

ARTÍCULO DE INVESTIGACIÓN

PHOTOSYNTHETIC PERFORMANCE AND LEAF WATER POTENTIAL OF GULUPA (*Passiflora edulis* Sims, PASSIFLORACEAE) IN THE REPRODUCTIVE PHASE IN THREE LOCATIONS IN THE COLOMBIAN ANDES

Desempeño fotosintético y potencial hídrico foliar de gulupa (*Passiflora edulis* Sims, Passifloraceae) en estado reproductivo en tres localidades de los Andes colombianos

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ABSTRACT

Gulupa, *Passiflora edulis* Sims (Passifloraceae), is an important fruit due to its organoleptic and nutritional characteristics and its demand in the international market; however, very few studies have been conducted for studying its Ecophysiology. Until now, this crop has spread throughout the country through empirical knowledge without data that indicate the zones that are more suitable for its cultivation. For this reason, gas exchange, chlorophyll fluorescence (photosystem II operating efficiency and maximum quantum efficiency of photosystem II photochemistry) and leaf water potential were measured in three different locations of Cundinamarca department (Chia [2610 m a.s.l., 14 °C], Granada [2230 m a.s.l., 15 °C] and Tena [2090 m a.s.l., 17 °C]), whose climatic conditions were monitored with meteorological stations to evaluate the physiologic performance in each location related to the environmental factors. The results indicate that, even though the photosynthetic capacity was similar and high in Granada and Tena, the water status of the plant, the stomatal control of water loss and recovery of photosystems during the night were more efficient in Granada ($p < 0.05$). In Tena, the small differences between day and night temperature, humidity, and vapor pressure deficit (VPD) would limited the night water recovery in the plants. Meanwhile, in Chia, the increase of VPD during the day and the low temperatures would decreased the water potential both during the day and during the night, as well as the recovery of photosystem II. Therefore, in conclusion the climatic conditions similar to Granada, which are 18/13 °C day/night, a VPD close to 0.5 KPa, and radiation that did not exceed 1000 $\mu\text{mol photons/m}^2\text{s}$ favored the good physiological performance of gulupa.

Keywords: chlorophyll fluorescence, crop, horticulture, passion fruit, photosynthesis, plant physiology, water.

RESUMEN

La gulupa, *Passiflora edulis* Sims (Passifloraceae) es un frutal importante debido a sus características organolépticas, nutricionales y su demanda en el mercado internacional; sin embargo, existen muy pocos estudios relacionados con su ecofisiología. Hasta el momento, el cultivo se ha extendido a través del país por medio de conocimiento empírico sin tener datos que sustenten las zonas más apropiadas para su cultivo. Por esta razón, en el presente estudio se midió el intercambio de gases, la fluorescencia de la clorofila (factor de eficiencia del fotosistema II y eficiencia cuántica fotoquímica máxima del fotosistema II) y el potencial hídrico foliar en tres localidades diferentes del departamento de Cundinamarca (Chía [2610 m s.n.m., 14 °C], Granada [2230 m s.n.m., 15 °C] y Tena [2090 m s.n.m., 17 °C]), cuyas condiciones climáticas fueron monitoreadas con estaciones meteorológicas para

evaluar el desempeño fisiológico en cada localidad y relacionarlo con los factores ambientales. Los resultados indican que aunque la capacidad fotosintética fue alta y similar en Granada y Tena, el estado hídrico de la planta, el control estomático de la pérdida de agua y la recuperación de los fotosistemas durante la noche fueron más eficientes en Granada ($p < 0,05$). En Tena, la estrecha diferencia entre los valores día/noche de temperatura, humedad y déficit de presión de vapor (DPV) limitarían la recuperación hídrica de la planta, mientras que en Chía el aumento de DPV en el día, y las bajas temperaturas disminuirían el potencial hídrico, tanto durante el día como durante la noche, así como la recuperación del fotosistema II. Por tanto, en conclusión, condiciones climáticas cercanas a las de Granada; 18/13 °C día/noche, DPV de 0,5 KPa, y una radiación que no exceda los 1000 μmol fotones/ m^2s favorecen el buen desempeño de la planta.

Palabras clave: agua, cultivo, fisiología vegetal, fluorescencia de la clorofila, fotosíntesis, fruto de la pasión, horticultura.

INTRODUCTION

Plant ecophysiology is the study of the behavior of plants in particular habitats which allow the understanding of physiological performance in the field (Lüttge and Scarano, 2004). This facilitates the determination of conditions that are helpful for the development of a crop (Solarte *et al.*, 2010), providing decision-making tools for crop management and sowing sites (Higgins *et al.*, 1992) because the genetic potential of the individual will only be reached if the environmental conditions are close to optimal (Rabbinge *et al.*, 1985).

Plant ecophysiology analyze variables such as photosynthetic rate, that provide the driving force for the metabolism of sink organs (Foyer, 1987) and at the same time, are linked to the transpiration rate or water loss through the stomata. Stomata are multisensorial structures that sense environmental and physiological factors (Zeiger *et al.*, 1987) for determining water use efficiency, which is reflected in the water status of the plant which can be measured through the water potential. The stomatal control and water status of plants change in accordance with the climatic conditions so they vary throughout the day (Pandey *et al.*, 2003) and throughout the phenological cycle of plants (Thomas and Winner, 2002; Kenzo *et al.*, 2006).

The use of light by the photosynthetic apparatus is measured through chlorophyll fluorescence, allowing for the understanding of processes such as the photoinhibition caused by excess radiation that affects photosystems, causing chronic or dynamic damage (Aro *et al.*, 1993). The evaluation of the response of horticultural crops to environmental factors such as temperature, water availability, light and carbon dioxide concentration is useful for determining the effect of suboptimal environmental conditions and for managing the crops for maximum productivity (Schaffer and Andersen, 1994).

Changes in environmental factors are more evident in field conditions where the plants can be subjected to minimal and inevitable stresses to which they must respond. Therefore, studies under uncontrolled conditions are necessary for understanding events such as the reproductive phase in plants at the agronomic level.

Gulupa, *Passiflora edulis* Sims, is among the fruit crops of high importance in Colombia due to the fact that it is highly sought after in the international market due to its organoleptic and physical properties, making up one of the primary export lines for fruit in Colombia (Pinzón *et al.*, 2007). Ecophysiological studies on passiflora are scarce although the importance of the studies have been recognized (Ocampo, 2013); most of the knowledge of the crop comes from empirical observations of crops sown in different zones. Although Jiménez-Neira (2006) and Jiménez *et al.*, (2009) report its growth between 15-20 °C and at an altitudinal range from 1400 to 2200 m a.s.l., the most suitable conditions within these ranges are unknown. Despite the fact that studies on topics such as phytopathology and postharvest physiology have increased, ecophysiological studies are scarce and most of them have been conducted under controlled conditions with passiflora hybrids. Only two photosynthetic rates have been registered in seedling phase (Turner *et al.*, 1996, Cruz-Aguilar, 2012) and two in adult *Passiflora* spp. hybrid plants with an ornamental use (Abreu *et al.*, 2014) and in different varieties of passion fruit (*Passiflora edulis* fv. *flavicarpa*) in the reproductive phase (Gama *et al.*, 2013).

For this reason, the present study aimed to describe and analyze the ecophysiological performance of gulupa in the reproductive phase under three environmental conditions in the field in order to produce tools that elucidate the conditions that result in better performance in the crop as linked to good agricultural practices, which will be reflected in fruit quality and yield. It is expected that climatic conditions such as high humidity and a low water deficit pressure result in a more efficient water use and a better water status in the plants, while the quantity of light of each location directly influence the photosynthetic rate.

MATERIAL AND METHODS

Study site

Experimental plots were sown with 100 gulupa plants at a distance of 6x3 m, in three different locations in the Department of Cundinamarca: Chia, located at 2610 m a.s.l., with an average temperature of 14 °C (04° 50.952' N 74° 04.343' W); Granada, located at 2230 m a.s.l. with an

average temperature of 15 °C (4°30.150'N 74° 21.532'W); and Tena, located at 2090 m a.s.l. with an average temperature of 17 °C (4° 41.234' N 74° 21.592'W).

A simple trellis system with double wires was used. The plants were managed with formation and maintenance pruning and were fertilized monthly in accordance with edaphic analysis. Irrigation was carried out at field capacity in periods of low precipitation in order to ensure water availability in the soil.

Meteorological stations were installed in each of the plots (Coltein Ltda, Bogotá, Colombia) with data loggers (Coltein Ltda, Bogotá and Hobo U12-006, Onset Computer Corporation, Bourne, Massachusetts, USA) that monitored the relative humidity (%) and temperature (THR-102 sensors, USA), and photosynthetically active radiation (PAR; LI 190 B sensors, LI-COR Inc. Lincoln, Nebraska, USA) every fifteen minutes. The vapor pressure deficit was determined by the method developed by Allen *et al.*, (2006).

Ecophysiological variables

The ecophysiological samplings were taken in the reproductive phase; in the flowering stage (flowering peak) and during fructification (fructification peak) in each of the locations during 2011. The measurements were taken in 10-21 months-old plants, in completely healthy and developed young leaves in tertiary branches directed towards the two wires of the trellis system. The ambient carbon dioxide (C_a) and the internal carbon dioxide (C_i), the transpiration rate (E) and the stomatal conductance (g_s) were measured with an IRGA gas analyzer (ADC LCPro+, Bioscientific Ltd, Hoddesdon, UK). The C_i/C_a index was determined to evaluate the photosynthesis stomatal limitations and the extrinsic water use efficiency was determined as photosynthetic rate/transpiration rate. The leaf water potential (Ψ) was measured with a Schölander pump, model 1000 (PMS Instruments Co, Albany, Oregon, USA). The photosystem II operating efficiency (Φ_{PSII}), which estimates the efficiency at which light is absorbed by PSII and is used by the first acceptor of electrons (plastoquinone A) (Baker, 2008), was measured with a modulated fluorometer (FMS2, Hansatech, King's Lynn, UK). In order to analyze the results related to the photosynthesis variables, the photon flow density (PPFD) was measured with the PAR sensors adjusted to IRGA gas analyzer and with modulated fluorometer, allowing registering the instantaneous incident radiation in the measuring moment.

All of the above measurements were taken in ranges of two hours, between 7:00 and 18:00 for two days in the two stages of the reproductive phase. The water potential and maximum quantum efficiency of photosystem II photochemistry (Fv/Fm) were measured at 4:00. The fluorescence measurements were taken in 20 plants and, in each one, 40 leaves were measured (20 leaves in each tertiary branch exposed on the trellis wire) and the water

potential and gas exchange measurements were taken in ten plants, six leaves of each plant (three leaves in each tertiary branch exposed on the trellis wire).

At the same time, HH2 soil moisture meters were installed (Delta T Devices Ltd, Cambridge, UK) in three different places in the plots of each location to measure the soil moisture content.

Photosynthetic light curves

The photosynthetic response light curves (A/PPFD) were done between 7:30 and 12:00 in three plants in each location, controlling the temperature at 25 °C and the CO₂ at 380 ppm. The plants were subjected to radiations of 1200, 1000, 800, 600, 400, 300, 200, 100, 50 and 0 $\mu\text{mol photons/m}^2\text{s}$ consecutively and the leaves in each radiation level were left to stabilize for a minimum of three minutes. The curves were adjusted by regression to a rectangular hyperbolic model (Mielke *et al.*, 2005; Solarte *et al.*, 2010) of the equation:

$$A = (A_{\max} * \text{PPFD}) / ((k + \text{PPFD})) - R_{\text{dark}}$$

Where A is the photosynthetic rate, A_{\max} the maximum photosynthetic rate, PPFD the photosynthetically active radiation, and k is half of the photosynthesis saturation radiation. The light compensation point, I_c , was determined by solving the equation for zero. The quantum efficiency, Φ_{PPFD} , was determined from the slope of the initial lineal portion of the A/PPFD curve (Bauerle *et al.*, 2006).

Statistical analysis

Lilliefors test was used to test the suppositions of normality. Due to the absence of normality of the data, the non-parametric tests of Kruskal-Wallis and Friedman were applied, using hour-location as factor. The differences were considered significant if the probabilities were less than 0.05. The area under the curve was determined to find the total fixed CO₂ and the total water loss through the foliar surface during the sampling days by using the disease progress curve method (AUDPC). All of the tests were carried out with the RStudio software (2012) with the R MESS (Ekstrom, 2013), MASS and Pgirmess packages (Venables and Ripley, 2002).

RESULTS

Climatic conditions

As can be seen in Figure 1, photosynthetically active radiation in Granada and Tena registered a tendency to increase in the morning hours and decrease at midday. Meanwhile, in Chia, the hours of higher radiation were registered at midday. The radiation in Granada was the highest, without exceeding 900 $\mu\text{mol/m}^2\text{s}$ on average, followed by Chia where the hours of high radiation reached an average of 800 $\mu\text{mol/m}^2\text{s}$. In Tena, the radiation in the morning hours reached an average of 700 $\mu\text{mol/m}^2\text{s}$ and decreased in the afternoon to values close to 500 $\mu\text{mol/m}^2\text{s}$ which is

avored by breaks provided by mist at some hours of the day, which considerably decreased the radiation. As can be seen in Figure 1b, the temperature in the day was similar from morning until afternoon in Granada and Tena (18 °C) but during the night the temperature decreased more in Granada, with a bigger difference between the day and the night (15 °C and 13 °C in Tena and Granada night respectively). By contrast, Chia presented lower temperatures for both the day

(13 °C) and the night (11 °C). As can be seen in Figure 1c, the relative humidity presented a higher fluctuation between day and night in Chia, decreasing considerably during the day to values near 65 %, while the night saw values of 95 %. Granada registered values similar to those of Chia in the night but, during the day, these values did not go below 80 %; meanwhile, Tena registered small differences between the day and the night, remaining close to 85 % throughout the 24

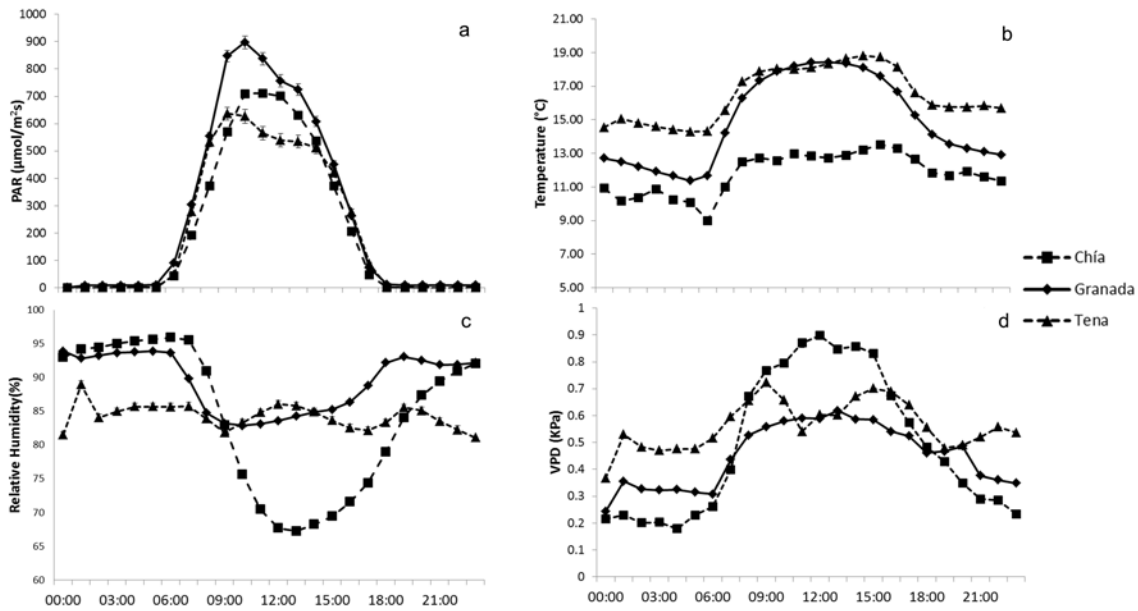


Figure 1. Climatic variables in the gulupa crops: (a) photosynthetically active radiation (PAR), (b) temperature, (c) relative humidity and (d) vapor deficit pressure (VPD). Each point represents the average of each location between 2009 and 2012 \pm standard error.

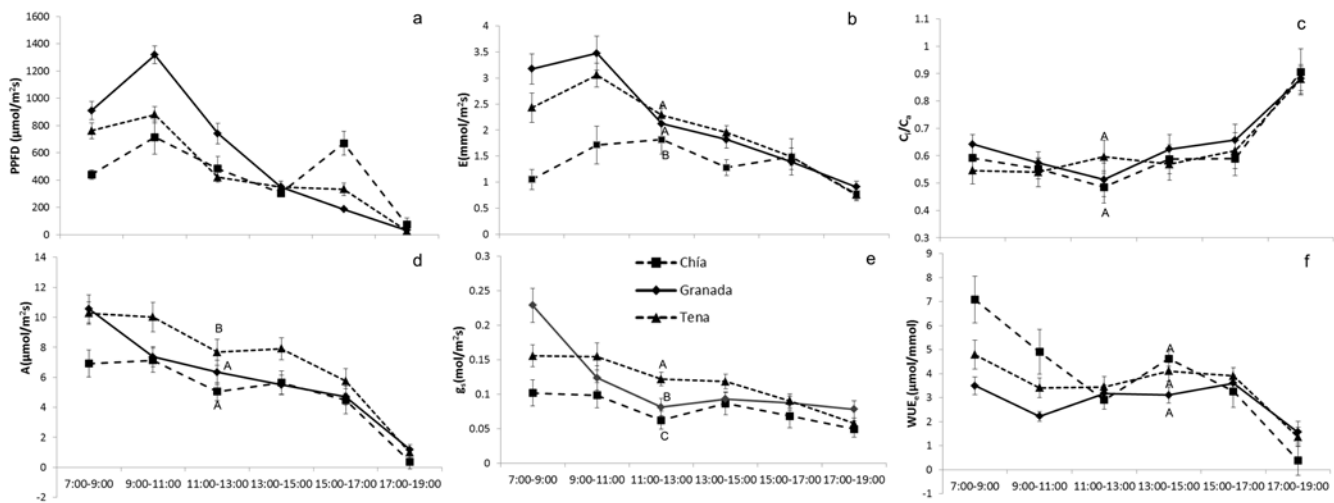


Figure 2. Daily record of (a) photosynthetic photon flux density (PPFD), (b) transpiration rate (E), (c) internal carbon/environmental carbon (C_i/C_a), (d) photosynthetic rate (A), (e) stomatal conductance (g_s), and (f) extrinsic water use efficiency (WUE_e) during the flowering stage in each of the locations. Each point represents the average of ten plants \pm standard error. Different letters indicate significant differences with $p < 0.05$.

hours of the day. Figure 1d shows that in Chia, there was a daily increase in VPD close to 0.9 KPa, related to the decrease in relative humidity but at night the VPD decrease below the other two locations. Granada presented a lower VPD during the day (0.6 KPa) while Tena registered a higher VPD during the night (0.5 KPa) and most part of the day (0.7 KPa).

The soil moisture content did not vary considerably throughout the day in the three locations during the sampling days. In Tena, an edaphic moisture content of between 0.42 and 0.48 m³/m³ was registered. The soil of Chia and Granada registered similar moisture content between 0.19 and 0.28 m³/m³.

Ecophysiological variables

Flowering stage

The photosynthetic rate (Fig. 2d) during the day was significantly higher in Tena than in Granada and Chia ($\chi^2=5.33$; $p<0.01$). The trend of the incident radiation (Fig. 2a) was similar to the photosynthesis trend in Tena and Chia while, in Granada, a decrease in the photosynthetic rate was registered in the hours of high radiation (close to 1400 $\mu\text{mol}/\text{m}^2\text{s}$), which was linked to a decrease in stomatal conductance (Fig. 2d) as well as for C_i/C_a (Fig. 2c), and a significant increase in the transpiration rate above of Tena and Chia locations was also registered, which generated a

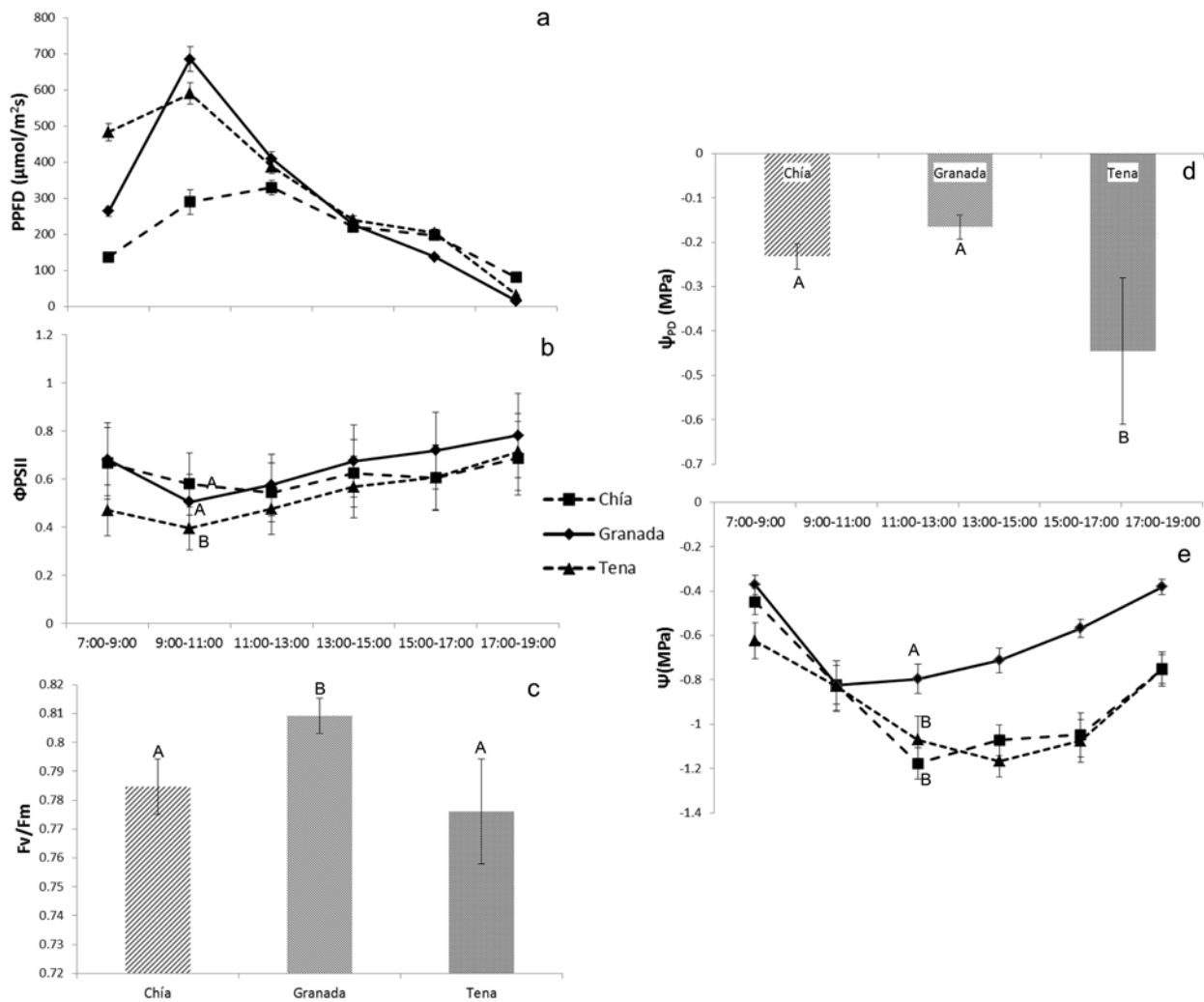


Figure 3. Daily record of the chlorophyll fluorescence and leaf water potential of the gulupa plants in the flowering stage in the three locations: (a) photosynthetic photon flux density (PPFD), (b) photosystem II operating efficiency (Φ_{PSII}), (c) maximum quantum efficiency of photosystem II photochemistry (Fv/Fm), (d) leaf water potential before dawn (Ψ_{pd}), (e) leaf water potential during the day (Ψ). In the water potential figure, each point represents the average of ten plants \pm standard error and, in the chlorophyll fluorescence figure, each point represents the average of twenty plants \pm standard error. Different letters indicate significant differences with $p < 0.05$.

decrease in the extrinsic water use efficiency that was not significant. The total CO₂ gain during the sampling days was 37.0 μmol CO₂/m²s in Tena, 29.8 μmol CO₂/m²s in Granada and 26.0 μmol CO₂/m²s in Chia.

The transpiration rate did not show significant differences in Granada and Tena and was significantly lower in Chia (χ²=9.00; p=0.011), which was reflected in the water loss during the two days that was 7.2 mmol H₂O/m²s in Chia, 10.42 mmol H₂O/m²s in Granada and 10.82 mmol H₂O/m²s in Tena; the radiation behavior was similar to the transpiration trend in the three locations (Fig. 2a and 2b). Although there were no significant differences (χ²=3.00; p=0.22), the water use efficiency was lower in Granada in the first hours of the day, followed by Tena and Chia (Fig. 2f). For its part, the decrease in photosynthesis in the midday hours

in Chia, similar to what occurred in Granada, was connected to a significant decrease in stomatal conductance (χ²=21.97; p<0.01) (Fig. 2e) and C_i/C_a (χ²=3.00; p=0.22) (Fig. 2c).

Figure 3b demonstrates a significant decrease of PSII operating efficiency in the plants of Tena (χ²=7.00; p=0.030) in high radiation hours of day, as compared to Granada and Chia, despite the fact that the PAR registered in Tena in the measurement points was similar to that of Granada (Fig. 3a). For its part, the maximum quantum efficiency of photochemistry (Fig. 3c) registered optimal values in Granada, while the plants grown in Chia and Tena had significantly lower values (χ²=71.70; p<0.01).

The leaf water potential during the day can be seen in Figure 3e, which was significantly higher in the plants of Granada (χ²=9.47; p=0.008), where the lowest value was

Table 1. Parameters derived from the photosynthetic light response curve, A/PPFD, in the flowering and fructification stages in the three studied locations (n=3). A_{max}=Maximum photosynthetic rate, I_c=Light Compensation Point, φ_{photons}=quantum efficiency.

Flowering stage					
Location	R ²	A _{max} (μmol/m ² s)	I _c (μmol/m ² s)	PAR sat (μmol/m ² s)	φ _{photons} (μmol CO ₂ /μmol photons)
Granada	0.85	10.13	26.59	243.08	0.034
Tena	0.96	19.93	13.37	419.54	0.042
Chia	0.93	8.88	26.90	230.66	0.030
Fructification stage					
Location	R ²	A _{max} (μmol/m ² s)	I _c (μmol/m ² s)	PAR sat (μmol/m ² s)	φ _{photons} (μmol CO ₂ /μmol photons)
Granada	0.92	15.84	15.31	1161.44	0.024
Tena	0.95	12.23	11.19	323.90	0.032
Chia	0.88	8.74	13.46	371.16	0.027

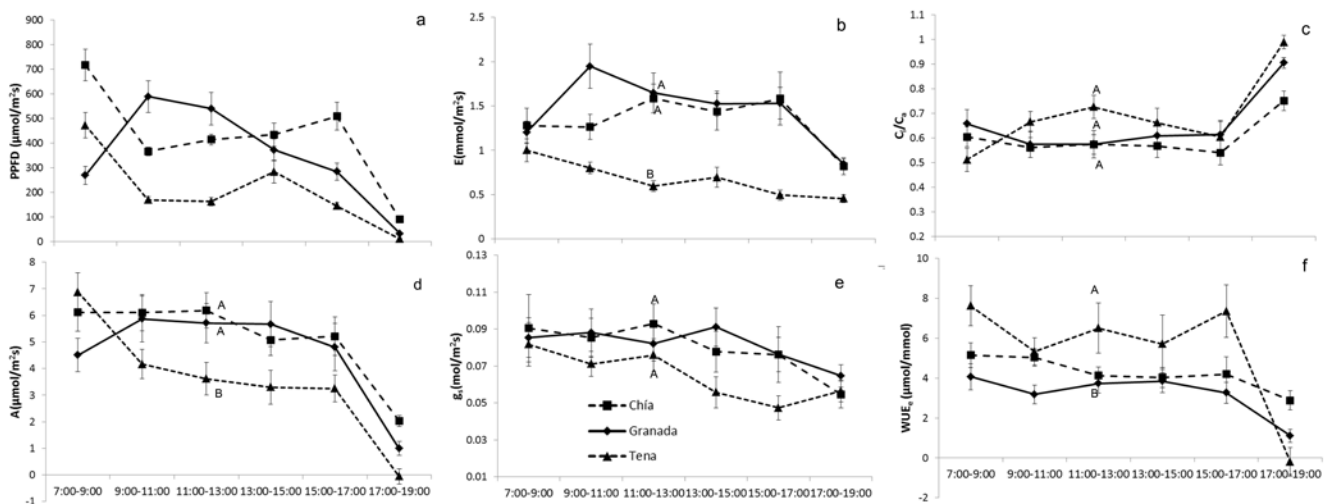


Figure 4. Daily records of (a) photosynthetic photon flux density (PPFD), (b) transpiration rate (E), (c) internal carbon/environmental carbon (C_i/C_a), (d) photosynthetic rate (A), (e) stomatal conductance (g_s), and (f) extrinsic water use efficiency (WUE_e) in gulupa plants during the fructification stage in each of the locations. Each point represents the average of ten plants ± standard error. Different letters indicate significant differences with p<0.05.

seen in the hours of the highest transpiration, which did not go under -0.8 MPa; followed by the plants sown in Tena and Chia, which did not present significant differences, registering values under -1.0 MPa between 11:00 and 15:00. The decrease in stomatal conductance and the increase in transpiration in the first few hours (Figs. 2e and 2b) were corresponded with a decrease in leaf water potential in Granada. The leaf water potential before morning (Fig. 3d) recovered in Chia, remained high in Granada, and remained low in Tena, with values close to -0.5 MPa ($\chi^2=81.14$; $p>0.01$).

The parameters found using the A/PPFD curve (Table 1) in the flowering stage indicated a higher photosynthetic capacity in Tena at a radiation near $420 \mu\text{mol}/\text{m}^2\text{s}$, a lower light compensation point and higher quantum efficiency, followed by Granada and Chia with similar values between them but with a high photosynthetic capacity in Granada.

Fructification stage

The photosynthetic rate was significantly lower in Tena ($\chi^2=7.60$; $p<0.01$), which was related to the low photosynthetically active radiation registered during the sampling days as seen in Figure 4a; only in the first range of the day where the PPFD was close to $500 \mu\text{mol}/\text{m}^2\text{s}$ did photosynthesis increased. The photosynthetic rate was similar in Granada and Chia and remained constant with a decrease in the midday hours (Fig. 4d). The total fixed CO_2 was $26.6 \mu\text{mol}/\text{m}^2\text{s}$ in Chia, $24.8 \mu\text{mol}/\text{m}^2\text{s}$ in Granada and $17.7 \mu\text{mol}/\text{m}^2\text{s}$ in Tena.

Figure 4d demonstrates that the low photosynthesis in Tena was related to the low transpiration (Fig. 4b) along with a very low stomatal conductance (Fig. 4e). This generated a significantly higher water use efficiency in Tena ($\chi^2=6.33$; $p=0.044$) (Fig. 4f). The decrease of g_s was not

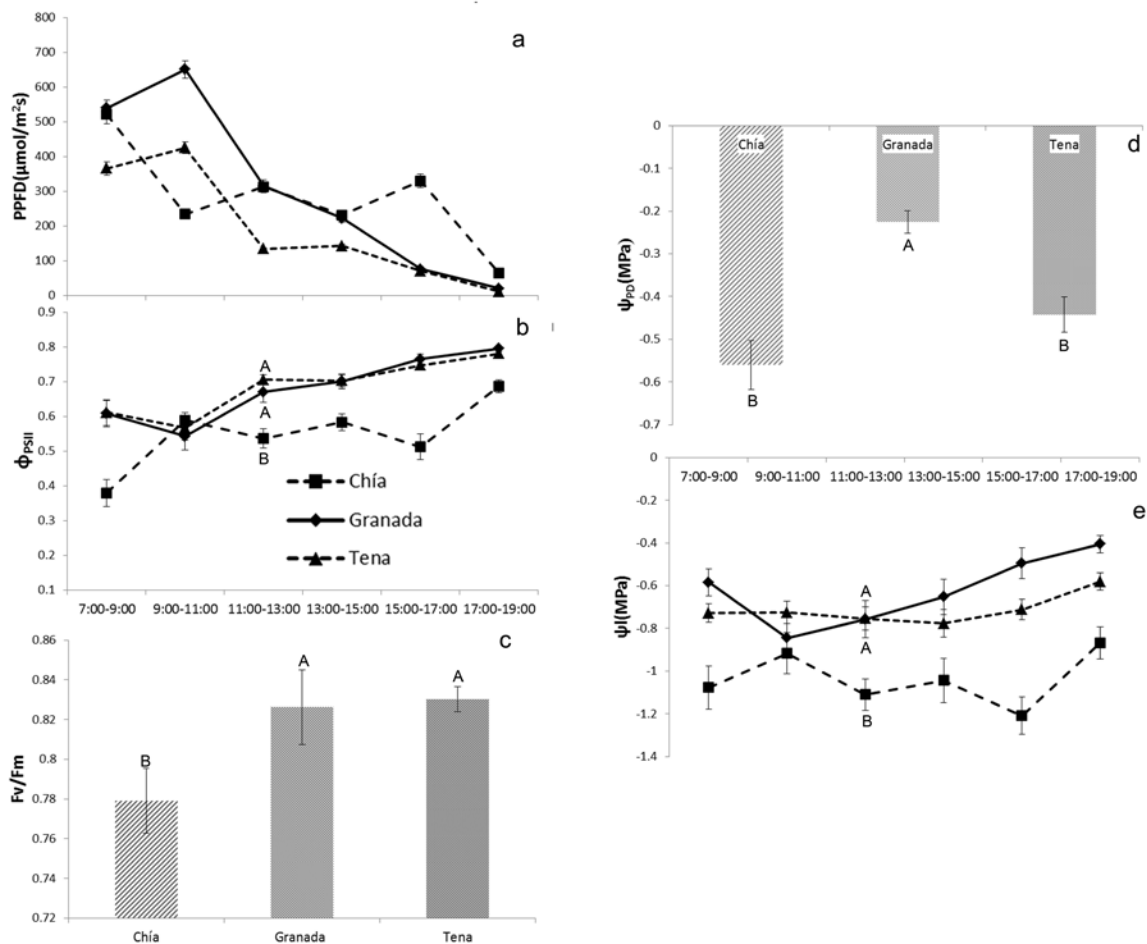


Figure 5. Daily record of the chlorophyll fluorescence and water potential of gulupa plants in the fructification stage in three environmental conditions: (a) photosynthetic photon flux flow density (PPFD), (b) photosystem II operating efficiency (Φ_{PSII}), (c) maximum quantum efficiency of photosystem II photochemistry (F_v/F_m), (d) leaf water potential before dawn (Ψ_{PD}), (e) leaf water potential during the day (Ψ). In the water potential figure, each point represents the average of ten plants \pm standard error. In the chlorophyll fluorescence figure, each point represents the average of twenty plants \pm standard error. Different letters indicate significant differences with $p<0.05$.

reflected in the decrease in C_i/C_a in Tena, which was similar in Granada and Chia (Fig. 4c). The transpiration rate and stomatal conductance were similar in Granada and Chia.

Figure 5a shows that, despite the fact that there was higher radiation in Granada, the PSII operating efficiency (Fig. 5b) was similar to that of Tena. At the same time, despite the fact that the radiation in Chia in the morning hours was lower than in Granada, the PSII operating efficiency was similar and for the next hours was significantly lower ($\chi^2=6.33$; $p=0.042$). For its part, F_v/F_m registered optimal values in Granada and Tena, however, in Chia, the values had significant differences ($\chi^2=144.76$; $p<0.001$) and indicated possible stress in the plants (Fig. 5c).

Figure 5e evidences a leaf water potential that was significantly lower during the day in plants grown in Chia ($\chi^2=61.50$; $p=0.0065$) than the plants grown in Granada and Tena. The slight changes in stomatal conductance were related to changes in the water potential, which were more evident in Granada. A high water recovery could be seen in Figure 5d for Granada ($\chi^2=81.14$; $p<0.001$), while the plants grown in Chia and Tena registered lower values and, therefore, a lower water recovery by the roots.

The parameters found by the A/PPFD curve for the fructification stage can be seen in Table 1. The maximum photosynthetic rate was higher in Granada, followed by Tena and lower in Chia. Nevertheless, the saturation radiation was considerably higher in Granada and much higher than in the flowering stage, while in Chia and Tena it was low and similar. The light compensation point was higher in Granada, followed by Chia and Tena, while the quantum efficiency was high in Tena but low and similar in Chia and Granada.

DISCUSSION

The higher photosynthetic rate values registered during the day were similar to those shown for passion fruit varieties FB2000 and Gigante Amarelo, but lower than other varieties (Gama *et al.*, 2013). In the three locations, the environmental conditions during the morning favored an increase in the WUE_g due to the fact that there are suitable radiation for an increase in photosynthesis while the VPD, temperature, and humidity conditions do not hazard an excessive loss of water by the leaf surface (Bucci *et al.*, 2003; Zweifel *et al.*, 2007; Mengistut *et al.*, 2011). This has also been observed in plants in temperate (Bassow and Bazzas, 1998), Mediterranean (Chaumont *et al.*, 1994; Gatti and Rossi, 2010) and tropical Savanna zones (Eamus *et al.*, 1999).

In the flowering stage in Granada, the instantaneous decrease in photosynthesis was connected to the an increase in radiation to over 1000 $\mu\text{mol}/\text{m}^2\text{s}$ (Fig. 2a), which brought about an increase in leaf temperature and a decrease in stomatal conductance, which have also been observed in *Actinidia deliciosa* (kiwi), another climbing fruit (Buwalda *et al.*, 1992). Nevertheless, if the average radiation

of Granada (Fig. 1a) is compared with the maximum value of the day during the sampling, over 1000 $\mu\text{mol}/\text{m}^2\text{s}$, it can be observed that it corresponds with values over the average and, therefore, would not be a recurring phenomenon in this location.

Although the water use efficiency was low in the reproductive phase in Granada, connected to a considerable transpiration rate, this did not induce a lower leaf water potential in the plants, indicating an effective water recovery that must be supported by a high water conductance (Hubbard *et al.*, 2001). This agrees with the fact that, in Granada, there are higher radiation, clear skies, and the soil is not water saturated (as was seen by the water soil content), which favor water uptake by the roots and its transport by the xylem due to the fact that it generates a high stomatal sensitivity to environmental changes (Rocha *et al.*, 2004). Cavatte *et al.*, (2012) reported that a low moisture content in the soil and high radiation in the day increase the nocturnal ability for hydration. When comparing the transpiration rate, the stomatal conductance and the water potential, a finer stomatal control was observed for Granada, evidenced by the fact that a slight decrease in stomatal conductance, caused a decrease in the transpiration that was clearly reflected in an increase in the water potential, which although also was observed in Chia, was less evident. The above facts reflected the fact that the best water status was found in the reproductive phase of the plants grown in Granada.

Despite the fact that clear skies are also found in Chia, VPD values that were close to 1.0 KPa (Fig. 1d) did not favor an adequate water recovery because they could generate cavitation in the xylem (Schultz and Matthews, 1997), which is evidenced in the water potential values during the day and the night, despite registering low transpiration rates. The low water potential values before morning that were registered in plants grown in Chia in the fruiting stage, could result from a low temperature during the night that decrease the permeability of the roots and its water conductivity (Matzner and Comstock, 2001; Norisada *et al.*, 2005); these values were close to those reported for grapevines (*Vitis vinifera*) under water deficit conditions (Tay *et al.*, 2007).

With respect to the chlorophyll fluorescence, the ϕ_{PSII} indicated a more efficient use of the light by the plants grown in Granada because a high incident radiation registered a low decrease of the efficiency factor of photosystem II. In the same manner, F_v/F_m was high in the flowering stage (in Tena only in fruiting stage), as in fructification, and its values indicated an optimal state of photosystem II (Maxwell and Johnson, 2000), which is supported by the climatic conditions of Granada, which include a low VPD both in the day and in the night, an average temperature of 18 °C in the day and 13 °C at night, and a considerable increase in relative humidity that does not decrease considerably in the day. This indicates

a high recovery capacity and light use by photosystem II in Granada, which is connected to a high efficiency in the conversion of light intercepted to the biomass, resulting from a high recuperation by photoprotection (Long *et al.*, 2006). Despite the low radiation in Tena, the Fv/Fm was not higher than in Granada and Chia, locations with higher radiation, indicating that other factors, such as the differences between the VPD, temperature and humidity for the day and for the night, which were small in Tena, are important for maintaining the capacity of photosystem II.

The photosynthetic rates in Tena are principally limited by the low average radiation (Fig. 1a) because the environmental conditions that presented during the sampling in the flowering stage and the first range measured in the fructification stage indicate that, with an increase of radiation to over 500 $\mu\text{mol}/\text{m}^2\text{s}$, photosynthesis increases. At the same time, the mist, besides limiting the available radiation, moistened the surfaces of the leaves, decreasing the diffusion of CO_2 to the interior of the leaves (Nobel, 1999; Guy-Letts and Mulligan, 2005). In addition, when radiation decreases considerably, as registered for the fructification stage sampling, the stomatal conductance remains very low, although the C_i/C_a data indicated that there were no stomatal limitations in Tena. Despite the fact that the VPD in Tena was not critical during the day, it increases to 0.7 KPa, which would favor an occasional high decrease in the water potential during the day with respect to Granada. In the flowering stage in Tena the Ψ maintained in the night time hours possibly due to a low difference in humidity, temperature, and VPD between the day and night, which would also be important for water recuperation. Additionally, the changing radiation conditions during the day, connected to the breaks provided by mist, caused instantaneous changes in other variables, such as temperature and humidity, to which the plants could not immediately respond because they need time to recover CO_2 uptake when radiation decreases (Long *et al.*, 2006).

In regards to the photosynthetic light curves, in general, with the exception of the PPFD_{sat} in Granada in the fructification stage, the low need for radiation in gulupa was evidenced, which is related to the behavior of subtropical plants in which light is not limiting due to the fact that the stomatal opening is maximum at a relatively low PPFD (Machado *et al.*, 2005; Ribeiro *et al.*, 2005), as verified with the daily tendencies of the three locations where, at low radiation, the photosynthesis increased to up to 7.0 $\mu\text{mol}/\text{m}^2\text{s}$ in the first hours of the day. Nevertheless, the optimal conditions that are supplied to the leaf when measuring A/PPFD curves, makes the difference between the results of daily curves (not environmentally controlled) and environmental controlled A/PPFD. For this reason, the A_{max} is higher than the maximum value of photosynthesis registered in the daily curve at similar or higher radiations.

The A/PPFD curves indicated that Tena has a high photosynthetic capacity, which was more evident in the flowering stage and indicated that the conditions are not stressful for the gulupa found there, but, better yet, are limiting for the increase of photosynthesis in environmental conditions. The results in the flowering stage are related to the fact that a high night temperature increases A_{max} because it increases the strength of the carbohydrate sinks due to the increase in respiration in darkness that reduces the concentration of carbohydrates in the leaves (Turnbull *et al.*, 2002). In the reproductive phase, in general, the high efficiency in the use of photons and the lower light compensation point registered in Tena are related to the low radiation of the location as seen in undergrowth plants adapted to low quantities of light (Kitao *et al.*, 2000). The photosynthetic capacity was lower in Chia in the two evaluated stages, a product of the low temperatures because in general, tropical species are vulnerable to temperature decreases (Crawford, 1989). Niyogi (1999) and Ribeiro *et al.*, (2005) reported that nighttime cooling decreased the maximum photosynthetic rate, probably due to decrease in the rate of chemical reactions that are part of the photosynthetic system. For its part, although the photosynthetic capacity increased in Granada in the fructification stage, the increase in the saturated radiation was considerable, which verified the plasticity of the plants to changing conditions in the long term because the data measured with the meteorological stations indicated that, during the months previous to the sampling, the radiation increased in Granada (data not shown). The results for the fructification stage were related to high radiation in Granada, which generated a higher saturated radiation as evidenced in Kiwi, *A. deliciosa* (Laing, 1985; Greer and Halligan, 2001).

Therefore, despite the fact that the photosynthetic capacity is suitable in Tena, as in Granada, in Tena, the specific limitations of the low radiation and the differences between the climatic variables, such as RH, temperature, and VPD, between day and night did not allow for the recovery of the water potential during the night, affecting the good physiological performance of the plants.

CONCLUSIONS

The conditions in Granada were more suitable for the development of gulupa, indicating that a low VPD (close to 0.5 KPa), high relative humidity, and average temperature of 18 °C favored the good ecophysiological performance of gulupa. The differences for humidity, temperature, and VPD between the day and night were important for the recovery of the leaf water status and the photosystems, but must be connected to a low VPD during the day. In Tena, although the low radiation was limiting, the photosynthetic capacity was suitable, indicating that the low water potential during the night has no effect. Nevertheless, the small differences between the day and night for the vapor pressure deficit

impeded the recovery of the water status at night. For their part, the low temperatures in Chia and the increase in the VPD in the day did not favor the water status of the plants, generating mechanisms that favor the conservation of water and impede the adequate recovery of photosystem II during the night.

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