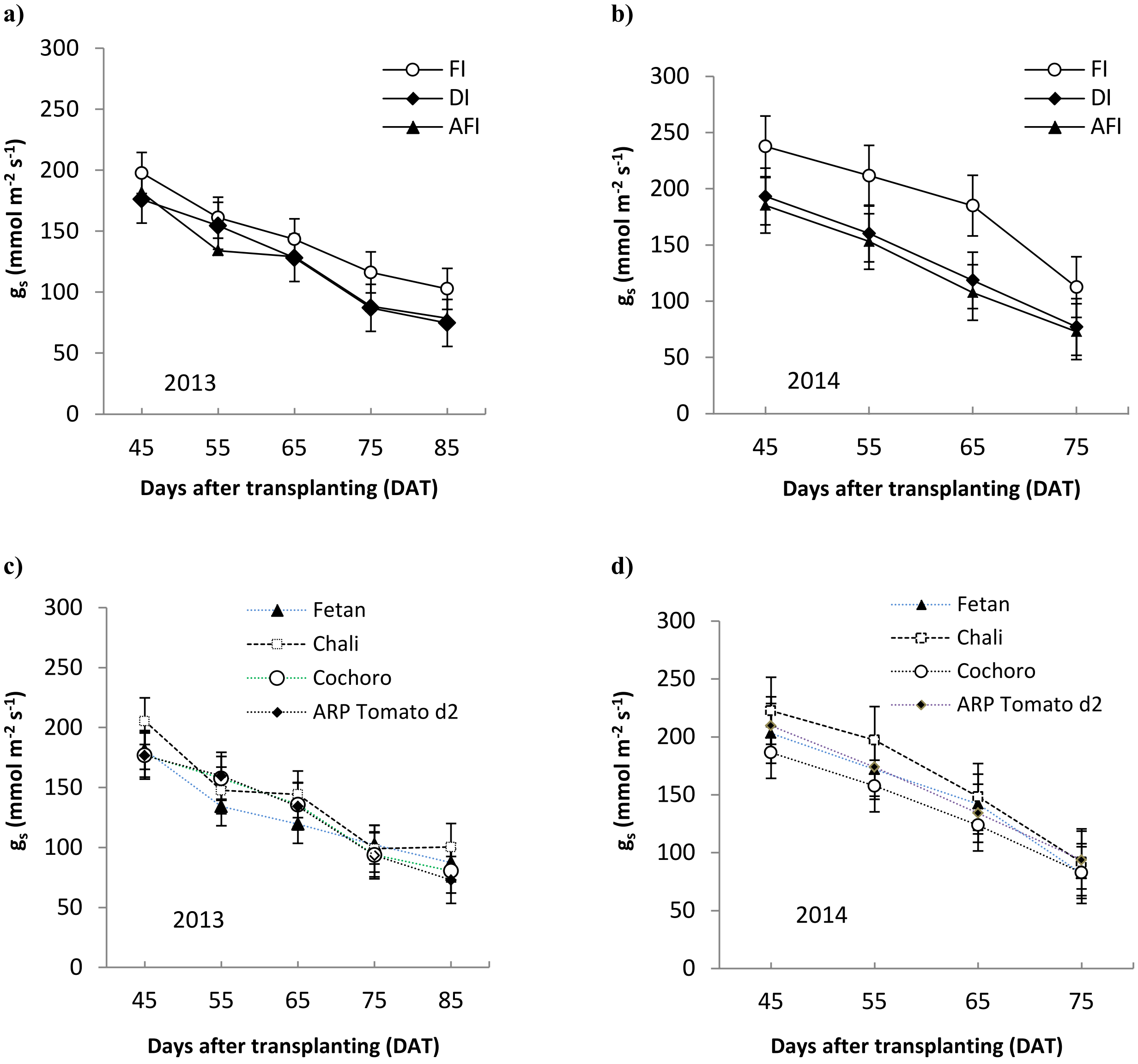

Fig. 2: *Stomatal conductances (g_s) vs. days after transplanting (DAT) of four tomato cultivars (c and d) grown under full irrigation (FI), deficit irrigation (DI), and alternate furrow irrigation (AFI) (a and b) during 2013 and 2014.*

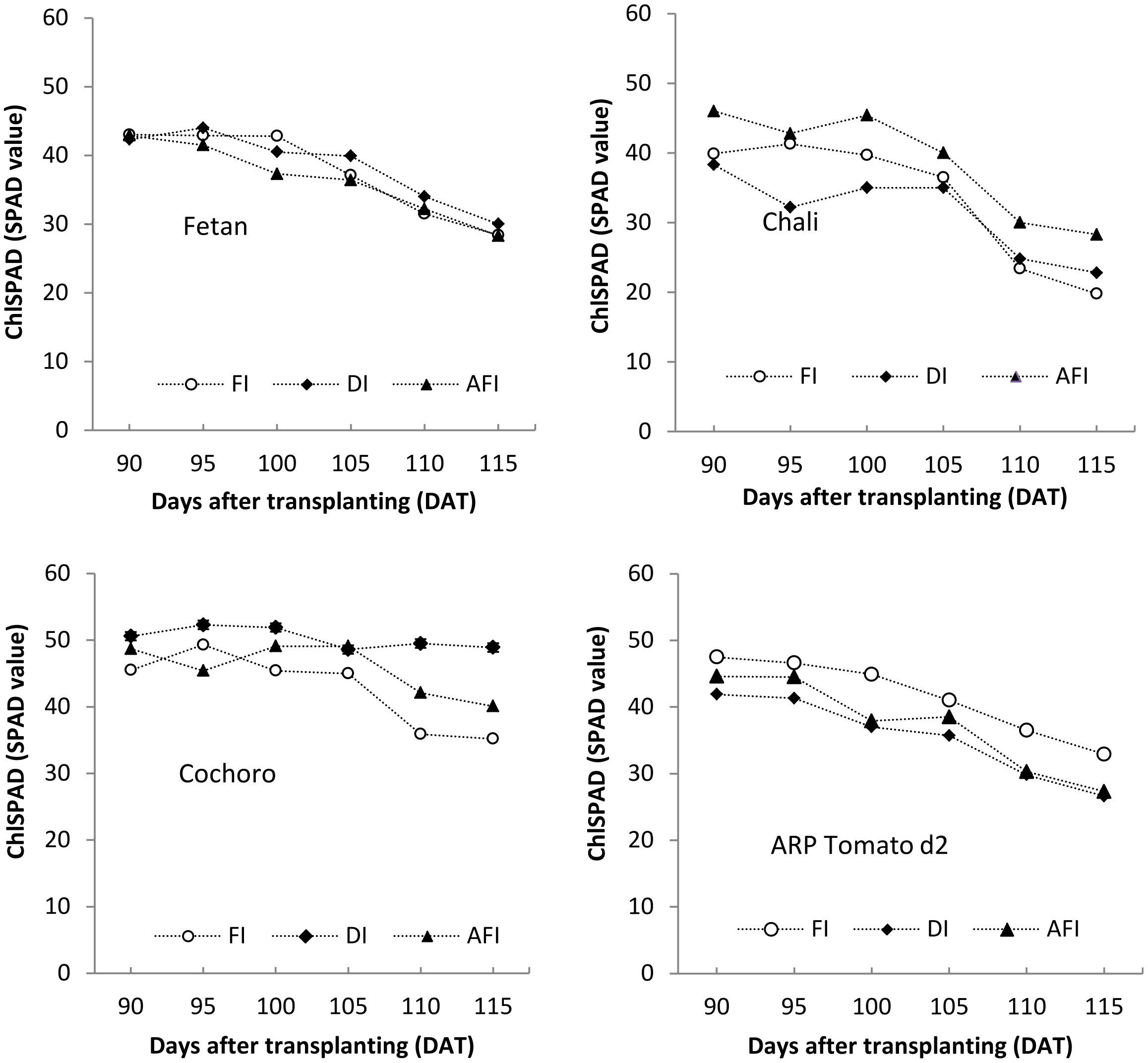

Fig. 3: *Chlorophyll content (Chl_{SPAD}) vs. days after transplanting (DAT) of four cultivars under full irrigation (FI), deficit irrigation (DI) and alternate furrow irrigation (AFI) in 2014.*

3.4 Chlorophyll contents (Chl_{SPAD}) and NDVI

In 2013, significant differences were found for Chl_{SPAD} between the irrigation treatments ($P < 0.001$) and cultivars ($P < 0.01$) (Table 2). However, irrigation by cultivar interaction was not significant ($P > 0.09$). Plants under AFI maintained significantly higher Chl_{SPAD} values whereas the values of FI and DI did not show any distinct differences. Significant differences in Chl_{SPAD} were found among cultivars under deficit irrigation treatments. *ARP Tomato d2* displayed lower Chl_{SPAD} whereas *Fetan, Chali* and *Cochoro* exhibited higher values.

In 2014, the Chl_{SPAD} values progressively declined over time. This trend was observed for all cultivars and irrigation treatments (Fig. 3). Different response of cultivars to irrigation treatments was exhibited by Chl_{SPAD} (Table 3). Except *Fetan*, the Chl_{SPAD} of the other cultivars was significantly affected by irrigation treatments. Chl_{SPAD} values of *Cochoro* and *Chali* were higher under DI and AFI relative to FI, while the values of *ARP Tomato d2* remained higher under FI and lower in deficit irrigation treatments. The comparison of the magnitude of the slope of the linear function of Chl_{SPAD}, indicated that significant differences were observed among the irrigation treatments (Table 4). However, no significant difference was detected between the slopes for AFI and FI.

Deficit irrigation treatments had no significant effect on leaf greenness when assessed by NDVI (Table 2), but the slope of NDVI was significantly higher for AFI than for FI and DI (Table 4). But NDVI varied between cultivars (Table 3). *ARP Tomato d2* displayed the most pronounced drop in the green canopy vegetation at late ripening stages while *Cochoro* maintained a relatively stable and higher NDVI (albeit at reduced level) during 95 to 115 DAT (Fig. 4). *Chali* consistently exhibited a lower NDVI.

Table 4: *Linear functions of chlorophyll contents (Chl$_{SPAD}$) and NDVI vs days after transplanting (DAT) for full irrigation (FI), deficit irrigation (DI) and alternate furrow irrigation (AFI) in 2014.*

Parameter	*Irrigation treatment*	*Equation*	R^2
Chl$_{SPAD}$	FI	$Y = -0.669x + 172.2$	0.879
	DI	$Y = -0.477x + 87.4$	0.963
	AFI	$Y = -0.565x + 97.5$	0.948
NDVI	FI	$Y = -0.008x + 1.294$	0.922
	DI	$Y = -0.008x + 1.326$	0.892
	AFI	$Y = -0.009x + 1.420$	0.882

3.5 *Chlorophyll fluorescence parameters*

A temporal trend of light adapted initial fluorescence (Ft) over time under different irrigation treatments in 2013 and 2014 is presented in Fig. 5. The value was consistently higher under both deficit irrigation treatments (Fig. 5a and b) and tended to decline over time (45 to 65 DAT). Irrigation treatment and cultivar had significant effects on Ft in both years. In 2013, no significant differences in Ft were found among cultivars under FI. Ft values of all cultivars were significantly higher under DI and AFI relative to FI (with exception of *ARP Tomato d2* under DI) (Table 2). In 2014, significant differences in Ft were found among cultivars only under FI and AFI (Table 3). Among the cultivars, *Cochoro* exhibited significantly the highest Ft values whereas *ARP Tomato d2* displayed the lowest under FI. The Ft values in *Cochoro* and *ARP Tomato d2* were higher under AFI and did not change in *Fetan* and *Chali* (Table 3).

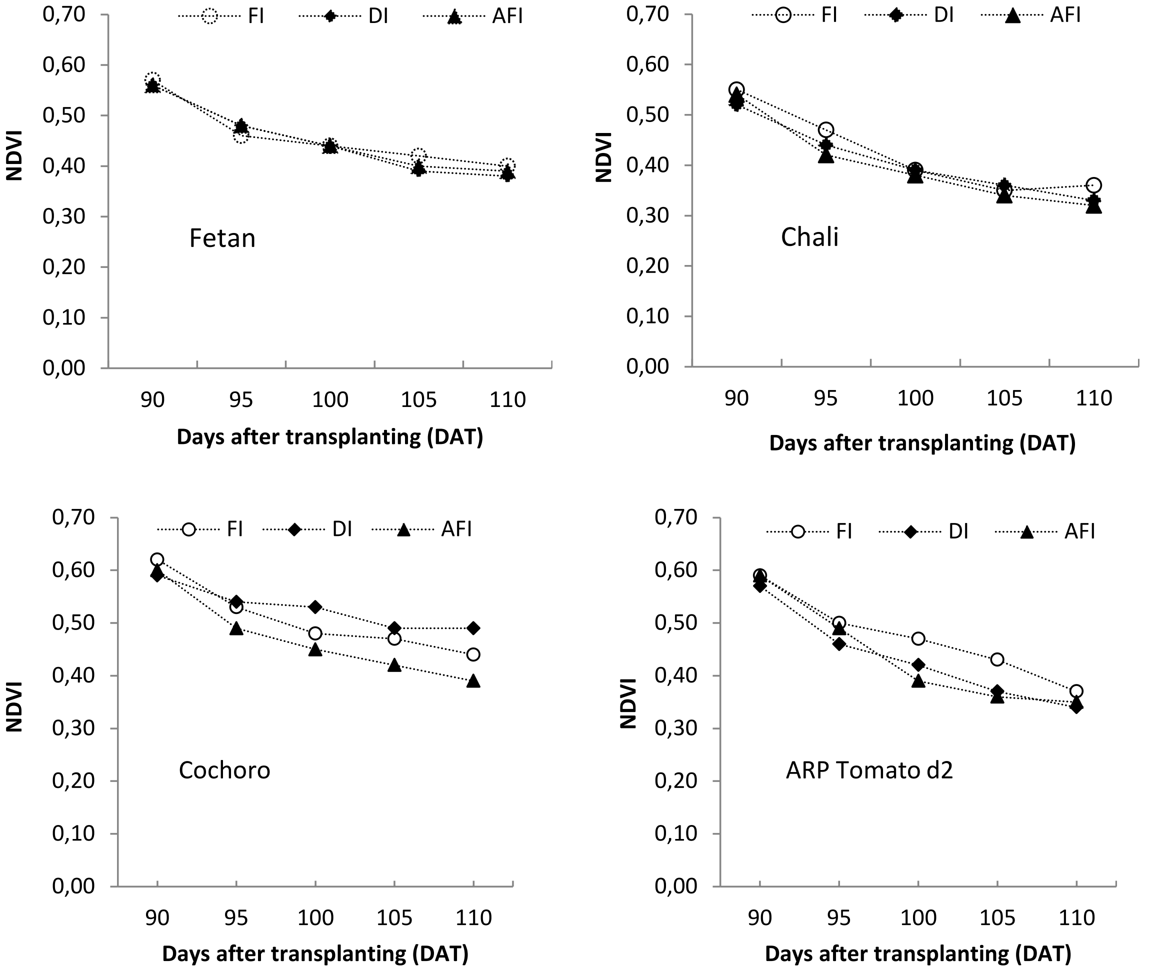

Fig. 4: *Normalized difference vegetation index (NDVI) vs. days after transplanting (DAT) of four cultivars under full irrigation (FI), deficit irrigation (DI) and alternate furrow irrigation (AFI) in 2014.*

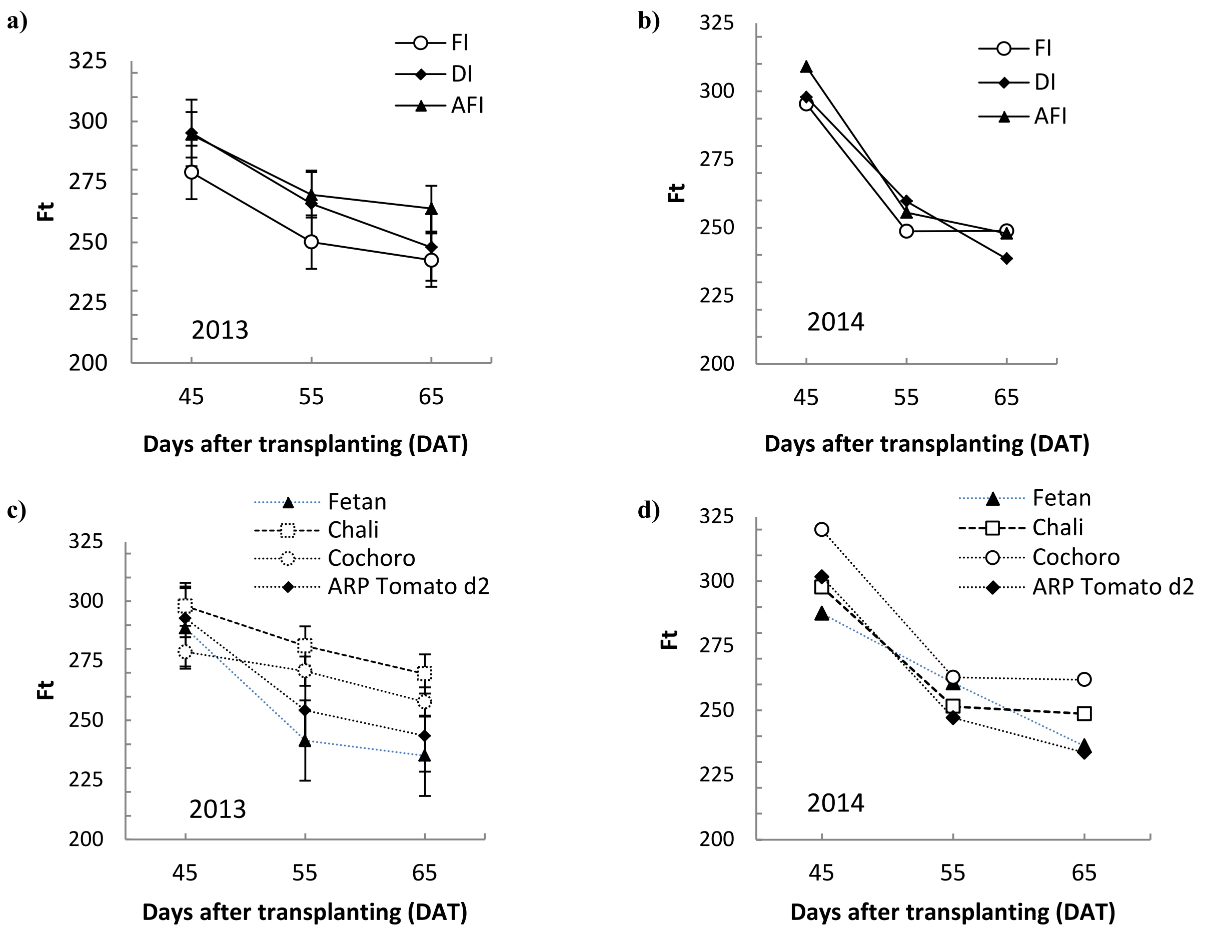

Fig. 5: *Light adapted initial chlorophyll fluorescence (Ft) vs. days after transplanting (DAT) in tomato growing under full irrigation (FI), deficit irrigation (DI) and alternate furrow irrigation (AFI) (a and b) and cultivars (c and d) in 2013 and 2014.*

Fv'/Fm' was not significantly influenced by irrigation and cultivars in 2013 (Table 2). However, significant cultivar differences were observed under AFI in 2014. *Cochoro* had the highest Fv'/Fm' value (0.58) (Table 2).

3.6 *Stem diameter and ash content*

Stem diameter was not significantly influenced by deficit irrigation treatments or cultivars. There were significant differences ($P < 0.05$) in leaf ash content among cultivars as well as irrigation treatments. However, cultivars variation in leaf ash content was only found under DI and AFI (Table 2 and 3). Overall, *Fetan* maintained the highest leaf ash content (27 %) while *Cochoro* showed the lowest (19.0 %) under DI.

3.7 *Relationship among physiological attributes, fruit yield and WUE*

There was an inverse relationship between WUE and g_s (Fig. 6). Further, a positive and significant correlation was found between average NDVI and final marketable fruit yield but the correlation with WUE was non-significant (Table 5). Positive and significant associations between NDVI and Chl_{SPAD} were noted and to each other at all sampling dates.

No correlation was found between ash content and fruit yield or any other physiological trait in 2013 (Table 5), but leaf ash content was significantly negatively correlated with marketable fruit yield and fruit weight in 2014 (Table 6). The correlation with WUE was weak negative. RWC exhibited positive and significant correlation with marketable fruit yield, WUE, fruit number per plant and average fruit weight (Table 5 and 6). Similarly, significant and positive correlations were found between light adapted initial fluorescence (Ft) and maximum quantum yield of PSII (Fv'/Fm') with a number of physiological and agronomic attributes, the latter were presented in part I. Fv'/Fm' was significantly positively correlated with marketable fruit yield, WUE, fruit numbers per plant, Chl_{SPAD} index, NDVI and RWC and inverse correlation with g_s. The positive Fv/Fm correlation with SPAD and NDVI indicated that photosynthetic performance is related to leaf greenness.

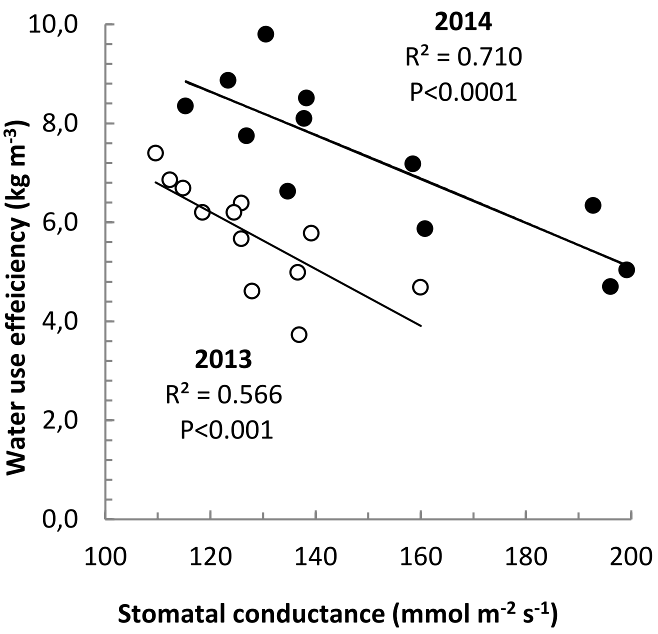

Fig. 6: *Relationship between water use efficiency (WUE) and stomatal conductance (g_s) of four cultivars and three irrigation treatments (full irrigation, regulated deficit irrigation and alternate furrow irrigation).*

Table 5: *Correlation coefficients between physiological attributes and fruit yield and their agronomical components of four tomato cultivars in 2013.*

	MFY	*WUE*	*FN*	*Avwt*
WUE	0.810***			
FN	0.606***	0.668***		
Avwt	0.218^{NS}	0.081^{NS}	−0.055^{NS}	
Chl$_{SPAD}$	0.007^{NS}	0.261^{NS}	−0.125^{NS}	−0.240^{NS}
RWC	0.362*	0.370*	0.079^{NS}	0.455**
g_s	−0.007^{NS}	−0.356**	−0.148^{NS}	−0.049^{NS}
Ash	0.165^{NS}	0.030^{NS}	−0.125^{NS}	−0.109^{NS}
Ft	0.172^{NS}	0.373*	0.316*	−0.342*
Fv‘/Fm‘	0.042^{NS}	0.230^{NS}	0.093^{NS}	0.133^{NS}

MFY: marketable fruit yield); WUE: irrigation water use efficiency; FN: numbers of fruit per plant; Avwt: average fruit weight; Chl$_{SPAD}$: SPAD chlorophyll content; g_s: stomatal conductance; Ash: ash content %; RWC: leaf relative water content; Ft: light adapted initial fluorescence; Fv‘/Fm‘: PSII quantum yield efficiency of light adapted leaf;
NS: non significant, *, **, ***: significantly different at 5 %, 1 %, 0.1 % probability level, respectively.

Table 6: *Correlation coefficients between physiological attributes and fruit yields and their agronomical components of four tomato cultivars in 2014.*

	MFY	*WUE*	*FN*	*Avwt*
WUE	0.751***			
FN	0.500**	0.490**		
Avwt	0.213^{NS}	0.106^{NS}	−0.551***	
Chl$_{SPAD}$	0.540***	0.425**	−0.072^{NS}	0.522***
NDVI	0.526***	0.278^{NS}	0.100^{NS}	0.437**
g_s	−0.156^{NS}	−0.730***	−0.235^{NS}	−0.096^{NS}
Ash	−0.317*	−0.227^{NS}	0.073^{NS}	−0.359*
SDM	0.061^{NS}	0.189^{NS}	0.284^{NS}	−0.257^{NS}
RWC	0.398**	0.474***	0.437**	0.117^{NS}
Ft	0.363*	0.400*	0.395*	−0.009^{NS}
Fv‘/Fm‘	0.465**	0.492**	0.414**	−0.064^{NS}

MFY: marketable fruit yield; WUE: irrigation water use efficiency; FN: numbers of fruit per plant; Avwt: average fruit weight; Chl$_{SPAD}$: SPAD chlorophyll content; NDVI: normalized difference vegetation index; g_s: stomatal conductance; Ash (ash content, %); SDM: stem diameter; RWC: relative water content; Ft: light adapted initial fluorescence; Fv’/Fm’: PSII quantum yield efficiency of light adapted leaf;
NS: non significant, *, **, ***: significantly different at 5 %, 1 %, 0.1 % probability level, respectively.

4 Discussion

Whenever water deficit occurs in plants, the water balance is disturbed and leaf RWC and water potential usually decreases. Indeed, significant difference was found among cultivars in RWC under deficit irrigation. *Fetan* and *ARP Tomato d2*, *Cochoro* consistently displayed the highest RWC and lowest g_s. The reduction in stomatal conductance under both deficit irrigated treatments was not related to plant water status as there was no significant change in leaf RWC between irrigation techniques. It may be assumed that root borne abscisic acid (ABA) triggered the stomatal closure; a well-documented effect to cause substantial water savings in PRD (Sun *et al.*, 2013; Wang *et al.*, 2010).

Though substantial variations exhibited between cultivars, all cultivars responded to water deficit irrigation by lowering g_s (Fig. 2c and d). Since g_s controls both photosynthetic assimilation and transpiration in plants, it was found as the main factor affecting WUE under moderate drought stress (Mei *et al.*, 2013). In this study, *Cochoro* gave the highest fruit yield and WUE along with the lowest g_s under deficit irrigation. This indicates that the cultivar combines higher productivity, WUE and stress avoidance mechanism. In contrast, *Chali* exhibited a lower fruit yield and WUE but with the highest g_s showing little adaptability to water stress. While g_s was considerably reduced under both deficit irrigation treatments (Fig. 2a and b), the photosynthetic capacity of the four cultivars, determined as Fv'/Fm', was not reduced under AFI and DI (Table 2 and 3). Several studies have also shown that g_s was substantially reduced while the photosynthetic rate was not greatly affected under deficit irrigation particularly in PRD treated plants (Campos *et al.*, 2009; Yang *et al.*, 2012). Mild drought associated with stomatal closure will often not result in a reduction of a photosynthetic capacity (Baker & Rosenqvist, 2004). Therefore, the apparent reduction in g_s of different cultivars is often greater than a respective change in photosynthetic rate under deficit irrigations resulting in differential WUE responses of the cultivars.

Under water deficit, *Fetan* and *ARP Tomato d2* had the highest relative fruit growth (Fig. 1). Remarkably, those cultivars maintain a higher growth rate under water deficit during the time of rapid fruit growth. Besides, *Fetan* was observed to react by pronounced stomatal closure and maintained higher yields under deficit irrigation. *Cochoro* had medium fruit growth rate but had longer fruit growth duration (Table 1), associated with the highest yield potential, while *Chali* had the lowest fruit growth rate and shortest duration, and produced smaller fruit under deficit irrigation. Differences in final fruit size among cultivars are effect of differences in fruit growth rates and fruit growth duration, concurring with earlier findings (Okello *et al.*, 2015). This was illustrated by spectral reflectance measurements of the leaf greenness of individual plants and at canopy level (Fig. 3 and 4). Cultivars which had higher $\mathrm{Chl}_{\mathrm{SPAD}}$ and NDVI values throughout the fruit development and ripening stages had higher fruit yields due to prolonged leaf metabolic activity. It can be seen from this study that the highest yielding cultivar, *Cochoro* maintained the highest $\mathrm{Chl}_{\mathrm{SPAD}}$ and NDVI whereas the low yielding cultivar, *Chali* had the lowest under DI and AFI, concurring with other previous studies, who reported that genotypes which delayed senescence rate often out yielded genotypes without this trait (Lu *et al.*, 2011; Lopes & Reynolds, 2012; Rolando *et al.*, 2015). On the other hand, *ARP Tomato d2* displayed a higher level of $\mathrm{Chl}_{\mathrm{SPAD}}$ and NDVI under FI, and this cultivar performed best in areas with better water availability. As $\mathrm{Chl}_{\mathrm{SPAD}}$ and NDVI are significantly correlated with average fruit weight (Table 6), differences in N mobilisation might partly explain genotype differences in delayed senescence (Shahnazari *et al.*, 2008; Gregersen *et al.*, 2013). Besides, significant positive correlations between photosynthetic performance measured by Fv'/Fm', $\mathrm{Chl}_{\mathrm{SPAD}}$ and NDVI indicate that plants can maintain source activity by delaying leaf senescence rate under deficit irrigation.

Defining the relationship between physiological functions and agronomic performance of different genotypes can be used to identify physiological traits that can assist as indirect selection criteria of genotypes with good adaptability to water deficit. Significant positive associations found between NDVI and $\mathrm{Chl}_{\mathrm{SPAD}}$ indicate that both physiological tools are good indicators for assessing the greenness or delayed senescence rate of different genotypes, and may be used either conjunctively or separately for phenotyping physiological traits. Besides, the heritability of NDVI was reported to be higher than that of grain yield in maize (Lu *et al.*, 2011), indicating its usefulness in the selection of secondary traits under water-limited environments. Leaf ash content (Misra *et al.*, 2010; Glenn, 2014) and stem diameter (Bhattarai & Midmore, 2007) were previously suggested as surrogates of WUE under water deficit, but significant correlations were not found between those traits and WUE in our study. Previous studies also showed that significant relationship between ash content and WUE was found only in drier environments and such relationships tend to disappear under moderate to non-water stress conditions (Monneveux *et al.*, 2005; Cabrera-Bosquet *et al.*, 2009). The result imply that the relationship between ash and yield depends more on stress intensity than stress modality and, consequently, ash content and stem diameter could not be reliable putative physiological reference for WUE under mild-water stress of AFI and DI.

5 Conclusion

The present study evidences that the differential responses of four tomato cultivars in terms of total fruit yield and WUE were ascribed to cultivars differences in physiological attributes. However, the overall differences in WUE were more accounted for by the variations in stomatal conductance (g_s). Therefore, g_s could be useful for breeders for screening large numbers of genotypes with higher WUE under deficit irrigation condition. Nevertheless, employing deficit irrigation strategies needs suitable cultivars that possess traits achieving higher yields and WUE. Due to combing higher productivity, WUE and stress adaptation mechanisms, the cultivar *Cochoro* can be used both, by producers and breeders under low water availability.

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