

Linking thermal imaging to physiological indicators in *Carica papaya* L. under different watering regimes[☆]



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ABSTRACT

Water deficit is the most limiting factor for yield and fruit-quality parameters in papaya crop (*Carica papaya* L.), deficit-irrigation (DI) strategies offering a feasible alternative to manage limiting water resources. When DI is applied, it is crucial to assess the physiological status of the crop in order to maintain the plant within a threshold value of water stress so as not to affect yield or fruit-quality parameters. The aim of this work was to evaluate the feasibility of thermal imaging in young papaya plants to assess the physiological status of this crop when it is subjected to different DI regimes, studying the relationships between the changes in leaf temperature (T_{leaf}) and in the major physiological parameters (i.e., stomatal conductance to water vapor, g_s ; transpiration, E ; and net photosynthesis, A_n). The trial was conducted in a greenhouse from March to April of 2012. Plants were grown in pots and subjected to four irrigation treatments: (1) a full irrigation treatment (control), maintained at field capacity; (2) a partial root-zone drying treatment, irrigated with 50% of the total water applied to control to only one side of roots, alternating the sides every 7 days; (3) a regulated deficit irrigation (50% of the control, applied to both sides of plant); (4) and a non-irrigated treatment, in which irrigation was withheld from both sides of the split root for 14 days, followed by full irrigation until the end of the study. Significant relationships were found between T_{leaf} and major physiological variables such as g_s , E and A_n . Additionally, significant relationships were found between the difference of leaf-to-air temperature ($\Delta T_{\text{leaf-air}}$) and gas-exchange measurements, which were used to establish the optimum range of $\Delta T_{\text{leaf-air}}$ as a preliminary step to the crop-water monitoring and irrigation scheduling in papaya, using thermal imaging as the main source of information. According to the results, we conclude that thermal imaging is a promising technique to monitor the physiological status of papaya during drought conditions.

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1. Introduction

Papaya (*Carica papaya* L.) is one of the most important fruit crops cultivated in tropical and subtropical worldwide areas, India, Brazil, and Indonesia being the leading producers.

The global production of papaya has increased to about 371,852 t year⁻¹ during 1998–2010. Within these countries, Brazil is the second largest producer with 31,989 ha and 43.3 t ha⁻¹ which represents 13% of total world-wide production (FAOSTAT, 2015).

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This crop is characterized by its special nutritional properties. That is, among a list of 38 fruits with high nutritional importance, papaya occupies the first position, based on the percentage of recommended daily intake in the USA, for Vitamin A and C, potassium, folic acid, niacin, thiamin, riboflavin, iron, and fiber (Ming et al., 2008). The papaya plant is also grown for production of papain, an important proteolytic enzyme found in the latex of the unripe fruits (Boshra and Tajul, 2013). This enzyme has multiple uses such as the textile industry for softening wool (Villegas, 1997), to prepare fish protein concentrate for animal nutrition, in cosmetics (soap, shampoo and toothpaste) is used in the softening meats, and is widely used in the brewing industry (Seelig, 1970).

Within the areas where this crop is grown, water availability is one of the most limiting factors, this being determined by natural climatic conditions of the growing areas, and the processes linked to the climate change. The frequency of extreme climatic events that cause water stress in plants have increased in the last few years, probably linked to global climate change, which is resulting in a global-warming phenomena in many areas of the world (Hoerling et al., 2012). Models of climate simulation predict an increase from 1.4 to in 5.8 °C in the average global air temperature (Hoerling et al., 2012) over the next century. In addition, incidence of more extreme weather events (droughts and high temperatures) and related stresses could reduce the potential production of many crops (Fedoroff et al., 2010). Thus, an understanding of the physiological processes related to plant responses to drought and high air temperatures is crucial to minimize the negative impacts under these conditions (Cavatte et al., 2011).

Although papaya can be considered a drought-tolerant crop, irrigation is crucial during the dry periods to increase the growth and final yield as well as to avoid extreme situations in these terms (Aiyelaadgbe et al., 1986; Malo and Campbell, 1986; Kruger and Mostert, 1999; Srinivas, 1996). Thus, when a water-stress situation is not properly managed, significant reductions in yield and fruit-quality parameters result (Kruger and Moestert, 1999; Sarwar et al., 2001; Lima et al., 2015; Mahouachi et al., 2007). In this sense, according to Kempe et al. (2014), it is crucial to keep the turgor pressure between 0.82 and 1.25 MPa for a proper flexural rigidity of the entire papaya stem, because this crop does not contain wood and it is identified as a giant herb. And hence, for a suitable crop-water development, it must grow within an optimum range of water availability.

Moreover, the effects of water stress varies in response to several factors, namely its severity and plant's phenological stage (Kramer and Boyer, 1995). A moderate to severe water stress in papaya plant may not only reduce crop development, by inhibiting the growth of stem and leaves, but may stimulate the production of sterile flowers (Marin et al., 1995; Bernardo, 1996; Coelho, 1999; Coelho et al., 2003).

In physiological terms, the first responses of plants subjected to water deficit are associated with a rapid growth reduction together with a reduction in transpiration due to the decline of stomatal conductance (Syvertsen and Lloyd, 1994; Nobel, 1999). In the case of papaya crop, stomata have significant regulatory control over the photosynthetic process (Clemente and Marler, 1996; Campostrini and Glenn, 2007; Campostrini et al., 2010). Therefore, an optimum management deficit-irrigation strategies that help to minimize the leaf stomatal conductance keeping the leaf photosynthesis rate within an optimum range, would be translated into the absence of significant yield reductions, even improving some fruit-quality parameters (Salazar, 1978).

Stomatal regulations of gas exchange in response to drought have a great importance in the plant adaptation to non-optimal situations. This regulation requires maintaining an equilibrium between photosynthetic rate, water loss, and leaf temperature (Chaves et al., 2003; Kaplan, 2007; Jones et al., 2009). A mod-

erate water stress can promote a water saving together with an improvement in some quality parameters of yield (García-Tejero et al., 2011a, 2013). However, severe water stress induces stomatal closure, significantly depressing assimilative activity and thus, reducing yield and harming crop development (Chaves et al., 2003). Hence, there is a strong interest in developing and improving different robust tools able to monitor the plant-water status, in order to keep the crop within of certain threshold values of moderate-to-mild water stress.

Associated with the leaf-transpiration process, a phenomenon known as 'evaporative cooling' occurs whereby heat is dissipated by water-vapor loss from the stomata. With lower transpiration levels, the evaporative-cooling process is significantly reduced, raising the leaf temperature (T_{leaf}) typically several degrees above the air temperature (Jones, 1999; Jones et al., 2002; Araus et al., 2008; Fuentes et al., 2012). These relationships establish the basis monitoring the crop-water based on leaf/canopy temperature, since any situation that causes a partial closing of the stomata (for example by a more or less prolonged water-stress situation) will result in a significant rise in leaf temperature. Therefore, T_{leaf} can be used as an indicator of the degree water stress with the advantage that it can be remotely measured and in plants of different sizes under field as well as controlled conditions.

Thermal imaging is a rapid and non-destructive technique that uses T_{leaf} as a component of crop physiological status related to water availability (Chaerle et al., 2004, 2007; Jones, 2004; Nilsson, 1995; Costa et al., 2013) and irrigation scheduling in several crops such as grapevine (Möller et al., 2007; Grant et al., 2006, 2007; Jones et al., 2002), olive trees (Ben-Gal et al., 2009) or citrus (García-Tejero et al., 2011b). However, according to Jones et al. (2009) and Jones and Vaughan (2010), there are many variables that determine the final value of T_{leaf} and therefore they must be taken into account when assessing the crop-water status using the T_{leaf} values. Variables such as the radiation level, air temperature, vapor-pressure deficit, the relative humidity or the angle of the radiation incident on the leaf surface decisively influence the absolute value of the leaf/canopy temperature. To optimize the use of T_{leaf} , various stress indexes have been developed with the aim of minimizing the effect of these variables in studies related to the temperature of the crops and their relationship to water-stress response. These indexes try to normalize the absolute values of temperature, providing a second value at which the effects of this set of potentially influential variables are partially minimized. Within these indexes, the $\Delta T_{leaf-air}$ index (this being the difference between leaf and air temperature) would be the most 'user-friendly' because it is only necessary to know the absolute value of air temperature at the timing measurements. However, for the optimization of this technique, the relationship between T_{leaf} and the thermal indexes with the most relevant physiological variables such as stomatal conductance to water vapor (g_s), net photosynthesis (A_n) or transpiration (E) must be established in order to quantify correctly the water-stress level endured by the crop.

We hypothesize that thermal imaging can serve as a good alternative to other classical physiological measurements to monitor the crop-water status, especially when this crop is subjected to deficit-irrigation strategies. To test this hypothesis, we undertook the following tasks: (i) an evaluation of the feasibility of thermal imaging in papaya crop to assess the physiological status for different deficit irrigation regimes; establishing the hypothetical relationships between T_{leaf} and the g_s , E and A_n ; in terms of studying whether possible changes in T_{leaf} are linked to physiological changes on the basis of gas-exchange measurements; (ii) and the determination of whether $\Delta T_{leaf-air}$ can be considered a feasible index to monitor the papaya physiological status as a preliminary step to schedule irrigation when this crop is subjected to DI strategies.

2. Material and methods

2.1. Plant conditions and experimental site

The trial was conducted from March to April of 2012, in a greenhouse at the Universidade Estadual do Norte Fluminense- UENF, Goytacazes Campus, Rio de Janeiro, Brazil (2°44'47"S 41°18'24"W), using 96-days-old papaya plants (*Carica papaya* cv. Gran Golden).

Prior to the establishment of the irrigation treatments, plant material was obtained from fruits of papaya cv. Gran Golden. This cultivar is characterized by bright-green leaves and fruits with a smooth fruit surface and some tolerance to skin freckles, making it a cultivar of greater acceptance in foreign markets. Seedlings were grown in tubes between the day of the year (DOY) 348 2011 to 31 DOY 2012. Seedlings were hand irrigated daily and transplanted into two 15-L polyvinyl chloride pots, filled with soil, sand, and cattle manure (2:1:2). Pots were connected to each other, with the root equally split between the two pots, in order to prevent water exchange between the two compartments. Additionally, 53 g pot⁻¹ of solid fertilizer was applied (Osmocote NPK 14:14:14) to avoid nutritional deficiencies in any treatment. Afterwards, plants were fully irrigated keeping the soil at field capacity until the irrigation treatments were applied.

2.2. Irrigation treatments

When plants were 96 days-old, 47 days after transplant (78 DOY 2012), with an average high of 0.55 m, the following irrigation treatments were applied: (1) full-irrigation (FI) with both sides of the split root kept at 100% of field capacity; (2) partial root-zone drying (PRD), in which water was initially applied daily to one side of the root (100% of field capacity), with no irrigation applied on the other side of the root, alternating the irrigation pattern between the two root sides every 7 days; (3) regulated deficit irrigation (RDI); in which both sides of the split root were simultaneously irrigated at 50% of field capacity; and (4) non-irrigated (NI) in which irrigation was withheld from both sides of the split root for 14 days, followed by full irrigation until the end of the study (Table 1).

Field capacity was determined before the irrigation treatments were applied. For this, three extra plants were used and irrigated with a known volume of water (just enough to saturate the soil). After 30 min, when drainage had finished, the difference between the amount of water applied and the drained volume was calculated, estimating the amount of water stored by the substrate (volume necessary to place the substrate at field capacity, which was between 0.24 and 0.26 kg kg⁻¹). FI plants were irrigated daily by hand with this amount of water. The remaining treatments, as FI were hand irrigated, with an amount of water according to the water applied in FI. At the end of irrigation period (21 days), FI plants received 47.5 L plant⁻¹, PRD and RDI plants received 23.8 L plant⁻¹. NI plants received 21.3 L plant⁻¹ and were irrigated only during the last 6 days of the experiment. To identify the time when NI should be irrigated, we determined the soil-water potential and measured the leaf-gas exchange every two days during the study. At 14 days after applying the irrigation treatment (DAT) the water potential of the NI substrate was around -180 kPa and the stomatal conductance (g_s) and net photosynthesis (A_n) reached values $\approx 0 \mu\text{mol m}^{-2} \text{s}^{-1}$. NI plants were re-watered with the same amount of water as FI. In the same vein, for the case of PRD, when soil-water potential in the non-irrigated PRD side was close to -100 kPa, with values of g_s and A_n close to $0.1 \text{ mol m}^{-2} \text{ s}^{-1}$ and $7 \mu\text{mol m}^{-2} \text{ s}^{-1}$, irrigation was withheld and applied to the other portion of the root zone.

2.3. Measurements of soil, climate and plants

Soil-water potential (Ψ_s) was monitored with 6450 WD probes (Watermark soil moisture sensor, Spectrum Technologies, USA), which were installed in four plants per irrigation treatment and in both sides of the root system at 0.15 m of soil depth and 0.1 m from the stem. Data were automatically collected every 30 min, using a Watchdog 200 datalogger (Spectrum Technologies, Inc., Illinois, USA).

Climatic conditions during the trial were monitored with a weather station (Model 450, Spectrum Technologies, Inc., Illinois, USA) installed inside the greenhouse. Air temperature (T_{air}), relative humidity (RH), vapor-pressure deficit (VPD) and photosynthetic photon flux density (PPFD) data were averaged every hour (Fig. 1). The average T_{air} during the experiment was $\sim 25^\circ\text{C}$, with maximal values around 40°C during some hours of the day. The relative humidity values were noticeably high, around 80%, even reaching values of 100% and with values of close to 30%. VPD values ranged between 0.8 and 1.2 kPa with occasional values of around 2.2 kPa during some hours. Light conditions (PPFD) were on average, close to $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$, sporadically reaching values of $1100 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

Leaf temperature was measured with a ThermoCAM™ Flir i50 (Flir Systems Inc., (USA), 7.5–13 μm , 140×140 pixels). The emissivity was set at 0.96 and the camera was placed at 0.3 m distance from the same leaves used in gas-exchange measurements. Data were collected between 12:00–14:00 h: (i) at the beginning (0 DAT), (ii) 9 DAT, when A_n values of NI plants were around to 50% of those measured for FI plants, (iii) and 14 DAT, when A_n values of NI plants were $\approx 0 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Thermal images were analyzed with FLIR QuickReport 1.2 (FLIR Systems, Inc., USA). The average T_{leaf} corresponding to the whole area of two leaves per plant was calculated and a total of five plants per treatment were measured. Once the T_{leaf} values were compiled for each treatment and sampling day, these values were normalized using the $\Delta T_{\text{leaf-air}}$, in order to try to exclude the environmental effects on T_{leaf} as stated by Jackson et al. (1988).

With the same periodicity as temperature readings, gas-exchange measurements (g_s , A_n , and E) were conducted using a portable infrared gas analyzer (Li-6400, Li-cor Biosciences, Inc., Nebraska, USA) equipped with an artificial light system equipped with two light-emitting diodes blue and red (Li-cor Biosciences, Inc., Nebraska, USA). Ten plants per treatment were measured under controlled conditions, with a photosynthetic active radiation (PAR) level of $1.500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ inside the leaf chamber ($2 \times 3 \text{ cm}^2$), a CO_2 level of $392 \pm 9 \mu\text{mol CO}_2 \text{ mol}^{-1}$, a block temperature of $24.5 \pm 1.6^\circ\text{C}$ and a relative humidity of $60 \pm 8.7\%$.

2.4. Statistical analysis

Data were subjected to a one-way variance analysis (ASSISTAT 7.6 beta, 2011) with four irrigation treatments and ten replicates per treatment, using a Tukey's test for mean separations ($p < 0.05$). An overall analysis was made to evaluate the relations between the parameters studied using the Pearson's correlation coefficient. This coefficient shows a linear relationship between two of the variables chosen and corresponded to the ratio of the covariance vs. the product of the standard deviations of the variables.

After this, using the average values for each irrigation treatment and sampling day, different functions were established to express the gas-exchange measurements in terms of $\Delta T_{\text{leaf-air}}$. Using a saturation model (Eq. (1)), two regions can be defined: a threshold value of A_n , g_s and E , corresponding with a certain range of $\Delta T_{\text{leaf-air}}$; and a second region (descending), in which the values of the gas-exchange parameters decline with the increment of $\Delta T_{\text{leaf-air}}$. This model was defined according the best fit found, using the software

Table 1
Timeline of irrigation treatments.

Treatment	Pot	Days after irrigation treatment application																					
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
FI	1																						
	2																						
PRD	1																						
	2																						
RDI	1																						
	2																						
NI	1																						
	2																						

Full irrigated (FI); partial-root-zone drying (PRD); regulated deficit irrigation (RDI); non-irrigated (NI). Dark-grey represents the period of days in which irrigation was applied at 100% of field capacity (FC). The light grey represents the days with irrigation at 50% of field capacity. The white color represents the period of time with no irrigation.

“CurveExpert Professional™ 2.0. (2013) and the Grapher™ Golden Software 11.0 (2014).

$$y = \frac{ax}{b+x} \quad (1)$$

where a and b , are the adjust coefficients for each model.

3. Results

3.1. Micrometeorological parameters and soil-water content

The average of T_{air} ranged between 23.5 and 30 °C, reaching the highest values on days 3, 9, 17, and 18 (Fig. 1A). The lowest values occurred on days 0, 1, and 10. Solar radiation ranged between 175 and 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the highest values being observed on days 2, 3, 4, 7, and 8 and the lowest on days 0, 1, 6, 10, 12, and 19 (Fig. 1B). Relative humidity varied between 70 and 90% and these values were high days 0, 6, 10, and 12 and lowest days 3 and 8 (Fig. 1C). Vapor–pressure deficit (VPD) values ranged between 0.2 and 1.3 kPa with the highest values observed on days 3 and 8, and the lowest on days 0, 6, 10, and 12.

The soil–water potential (ψ_{soil}) in the NI and PRD treatments declined beginning on 3 DAT. The NI treatment reached the minimum value of ψ_{soil} (–180 kPa) 14 DAT and was re-watered and returned to $\psi_{\text{soil}} = 0$ kPa (Fig. 2).

In relation to the sampling days of thermal imaging, at the beginning of the experiment (0 DAT), the maximum value of T_{air} was 25 °C, with a minimum relative humidity of 80%; and a maximum solar radiation of 257 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These values were significantly less severe than those detected the following sampling day (9 DAT), with values of maximum T_{air} of 44 °C, a minimum RH of 26% and a maximum PAR of 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Finally, 14 DAT climatic data were similar to those detected the previous day; with values of maximum T_{air} of 36 °C, minimum values of RH of 39%, and maximum values of PAR = 830 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

3.2. Leaf-gas exchange measurements

The highest values of g_s , A_n , and E were detected in FI plants, and the lowest in NI plants (Table 2). There was a gradual reduction in g_s and A_n for the PRD treatment during the study. At 9 DAT, a significant decrease was detected in A_n , from 14.3 to 6.38 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, with a parallel decrease of g_s (from 0.24 to 0.07 $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$). Similarly, leaf transpiration fell from 4.1 to 1.8 $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$, with significant differences between FI and NI.

Net photosynthesis markedly dropped in NI plants (from 10 to 1.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and these low values remained stable until the day of maximum stress (14 DAT). The g_s diminished from 0.42 to 0 $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ and E varied between 4 and 0.06 $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$. NI plants demonstrated a partial recovery after being irrigated with the same amount of water as FI (14

days after the beginning of the water stress). That is, 48 h after re-watering, in NI treatment, A_n values were a 54% of the initial value and 72 h after re-watering, these values rose to 72% of the initially value, a level that remained constant until the end of the trial.

Comparing the photosynthetic rates values of NI, PRD, and RDI, we found that values of NI plants were 43 and 54% lower 48 h after re-watering and 37 and 24% 72 h after re-watering, respectively. In addition, we observed a slower recovery of g_s and E for the NI plants during re-watering than the recovery of A_n .

Meanwhile, g_s values in FI ranged between 0.3 and 0.6 $\text{mol m}^{-2} \text{s}^{-1}$, whereas in the case of A_n and E , these values ranged between 9.3 and 18.8 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ and 3.7 and

Table 2
Physiological responses to irrigation treatments in papaya.

DAT	Parameter	Treatments			
		FI	PRD	RDI	NI
0	g_s	0.39a	0.42a	0.42a	0.42a
	A_n	9.32a	11.21a	10.01a	9.88a
	E	3.73a	4.09a	3.95a	4.00a
3	g_s	0.45a	0.25c	0.39b	0.36b
	A_n	16.06a	15.25a	14.32a	10.90b
	E	6.67a	4.15a	6.77a	5.97a
6	g_s	0.40a	0.34a	0.36a	0.04b
	A_n	12.71a	14.33a	13.31a	6.01b
	E	4.84a	4.92a	4.70a	0.96b
9	g_s	0.34a	0.07b	0.09b	0.00b
	A_n	13.19a	6.39b	8.38b	1.84c
	E	5.70a	1.89b	2.26b	0.06c
12	g_s	0.63a	0.49b	0.62a	0.01c
	A_n	14.65a	15.17a	13.36a	2.69c
	E	9.09a	8.63a	9.08a	0.56c
14	g_s	0.68a	0.10c	0.28b	0.02c
	A_n	18.84a	9.07c	12.47b	2.42d
	E	11.44a	3.72c	6.30b	0.89c
16	g_s	0.44a	0.11c	0.25b	0.06c
	A_n	14.86a	10.27a	12.76a	5.90b
	E	5.96a	2.76c	4.24b	1.67c
17	g_s	0.43a	0.15b	0.20b	0.10b
	A_n	14.33a	10.44a	12.50a	7.95a
	E	6.59a	3.55b	3.97b	2.72b
21	g_s	0.39a	0.14b	0.19b	0.26b
	A_n	14.33a	10.44a	12.52a	7.95a
	E	6.18a	2.49b	3.52b	3.52b

Stomatal conductance to water vapor (g_s , $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); leaf net photosynthesis (A_n , $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and transpiration rate E ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) measured over the trial, on different days after irrigation treatment (DAT) and for the different irrigation regimes: full irrigation (FI), partial root drying (PRD), regulated deficit irrigation (RDI) and no irrigation (NI). Values are the averages of 10 measurements per treatment ($n = 10$). Different letters in the same row indicate significant differences.

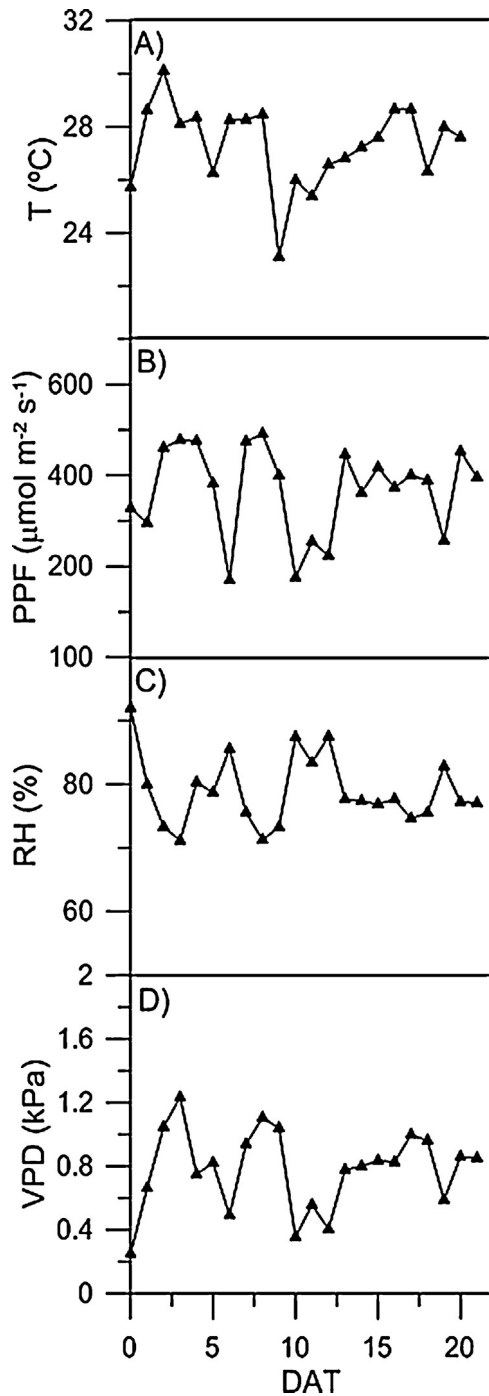


Fig. 1. Micrometeorological conditions after irrigation treatment application (DAT) (A) average air temperature (T), (B) average photosynthetic photon flux (PPF); (C) average relative humidity (RH) and D) average air–vapor pressure deficit (VPD).

$11.4 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$. These results show a wide range of data under FI conditions.

In the case of the worst irrigation conditions (detected in NI treatment prior to its recovery), it is notable that even for days on which the stomatal conductance and transpiration were very low (even zero), only slight photosynthesis activity was detected. However, considering that this treatment was recovered 14 DAT, neither stomatal conductance, transpiration values, nor photosynthesis activity reached values similar to those detected in FI treatment during the same days. In fact, these values were below those recorded in PRD and RDI during the last days of the experi-

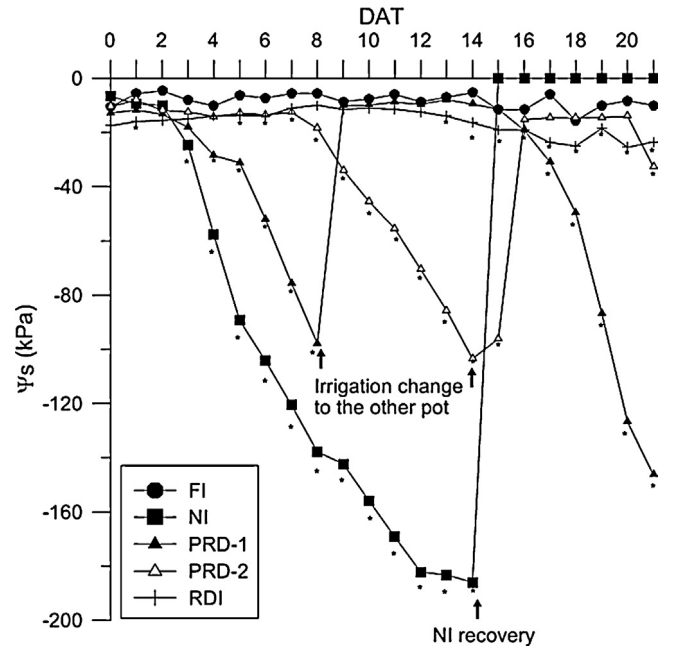


Fig. 2. Soil–water potential (Ψ_s) during study for each irrigation treatment. DAT, Day after irrigation treatment application; FI, full irrigation; NI, no irrigation; PRD-1 and PRD-2, partial root drying, sides left and right, respectively; RDI, regulated deficit irrigation. Each point represents the average of four single values ($n=4$). Asterisks represent significant differences ($p < 0.05$) with the values recorded in FI treatment.

ment, when NI was being irrigated with the same amount of water as in FI, and the remaining with the 50% of water applied in FI and NI treatment.

Some effects in gas-exchange measurements were observed in relation to the climatic conditions registered during the sampling days (Fig. 1; Table 2), although these variations differed within each treatment. Nevertheless, high values of VPD were associated with higher g_s and E values, this being indirectly reflected in the final values of T_{leaf} .

3.3. Leaf temperature response

T_{leaf} response was contrary to leaf stomatal conductance and leaf net photosynthetic rates (Fig. 3, Table 2). At the beginning of the study (0 DAT), T_{leaf} ranged between a minimum of $23.6 \pm 0.4^\circ\text{C}$ in FI and a maximum of $24.2 \pm 0.3^\circ\text{C}$ in PRD. T_{leaf} in RDI and NI was 24.2 ± 0.3 and $24.1 \pm 0.5^\circ\text{C}$, respectively. At 9 DAT, when photosynthetic rates of NI plants were about half of FI, we found significant differences were found between NI ($41.2 \pm 0.3^\circ\text{C}$) and PRD ($40.3 \pm 0.4^\circ\text{C}$) in comparison to FI ($35.6 \pm 0.5^\circ\text{C}$) and RDI ($36.4 \pm 0.8^\circ\text{C}$) (Fig. 3A). T_{leaf} values for FI increased 5.6°C in relation to the beginning of the experiment, whereas PRD values rose 4.7°C . At maximum stress (14 DAT (Fig. 3A), T_{leaf} values of NI plants were $35.3 \pm 0.4^\circ\text{C}$, showing significant differences as compared to the remaining treatments, which showed values of $28.5 \pm 0.7^\circ\text{C}$, $32.1 \pm 0.5^\circ\text{C}$ and $33.5 \pm 0.6^\circ\text{C}$ in the case of FI, PRD and RDI plants, respectively.

According to this, neither T_{leaf} nor $\Delta T_{\text{leaf-air}}$ showed similar values over the experiment in the FI treatment. This finding agrees with the high variability of data recorded for gas-exchange measurements. In this sense, although the T_{leaf} values found in this treatment were significantly lower than at the beginning of the experiment 9 at 14 DAT; this treatment offered $\Delta T_{\text{leaf-air}}$ values lower than those reached the first day (almost 6°C lower than 0 DAT (Fig. 3). Considering the gas-exchange measurements, the values of

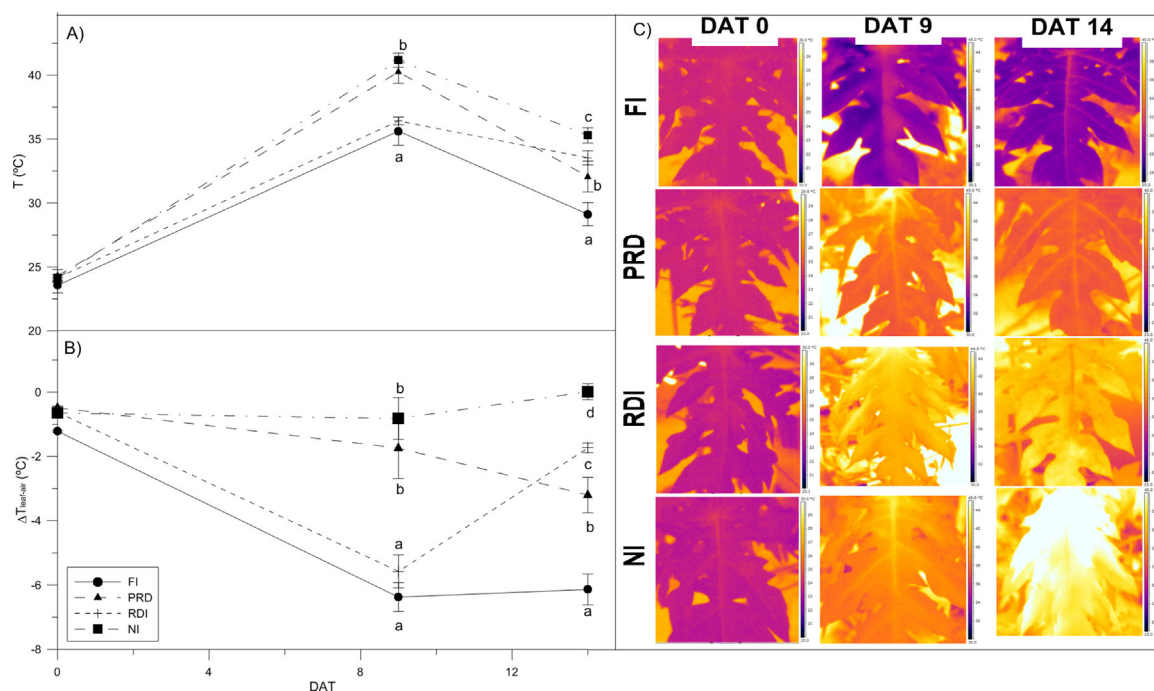


Fig. 3. (A) Leaf temperature (T_{leaf}) derived from IR measurements during the study (DAT); (B) difference of leaf to air temperature ($\Delta T_{leaf-air}$), and (C) false-colored IR thermal images showing a selected fully expanded leaf, along the experiment for the different treatments: fully irrigated (FI); partial root drying (PRD); regulated-deficit irrigation (RDI); non-irrigated (NI). Climate conditions at 0 DAT (T_{air} max: 25 °C, RH_{min} : 80%, ψ_{soil} = -10 kPa, PAR_{max} = 257 $\mu\text{mol m}^{-2} \text{s}^{-1}$); 9 DAT (T_{air} max: 44 °C, RH_{min} : 26%, PAR_{max} = 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and 14 DAT (T_{air} max: 36 °C, RH_{min} : 39%, PAR_{max} = 830 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Leaf temperature scale is identical for four treatments in the same day of observation. Different letters indicate significant differences at $P < 0.05$ by the Tukey's test ($n = 10$).

E registered were higher than those detected at the beginning of the experiment. These higher transpiration values could be the reason for a more pronounced effect of evaporative cooling in FI during the 9 and 14 DAT (Fig 3, Table 2). Moreover, comparing the $\Delta T_{leaf-air}$ values registered in NI, which were unchanged over the study, with those found in FI, we can see that, at 9 and 14 DAT the transpiration values were very low (close to zero) and this absence of transpiration promoted values of $\Delta T_{leaf-air}$ similar to those detected at 0 DAT (before to the desiccation process). The only explanation for this finding would be the weather during the measurement days.

After the study of the time course of T_{leaf} and the thermal index $\Delta T_{leaf-air}$, together with the gas-exchange measurements, the second step in this experiment was to define the hypothetical relationships between these parameters. If significant relationships were defined, then, we could conclude that an easy way to monitor the crop-water status is to use the leaf (or canopy) temperature as the main source of information. In agreement with this, no signif-

icant correlations between temperature related parameters (T_{leaf} and $\Delta T_{leaf-air}$) and leaf gas exchange measurements were found at the beginning of the experiment (0 DAT) (Fig. 4A–C; Table 3). By the contrast, these correlations were highly significant ($p < 0.05$) at 9 and 14 DAT (Fig. 4A–C; Table 3). According to these linear correlations; higher T_{leaf} values were related to lower transpiration, stomatal conductance and net photosynthesis. However, these linear regressions were different for 9 and 14 DAT, and even more for those determined with the dataset corresponding to 0 DAT.

The same relationship between T_{leaf} and gas-exchange measurements were found using the values of $\Delta T_{leaf-air}$ (Fig. 4D–F). Although these relations were not similar for each timing measurement, there was a grouping of dataset, mainly for the data from the beginning of the experiment (0 DAT) in relation to the rest. When these same relationships were calculated using the average values, as described in the model of Eq. (1), the optimum ranges of $\Delta T_{leaf-air}$ related to gas exchange measurements were identified

Table 3

Linear regression analysis between physiological parameters and temperature measurements in relation to sampling days.

Physiological parameters		0 DAT		9 DAT		14 DAT	
		T_{leaf}	$\Delta T_{leaf-air}$	T_{leaf}	$\Delta T_{leaf-air}$	T_{leaf}	$\Delta T_{leaf-air}$
E	a	–	–	–0.79	–0.79	–1.35	–1.35
	b	–	–	33.85	0.49	50.50	2.79
	r	ns	ns	0.88**	0.88*	0.89**	0.89**
g_s	a	–	–	–0.045	–0.045	–0.086	–0.086
	b	–	–	1.90	0.020	3.132	0.103
	r	ns	ns	0.85**	0.85**	0.88**	0.88**
A_n	a	–	–	–1.082	–1.082	–1.601	–1.601
	b	–	–	50.456	4.99	64.266	7.81
	r	ns	ns	0.78*	0.78*	0.73*	0.73*

DAT, day after treatment; T_{leaf} , leaf temperature; $\Delta T_{leaf-air}$, difference of leaf and air temperature; a and b are the regression coefficients according to $y = ax + b$; E , transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$); g_s , stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); A_n , photosynthesis ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$); r , Pearson's correlation coefficient.

* $p < 0.05$.

** $p < 0.01$.

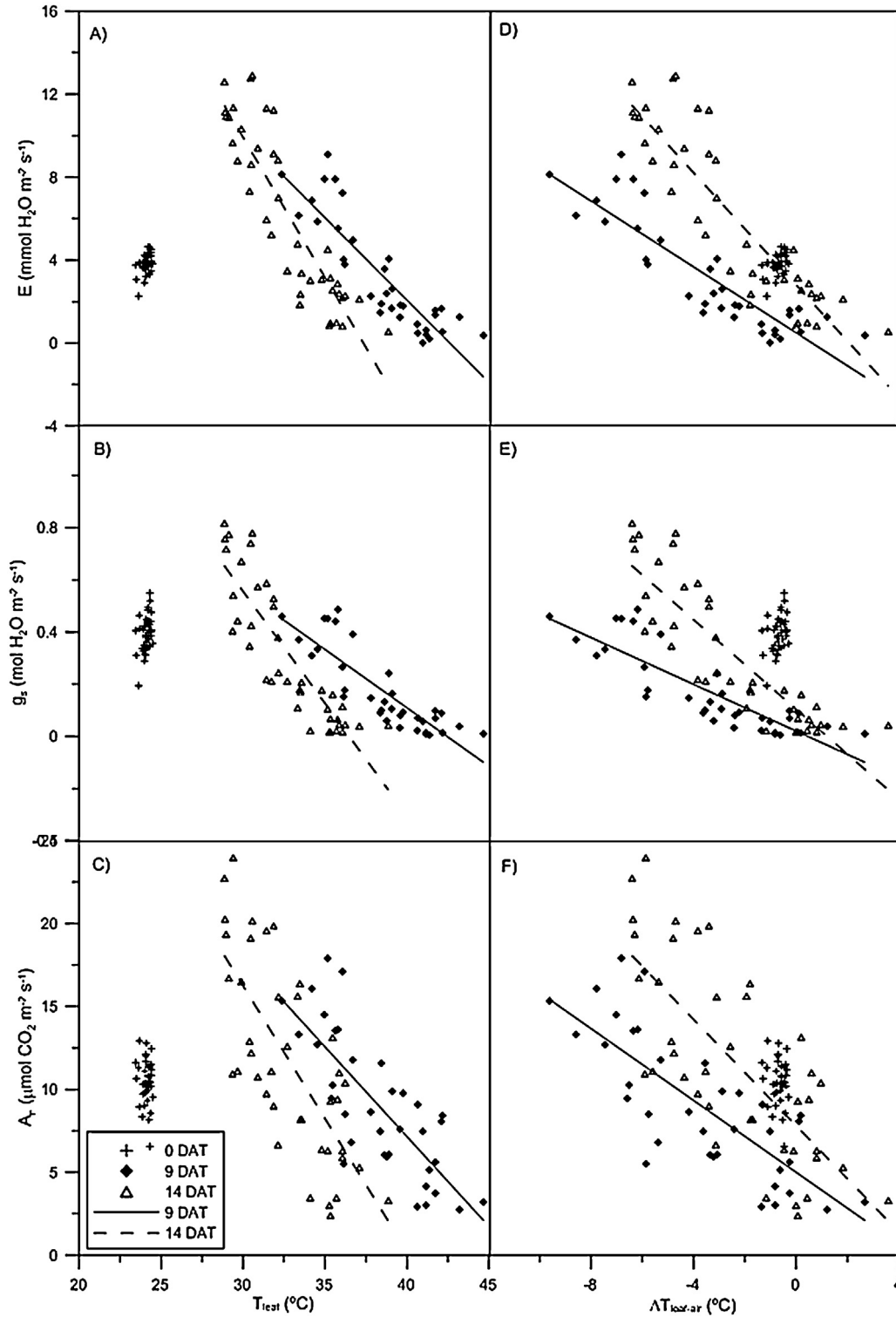


Fig. 4. Relationship between transpiration (E), stomatal conductance to water vapor (g_s) and net assimilation (A_n) vs. the leaf temperature (T_{leaf}) and the difference between T_{leaf} and air temperature ($\Delta T_{leaf-air}$). Each linear function was determined with 80 pair of data ($n = 80$).

(Fig 5, Table 4), that is, those in which a minimal increase was detected in gas-exchange responses. According to these results, $\Delta T_{leaf-air}$ values below to -2 °C would be accompanied with maximum values of A_n and g_s the maximum values of E would be reached for values of $\Delta T_{leaf-air}$ close to -4 °C.

4. Discussion

Taking into account the hypothesis and the tasks of this work, two questions arise: the first concerns the capability of thermal imaging to reflect changes in the plant–water status of papaya, and the second, whether T_{leaf} or $\Delta T_{leaf-air}$ can be considered feasible

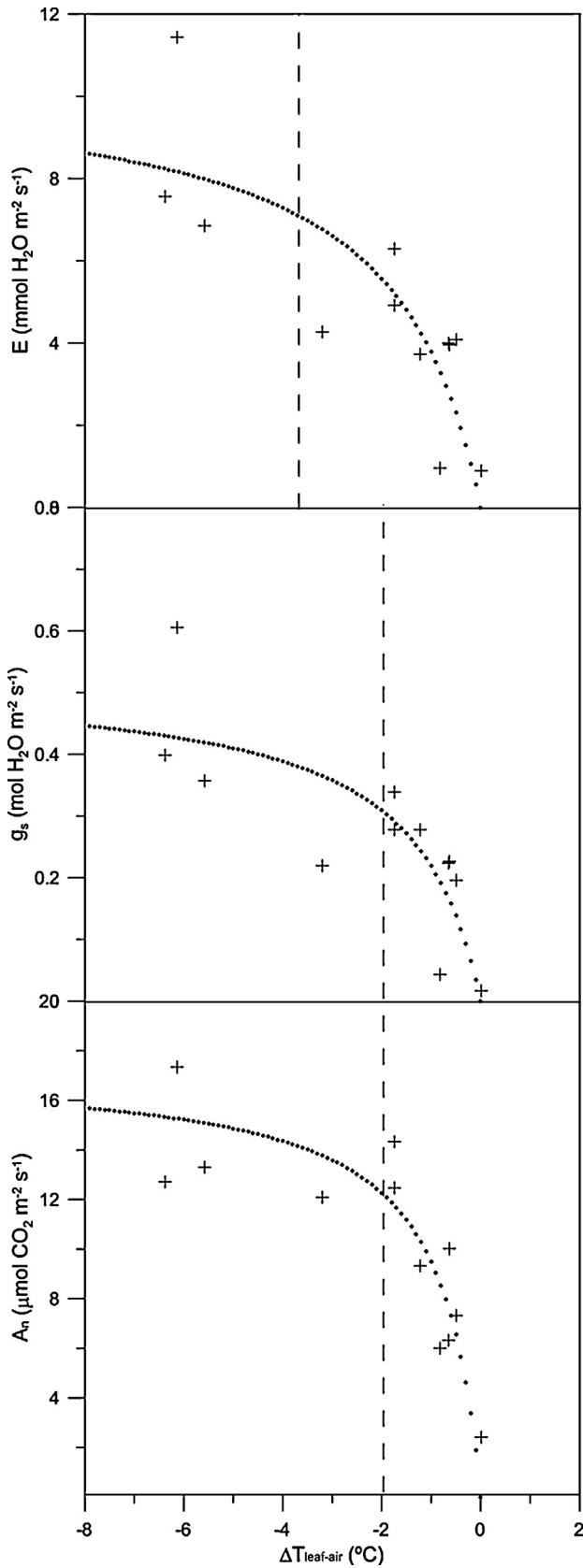


Fig. 5. Relationship between air temperature ($\Delta T_{\text{leaf-air}}$), stomatal conductance (g_s), and net photosynthesis (A_n).

Table 4

Regression coefficients and threshold values for the different adjust functions of plant physiological indicators.

$f(x)$	$\Delta T_{\text{leaf-air}}$		
	E	g_s	A_n
a	10.5	0.52	17.3
b	-1.79	-1.39	-0.82
r^2	0.64	0.64	0.86

$\Delta T_{\text{leaf-air}}$, difference between leaf and air temperature; a , and b are the regression coefficients according to the defined functions; E , transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$); g_s , stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); A_n , photosynthesis ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$); r^2 , regression coefficient.

indicators to monitor the crop physiological status of papaya when this is subjected to deficit-irrigation regimes.

Responding to the first question is not easy, as it is necessary to identify what are the main physiological changes in papaya in terms of gas-exchange measurements when this plant is subjected to deficit-irrigation regimes. Under a situation of water scarcity, many crops have a high capability of regulating leaf transpiration through stomata, reducing water loss from the plant tissues, and thereby avoiding severe plant dehydration or the total or partial embolism in the xylem vessels (Chaves et al., 2010). Because of this, there is a decline in CO_2 fixation declines, and therefore so does the photosynthetic activity of the plant (Chaves et al., 2007). Associated with lower transpiration levels, the process of evaporative cooling diminishes, raising leaf temperatures typically several degrees above the air temperature (Fuentes et al., 2012). These relationships establish the basis for monitoring the crop-water status using thermal information, since any situation that triggers a partial closing of the stomata (for example by a water-stress situation more or less prolonged) will result in a significantly higher leaf temperature.

According to Marler and Mickelbart (1998), a soil-water deficit promotes a significant drop in photosynthetic activity in papaya together with a lowering of g_s levels. Similarly, Mahouachi et al. (2006) demonstrated that when this crop was subjected to a drought period, the first effects were reflected in terms of gas-exchange parameters, with no significant changes in the leaf-water potential values, these being only affected only after a long and severe water-stress period. These findings are supported by Marler and Mickelbart (1998), who also demonstrated that the leaf relative water content and the xylem pressure potential were initially unaffected by drought in young papaya plants. Moreover, these considerations are in line with the results reported by Kempe et al. (2014), who argued that papaya needs to maintain a certain turgor-pressure values for an optimum flexural rigidity of the entire stem, this specie responding to drought via dehydration postponement. In agreement with these results, data from several authors such as Campostrini and Glenn (2007), Campostrini et al. (2010) or Maouachi et al. (2007) have demonstrated a high sensitivity of papaya leaves to water deficit, observing significant increases of ABA concentrations both in the leaves and in the roots, which promotes stomatal closure (Davies et al., 2002) and a significant slowing of the photosynthesis rate (Clemente and Marler, 1996; Lima et al., 2015). In the present study, at 9 DAT, all the deficit irrigation treatments showed significant differences in terms of gas-exchange measurements with the FI (Table 2), and these dissimilarities were reflected also in the T_{leaf} values (Fig. 3).

At first sight, low values of T_{leaf} were expected to correspond to high values of stomatal conductance or transpiration, because of the evaporative cooling process is associated with these parameters (Costa et al., 2013). However, low values of T_{leaf} are not due exclusively to high transpiration rates. Other factors such as low values of T_{air} or solar radiation, together with high values of relative

humidity could promote low values of T_{leaf} . However, we could have low values of T_{leaf} together with levels of gas exchange lower than the expected because these might not be the optimum weather conditions for the crop.

Many authors have reported that a crop's gas-exchange response is related to the different effects of micrometeorological variables such as T_{air} , PAR, RH, wind speed or VPD on T_{leaf} (Jones, 2004; Grant et al., 2007; García-Tejero et al., 2011b; Costa et al., 2013). Campostrini et al. (2010) and Campostrini and Glenn (2007) evidenced that photosynthesis activity in papaya was significantly affected by many environmental factors such as photosynthetic active radiation (PAR), air and leaf temperature, water availability or wind speed, among others. Moreover, according to Clemente and Marler (1996), stomatal conductance is widely affected by the radiation levels, arguing that abrupt changes in PAR promoted changes in leaf stomatal conductance and effects on the photosynthetic process.

These findings are consistent with the obtained results in the present work given that significant relationships between T_{leaf} and gas exchange parameters proved significant only when these were monitored for a single day and under different water-stress situations (Table 3, Fig. 4A–C). Moreover, no significant relationships were found using the values for 0 DAT, whereas these relationships improved when they were defined using the values for 9 and 14 DAT (Table 3). However, these relationships were not equal for the measurement days, as it was difficult to monitor the crop water status exclusively using the T_{leaf} values.

Once the main relationships between T_{leaf} and gas-exchange measurements were defined, there were established those using the $\Delta T_{leaf-air}$ index with the aim of normalizing the T_{leaf} values obtained during the measurements, trying to exclude the environmental effects in T_{leaf} . Within the most widely used thermal indexes, $\Delta T_{leaf-air}$ is the most user friendly because it requires only the absolute value of the air temperature (García-Tejero et al., 2014). However, this index raises the problem that its variation with the atmospheric conditions, such as the VPD (Idso et al., 1981; Idso, 1982; Jackson, 1982), is relative high. Other thermal indexes such as the CWSI or I_g are able to exclude the environmental effects, using wet and dry reference leaves (as stated in the thermal indexes of CWSI or I_g), or using non-water-stressed baselines. However, establishing these relationships is complex, because there is a high sensitivity to several climate factors such as radiation and wind speed (Jones, 1999; Jackson et al., 1988). For this reason, the selection of the most proper thermal index must take into account all the factors involved, such as the time spent in the process, as well as the robustness of the results. It is not easy to define this fact, because as it has been previously described, numerous interferences and variables could affect to the canopy temperature values.

Considering the limitations of $\Delta T_{leaf-air}$, we might ask how we can decide whether this index is the most profitable one in terms of the crop-water status monitoring. To date, many authors suggest that the main criteria to choose the best thermal index should be based on the study of the relationships between thermal indexes and crop-water stress measurements taken at the plant scale (i.e., gas-exchange measurements or crop-water potential). Thus, data on these relationships is required in order to apply this technique for a precise and robust estimation of crop-water status and irrigation scheduling (Jones et al., 2002; Costa et al., 2012; Pou et al., 2014).

Until now, the main difficulty has been to draw robust and general relationships between the main thermal indexes and the most widely studied physiological variables. The causes are not very clear, although some aspects such as the crop-response variability to water stress under different edaphic and climate conditions, the different performance of different varieties for a same crop, and the effects of weather on leaf temperature (as discussed above), would

be some of the reasons for having been unable to obtain to establish robust relationships and generalize this technique for crop-water monitoring.

These limitations hamper defining the optimum ranges in function of T_{leaf} or some thermal index. In the present work, the use of $\Delta T_{leaf-air}$ is an improvement in terms of grouping data, in comparison to the obtained for T_{leaf} ; and if these relations were drawn using the average values, we could conclude that for values of $\Delta T_{leaf-air}$ below to -2 °C gas-exchange values stabilized. Nevertheless, further research is necessary at the field scale, comparing other thermal indexes in order to establish more robust information on the use of infra-red thermography to monitor the crop-water status and irrigation scheduling.

In this sense, defining an optimum range of $\Delta T_{leaf-air}$ would be more feasible than in terms of T_{leaf} , because the former parameter would be more directly affected by the weather conditions, as discussed above. Thus, the use of $\Delta T_{leaf-air}$ in comparison with the absolute values of T_{leaf} would improve thermal-imaging analysis in papaya to monitor the crop water-status.

According to the results found in the present experiment, we can conclude that thermal imaging can be used for irrigation scheduling and water-stress monitoring of papaya, this system being particularly useful when deficit-irrigation strategies are adopted. In view of the importance of fostering the water-use efficiency and more precise water use in modern agriculture, the present study reveals improved knowledge on papaya water-stress behavior, physiological responses, and on the usefulness and robustness of remote measurements of leaf temperature to monitor water stress in the crop. This study should be complemented by future field trials, under field conditions, in order to define more robust relationships and establish more effective protocols regarding the use of thermal imaging for irrigation scheduling of papaya.

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