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ORIGINAL ARTICLE

Photochemical metabolism and fruit quality of Ubá mango tree exposed to combined light and heat stress in the field

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Abstract Several experiments have highlighted the complexity of stress interactions, in field conditions, involved in plant response. However, these impacts on the mechanisms involved in plant photosynthetic response remains understudied. The aim of this work was to compare the photosynthetic efficiencies and fruit quality of mango tree (*Mangifera indica* L.) cv. Ubá harvested from plants cultivated on the east and west sides of a commercial orchard, according to the position of plants in relation to sunrise. Chlorophyll a fluorescence, was analyzed in leaves in four different periods: fruit growth phase, fruit ripening phase, post-harvest period and after plant pruning. Photoinhibitory damage was detected by the trapped energy flux and transported electron flux per reaction center during the fruit ripening phase, and by specific energy fluxes and yield quantum efficiency after plant pruning. Although high radiation caused photoinhibition on leaves from plants cultivated on the west side of the orchard, it provided sweeter fruits. In contrast to our initial hypothesis, it was verified that plants cultivated on the west side of the orchard presented better photochemical performance in periods with the greatest requirements of photoassimilates. In addition, plants demonstrated different abilities to deal with changes on photosynthetic active radiation and high temperature. This information suggests that the phenotypic plasticity of the Ubá mango cultivar is considerable, which can be exploited to be used in regions with great relief variations and the combination of increased irradiance and high temperature.

Keywords *Mangifera indica* L. · Chlorophyll *a* fluorescence · Photoinhibition · Sweeter fruit

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Introduction

Ubá mango (*Mangifera indica* L.) is a cultivar that produces fruits with excellent nutritional properties due to its carotenoid and ascorbic acid contents, which are efficient antioxidants against free radicals (Rosalie et al. 2015). In addition to these characteristics, high yield, attractive pulp color and high soluble solids content make the Ubá mango preferable by pulp processing and juice production industries. With the increase of crop-growing areas, studies on the quality of Ubá mango fruit have intensified. The exposure of mango fruits to high temperature and intense light conditions may lead to metabolic and physiological disorders and affect fruit yield and quality (Léchaudel et al. 2010, 2013). Therefore, little is known about the

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Table 1 Total soluble solids (TSS) content, titratable acidity (TA), ratio TSS/TA and β-carotene of the Ubá mango fruit of each light condition (plants grown on the east side—ES and plants grown on the west side—WS) in different maturation stages

Parameters	Maturation stages	Plants grown on the east side (ES)	Plants grown on the west side (WS)
TSS (°Brix)	0	7.27 ± 0.70d	11.58 ± 0.81c*
	2	11.30 ± 1.40c	10.40 ± 1.32c
	4	16.27 ± 0.49b	17.20 ± 0.10b*
	Ripe	19.12 ± 0.28a	21.27 ± 0.31a*
TA (% citric acid)	0	1.63 ± 0.16a	1.44 ± 0.11b
	2	1.56 ± 0.06a	2.02 ± 0.19a*
	4	1.04 ± 0.04b	1.14 ± 0.08c
	Ripe	0.48 ± 0.02c	0.43 ± 0.05d
TSS/TA	0	4.48 ± 0.30c	8.10 ± 1.15c*
	2	7.25 ± 0.66c	5.20 ± 1.09c
	4	15.72 ± 1.03b	15.18 ± 1.20b
	Ripe	39.99 ± 1.83a	51.06 ± 5.63a*
β-caroteno (mg/100 g)	0	10.90 ± 2.52b	15.78 ± 2.69b
	2	17.31 ± 5.85b	18.08 ± 0.97b
	4	17.22 ± 3.08b	19.25 ± 0.07b
	Ripe	54.27 ± 1.74a*	29.51 ± 6.72a

Values represent the mean ± SE ($n = 10$)

* Significant differences at $p < 0.05$ according to Duncan's multiple range tests

physiological responses of these plants to stressful factors generated by the different fruit growing areas, combined with changes in the rain and luminosity regime.

The increase in photosynthetically active radiation (PAR) results in higher CO_2 assimilation, although this increase also depends on the CO_2 concentration in the atmosphere and the light saturation level (Gama et al. 2013; Rakić et al. 2015). Excess luminosity on leaves, followed by high temperatures, can lead to irreparable damage to the structures of both photosystem II (PSII) and photosystem I (PSI) and is known as photoinhibition (Adir et al. 2003; Mlinarić et al. 2016). Different strategies are used by plants to escape photoinhibition and one of them is the production of accessory pigments such as carotenoids. Carotenoids can participate in the absorption of excess energy in the light-collecting complex of plants and plays an essential role in photoprotection (Demmig-Adams and Adams 1996; Kyzeridou et al. 2015; Park and Jung 2017).

Severe and prolonged photoinhibition, usually called photodamage or chronic photoinhibition, decreases the energy capture efficiency, not only because it damages the oxygen evolution complex, but also because it degrades D1 protein. This leads to an over-reduction of Q_A caused by the unbalance between Q_A reduction rate by PSII and Q_A reoxidation rate by PSI (Murchie et al. 2015).

There is consistent evidence that the decrease in quantum yield resulting from photosynthesis inactivation during periods of high luminosity and high temperatures can significantly affect the yield and productivity of important cultures (Gomes et al. 2012; Murchie et al. 2015; O'Sullivan et al. 2017).

One of the tools most frequently used to verify the photochemical yield in relation to adverse environmental conditions is the chlorophyll *a* fluorescence (Strasser et al. 2004; Lukatkin et al. 2017; Park and Jung 2017), measured in a non-destructive way through portable fluorometer. This technique allows the extrapolation of details from the photochemical phase to the biochemical phase, providing qualitative and quantitative information on the physiological conditions of the photosynthetic apparatus (Stirbet et al. 2014; Van Wittenberghe et al. 2015).

Several researchers have focused on the seasonal changes of light and temperature in cultivated and wild plants (Czyczyło-Mysza and Myśków, 2017; Chuyong and Acidri 2017; Léchaudel et al. 2013). Recently Xue et al. (2017), suggested that the productivity of rice crops is dependent not only on biophysical factors, but also on the photosynthetic capacity and stage of crop development. In this context, our hypothesis was that the physiological performance of the Ubá hose, i.e., the photochemical efficiency and the quality of the fruit would be better in the plants that received the morning sun. Thus, the leaves that received higher radiation and higher temperatures would have a higher photoinhibition and, consequently, would produce fruits of low quality. Knowing that the changes in solar radiation intensity in the structures of photosystems can alter the photochemical efficiency and also the quality of

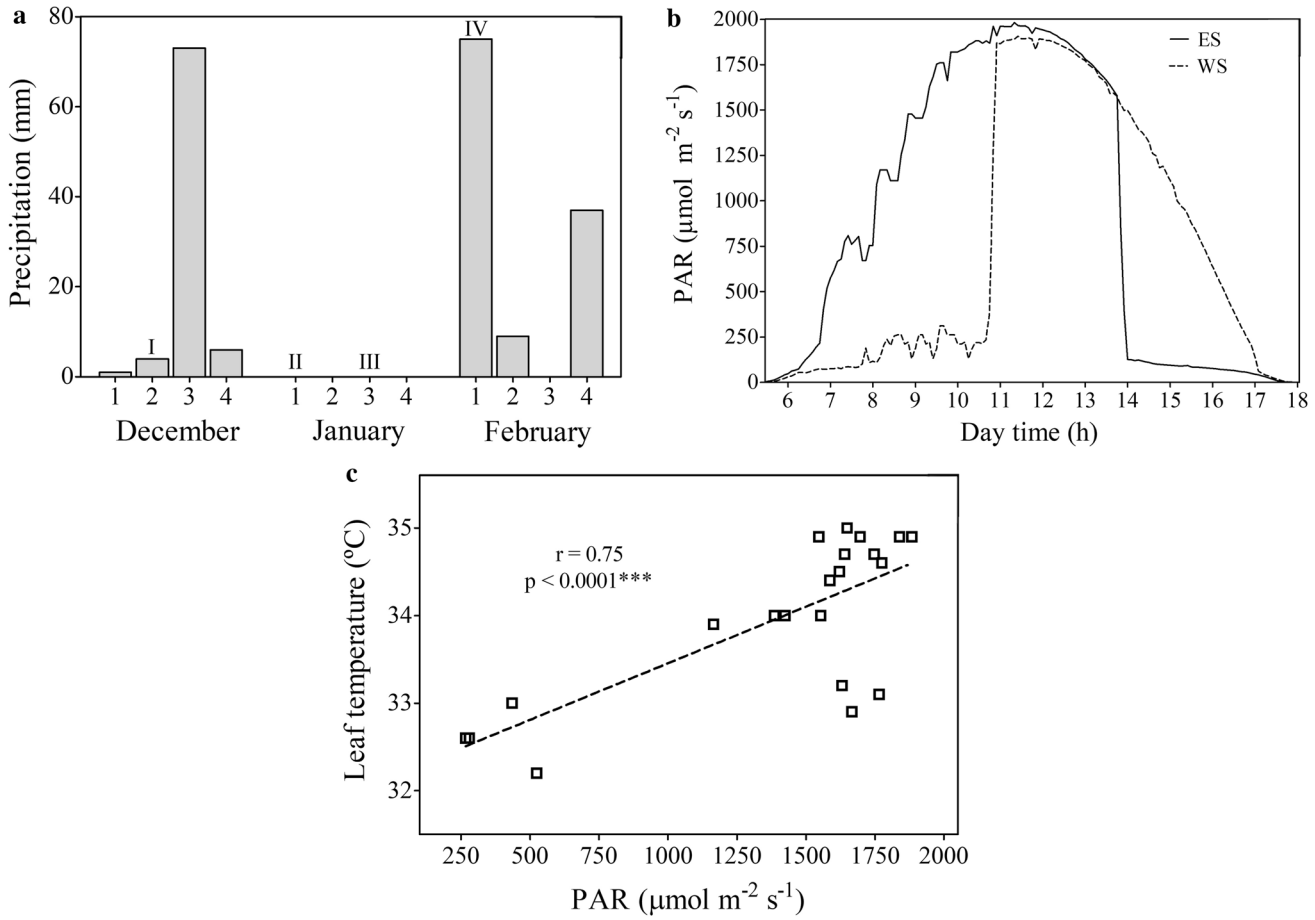

Fig. 1 **a** Precipitation of each period of analysis (I—fruit growth phase; II—fruit ripening phase; III—after fruit harvesting and IV—after plant pruning). **b** Photosynthetic Active Radiation, PAR, in the orchards of mango tree grown on the east side (ES) and the west side (WS). **c** Correlation between PAR and temperature on the leaf of east side plants and west side plants

fruits produced by the plant, the aim of this work was to evaluate and discuss the effects of contrasted temperature and light conditions on the photochemical parameters of Ubá mango leaves and fruit quality associated to the different stages of plant development.

Materials and methods

Plant material and growth conditions

The work was carried out during the reproductive and vegetative phases of mango cultivar Ubá (*Mangifera indica* L.) from December to February. Data collection was done at an orchard belonging to the 'Mango Pole' for the Industry of Northwestern state of Espirito Santo (19°33′53″S, 40°44′23″W, alt. 80 m). Plants aged 8 years and were grown in rainfed conditions on a hill. The recorded average rainfall was 85 mm in December, 0 mm in January and 120 mm in February. Precipitation data were obtained from the meteorological station of the National Institute of Meteorology (INMET) (Fig. 1).

Plants were cultivated on a hill and, considering that the movement of the sun during the day from east to west, shadow of one plant to the other occurs. Mango trees were evaluated at both positions: trees facing east fully exposed to sunlight in the morning and shaded in the afternoon (ES) and trees facing west that were shaded in the morning and fully exposed to sunlight in the afternoon (WS). In summary, the following two light conditions were established: trees facing east, fully exposed to sunlight in the morning (ES) and, trees facing west fully exposed to sunlight in the afternoon (WS). (see representative scheme—Online Resource 1).

Data were collected during four periods, the first two in the reproductive phase and the following two in the vegetative phase: I—fruit growth phase (before fruit reaches the point of physiological maturity); II—fruit ripening phase (after fruit has reached the point of physiological

maturity); III—after harvest (1 week after fruit harvesting), and IV—after plant pruning (1 week after plant pruning).

Photosynthetically active radiation (PAR) was recorded between 5 a.m. and 6 p.m. (solar time), with LI-190SA sensors (LI-COR, Lincoln, NE) connected to LI-1400 (LI-COR Biosciences) data logger. Sensors were fixed externally to the orchard, out of the projection of the canopy of the first row of plants, 1.5 m above ground throughout the analyses. The temperature in leaves was monitored with an infrared digital thermometer (TFA) in the same leaves used in all analyses (Fig. 1).

Chloroplast Pigments

To determine the content of photosynthetic pigments, 100 mg of leaves corresponding to 8 discs of 0.5 cm^2 were ground together with 7 mL of 80% acetone. The macerate was filtered through filter paper in a volumetric flask and the volume was completed to 25 mL, under light protection to avoid photodegradation. Extracted pigments were submitted to spectrophotometric analysis at 470, 646.8 and 663.2 nm (Genesys 10S UV–Vis, Thermo Scientific) at room temperature. The chlorophyll *a*, chlorophyll *b* concentrations, in μg mL^{-1}, and total carotenoids content $x + c$ (xanthophylls + carotenes) were obtained using equations suggested by Lichtenthaler and Buschmann (2001).

The carotenoid content in fruit pulp was determined using method based on Sérino et al. (2009). A total of 0.2 g of freshly lyophilized, homogenized mango pulp was added to 100 μL of 30% NaCl (w:v) solution. The mixture was stirred for 1 min on a linear agitator and then 200 μL of dichloromethane was added and stirred for 1 min. Subsequently, 500 μL of hexane:ether (1:1) was added and the mixture was stirred for 1 min and centrifuged (13,000×*g*, at 4 °C, for 5 min). The supernatant was collected in a 2 mL microtube; the procedure was repeated three times and the organic phases were pooled together. The remaining hexane phase was evaporated under low pressure. The concentrated carotenoid extract was reconstituted in 200 μL ethyl acetate, filtered with 0.45 μm disc and injected into a high pressure liquid chromatography (HPLC) apparatus (Dionex Ultimate 3000, Dionex Co., Sunnyvale, CA, USA).

The assay was performed using HPLC with DAD UV–Vis detector (UV6000LP, Thermo Separation Products, Riviera Beach, FL) under the following conditions: coupling of two columns, Chromolith Performance RP-18e column (100 4.6 mm, Merck, VWR International, Fontenay-sous-Bois, France); precolumn, Chromolith (Merck, VWR International); column oven temperature, 28 °C; mobile phase, ACN:UP water: EA (53:7:40, v/v/v); flow rate of the mobile phase, 1 mL min^{-1}; injection volume, 10 μL; wavelength range, 200–750 nm; 454 nm for β-carotene, and quantifications were established based on standard curves.

Fast chlorophyll *a* fluorescence measurements

The kinetic of fast chlorophyll *a* fluorescence was measured with a Plant Efficiency Analyzer (Handy PEA fluorometer, Hansatech Instruments Ltd, King's Lynn, Norfolk, UK) and viewed with dedicated software. To make the light-collecting system of leaves fully receptive, that is, for the complete oxidation of reaction centers, three young leaves, fully expanded (fourth to sixth leaf starting from the apex), located in branches of the third medium of each plant were adapted to the dark for 40 min (Gama et al. 2013). Measurements were performed between 7 a.m. and 10 a.m. The kinetics of chlorophyll *a* fluorescence was estimated after submitting samples to a saturating red light pulse of about 3000 μmol m^{-2} s^{-1}. Fluorescence intensities were recorded between 20 μs and 1 s, where: 20 μs was the initial fluorescence (F_0) and 300 ms was the maximum fluorescence (F_M). Fluorescence intensities, parameters established by the JIP test (Strasser and Strasser 1995; Strasser et al. 2004, 2010) and calculations are shown in Material Suplementar Eletrônico (Table A1).

Fruit quality measurements

Fruit sampling was performed at two ripeness stages (unripe, but physiologically mature and ripe). Fruit was considered to have reached physiological maturity when it presented dark green with a less shiny peel, and a more prominent wavy shape near the insertion of the petiole, called the "shoulder". Fruit was considered ripe when the peel was yellow with black dots, and the petiole was easily detached from the plant (Yashoda et al. 2006). Unripe fruits were analyzed at days 0, 2 and 4 after harvesting, while ripe fruits were analyzed on the day of harvest.

Fruit was peeled, cut, and part of the pulp was ground in a blender to obtain juice to measure the content of total soluble solids (TSS) and titratable acidity (TA); the other part was immediately dipped in liquid nitrogen. The frozen pulp was ground and the powder was stored at −20 °C. A sample of each frozen powder was lyophilized over 48 h at −52 °C, and stored in plastic pots with desiccation pastille at −20 °C until carotenoid analysis. Titratable acidity (TA) was measured through titration with a 0.1 N NaOH solution and expressed in % of citric acid. Total soluble solids (TSS) were determined using refractometer (Biobrix 103, Japan).

Statistics analysis

The experimental design used for all variables was fully random. Data obtained were submitted to analysis of

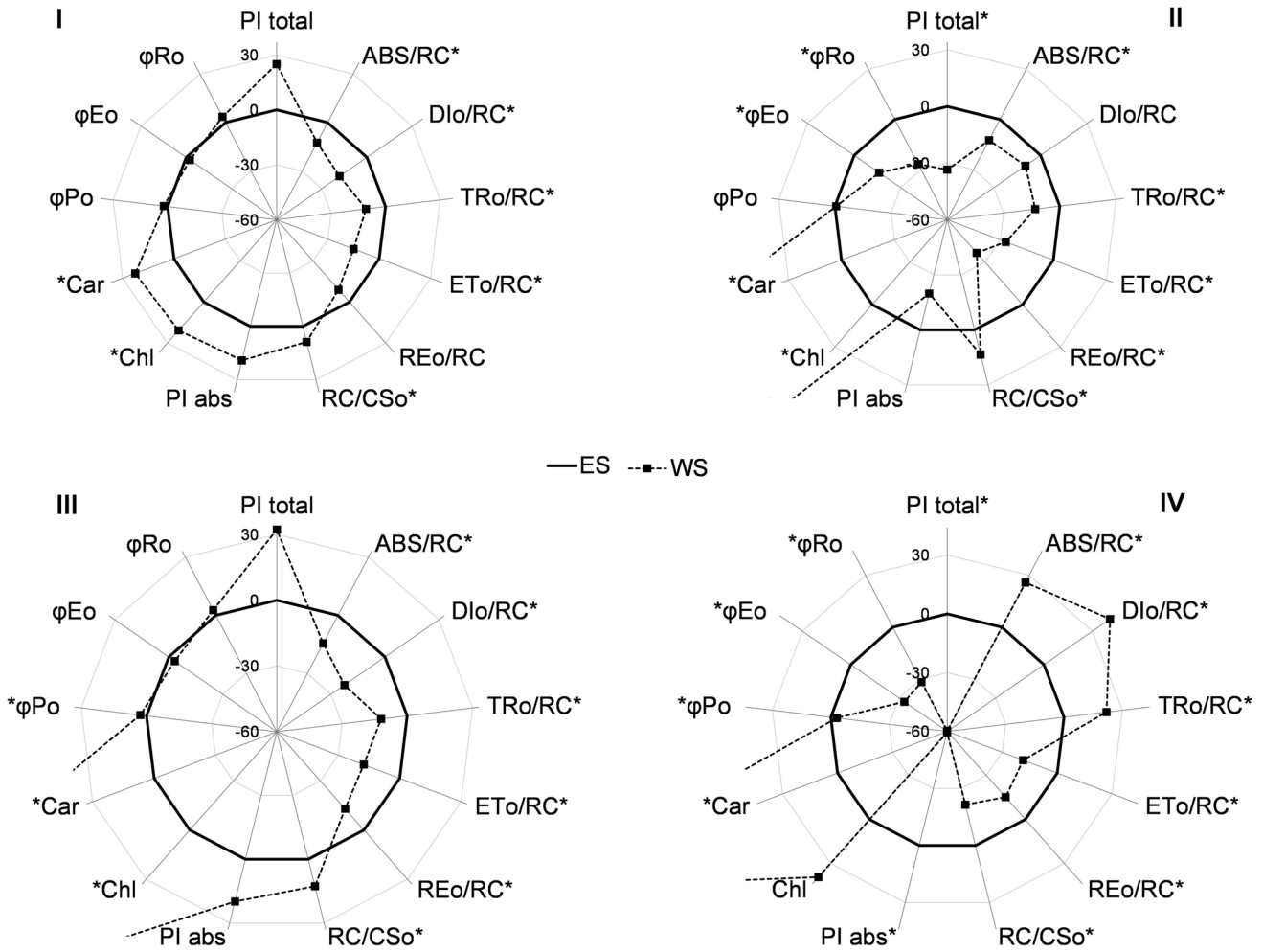

Fig. 2 Photosynthetic parameters deduced by the JIP test analysis of fluorescence transients and chlorophyll (Chl) and carotenoids (car) of the leaves collected of each period of analysis (I—fruit growth phase; II—fruit ripening phase; III—after fruit harvesting and IV—after plant pruning) of the plants grown on the east side (ES) and on the west side (WS). The parameters (for their definition and, calculations see Table 1a, Online Resource 2) were normalized using as reference (=0%) the corresponding values of ES. Asterisk indicate significant differences between ES and WS by Duncan test ($\alpha = 0.05$)

variance (ANOVA) and the means to Duncan's test at 5% probability, using Statistical Analysis Software (SAS, version 9.0). The relative fluorescence variable of east-side plants (ES) was used as reference because the PAR variation in these plants was gradual throughout the day. Thus, means were represented in percentages in relation to data of ES plants (0%) and presented in radar-type charts. Pearson's correlations were used on the GraphPad Prism software version 5.03.

Results

Chlorophyll fluorescence measurements

In the first three periods (I, II and III), it was observed that the total chlorophyll content was higher in WS plants, while similar values were obtained in both fields in period IV (Fig. 2).

The Chl a fluorescence parameters in ES and WS of Ubá mango measured in the morning are shown in Fig. 2. Gradual increase of irradiance and temperature in the morning revealed significantly higher values in ES compared to WS in the period I in the specific energy flows of absorption (ABS/RC) and trapped (TR_0/RC) of electrons for reduction of Quinone A (Q_A). The same occurred with the transport of electrons after reduced Quinone A (ET_0/RC) in all periods of analysis, and with the dissipated energy flux (DI_0/RC) in periods I and III. The opposite was observed in period IV, when WS plants showed higher ABS/RC, TR_0/RC (approximately 25% higher) and DI_0/RC values (40% higher) (Fig. 2).

The quantum yield for electron transport ($\varphi E_0 = ET_0$/ABS) in ES plants was 15% higher in period II and 30%

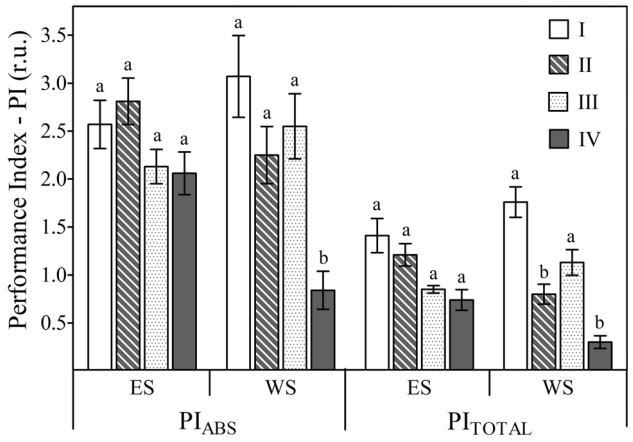

Fig. 3 Performance index (PI) expressed in relative units of the fluorescence, on the leaves collected of each period of analysis (I—fruit growth phase; II—fruit ripening phase; III—after fruit harvesting and IV—after plant pruning) in the plants grown on the east side and on the west side. Different letters indicate significant difference for each one of the parameters (PI_{ABS} and PI_{TOTAL}) for ES and WS plants by Duncan test ($\alpha = 0.05$). The bars indicate the standard error of the mean

higher in period IV. The electron flux reducing end electron acceptors at the PSI acceptor side, per RC (RE_0/RC) in ES plants presented values 35% higher in period II and, 15% higher in periods III and IV.

The results showed a positive correlation between number of active reaction centers (RC/CS_0) and chlorophyll (Chl) across all data sets ($r = 0.91$; $p < 0.0019$) although was observed a negative correlation between the maximum quantum yield of oxidation–reduction reactions occurring in PSII ($\varphi P_0 = F_V/F_M = TR_0/ABS$) and DI_0/RC (dissipated energy flux, per RC) ($r = -0.84$; $p < 0.0085$).

The performance index (Fig. 3) allowed us estimating the severity of PSII photoinhibition. Only in period IV, the PSII performance index (PI_{ABS}) was statistically different between ES and WS plants, while the total photochemical performance index (PI_{TOTAL}) was higher in ES plants in periods II and IV.

Postharvest fruit quality

Fruits harvested from mango trees under predominantly west side (WS) light conditions were sweeter than fruits harvested from mango trees under predominantly east side (ES) light conditions (Table 1). The effect of light conditions on fruit quality was perceptible at the moment of sampling characterization. On the day of harvesting of unripe fruits (stage 0), it was observed that WS fruits showed higher TSS content compared to ES fruits (11.58° and 7.27° Brix, respectively). The significant difference in fruit sweetness also occurred when fully ripe fruits were harvested, when TSS content of 21.27° Brix was reached on WS fruits and 19.12 on ES fruits.

Titratable acidity (TA) was statistically equal ($p < 0.05$) in ES and WS fruits at all maturation stages, except for stage 2, when WS fruits showed 30% higher acidity. The difference in titratable acidity content was observed with fruit ripening, with a decrease in TA under both light conditions, where the average values obtained were 1.53% of citric acid on the first day of analysis and 0.45% in ripe fruits.

There was a significant increase ($p < 0.05$) in the TSS/TA ratio with fruit ripening; during the ripe stage, the average value observed was 145% higher than during stage 0. It is noteworthy that ripe fruits showed significant difference in the TSS/TA ratio, with average value of 39.99 in ES fruits and of 51.06 in WS fruits.

When harvested unripe, fruits showed no statistical differences in β-carotene content at any maturation stage (0, 2 and 4). However, ripe ES fruits showed β-carotene content 80% higher than WS fruits (54.27 mg/100 g and 29.51 mg/100 g, respectively).

Discussion

Impact of combined stresses on the photochemical performance of leaves

High-temperature tolerance in plants is important in a tropical world, with extreme heat waves predicted to increase in frequency and duration, potentially leading to lethal heating of leaves (O'Sullivan et al. 2017). In the southeastern region of Brazil, light and temperature have a strong positive correlation, and their effects could be observed throughout this study. The combination of increased irradiance and high temperature is among the most commonly experienced stresses under field conditions (Mlinarić et al. 2017; Rodríguez-López et al. 2013; Wayne and Bazzaz 1993). In the morning, leaf temperature of ES plants was 34.0 ± 2.0 °C and received about five times more PAR (mean 1480 µmol m^{-2} s^{-1}) than WS plants (temperature 30 ± 2.0 °C and 595 µmol m^{-2} s^{-1}). In the afternoon, ES plants received about three times less PAR (temperature 30 ± 2.0 °C mean of 440 µmol m^{-2} s^{-1}) than WS plants (temperature of 40 ± 2.0 °C and average of 1150 µmol m^{-2} s^{-1}).

The relative effect of temperature on RC/CS_0 was 15% lower in periods I, II and III in ES plants and it was only lower in period IV in WS plants (25%). This means that the tolerance of the PSII active reaction centers to high temperatures and/or rapid radiation increase were higher in the west side (WS) plants than in the east side (ES) plants. Heat-induced or light-induced RC/CS_0 is consistent with

the results obtained for pea (Strasser et al. 2000) and apple leaves (Chen and Cheng 2009). The high ABS/RC, TR_0/RC, ET_0/RC and RE_0/RC values in ES plants are at least in part due to their smaller number of PSII active reaction centers, as indicated by the smaller RC/CS_0 ratio in periods I, II and III (Fig. 2).

In contrast to our initial hypothesis, our results demonstrate that plants cultivated on the west side (WS) presented better photochemical performance in periods with the greatest need for photoassimilates, i.e., in period I—fruit growth phase (before fruit reaches the point of physiological maturity) and period III—after fruit harvest (1 week after fruit harvest) (Fig. 2). In addition, it was demonstrated that there were different abilities to deal with PAR changes between cultivation sides analyzed. This information suggests that there is considerable phenotypic plasticity in Ubá cultivar, which can be exploited for to be used in regions with great relief varieties and the combination of increased irradiance and high temperature.

Little, if any, differences in the maximum quantum yield of primary photochemistry ($TR_0/ABS = F_V/F_M = \varphi P_0$) were found in leaves when comparing ES and WS plants. A rapid increase in PAR and leaf temperature may lead to a significant photosynthesis inhibition. The transport of photosynthetic electrons through PSII is inhibited, the PSII complex and the PSII reaction centers associated with D1 protein degradation are damaged (Zlatev 2009). Therefore, the ability to maintain the functionality of photosynthetic machinery under light and temperature stress is of great importance in environmental stress tolerance. The rapid increase in temperature or light (Yusuf et al. 2010; Huang et al. 2017) leads to the inactivation of OEC and increase in the functional size of the antenna. Therefore, it was expected that WS plants exhibited greater inactivation of OEC, which led to a discrepancy between the receptor and the PSII donor side as suggested by Oukarroum et al. (2007). In addition, ES, contrasting with WS, showed lower PSII photochemical efficiency (PI_{ABS}) at periods I and III, suggesting that higher temperature and intense light at midday induced a prolonged negative effect on the capacity of PSII donor side in ES (Gomes et al. 2012). In fact, Force et al. (2003) suggest that a more accurate assessment of the photoinhibition process can be obtained through the changes between flux ratios and specific fluxes per RC rather than some in TR_0/ABS ($=F_V/F_M = \varphi P_0$) change. This is because specific flows consider only active RC that can reduce Q_A (Strasser et al. 2004). A significant decrease in TR_0/ABS (in period III in ES and in period IV in WS) was accompanied by an increase in ABS/RC and TR_0/RC (Fig. 2). This indicates inactivation of part of RC. Q_A-non-reducing centers can efficiently absorb excitation energy, but they are unable to reduce Q_A. Instead, excess excitation energy is mostly dissipated as heat (Strasser et al. 2004; Yusuf et al. 2010). This was corroborated with increased DI_0/RC in periods I and II in ES and about 40% higher in WS in period IV. However, a much more pronounced increase in DI_0/RC in WS in period IV, accompanied by a decrease in ET_0/RC and reduction of electron transport capacity (φE_0) indicated higher susceptibility to photoinhibition.

According to Tikkanen et al. (2014), in the particular case of PSI, the structures are hardly ever damaged because the active reaction centers (RC) are efficiently protected. However, when affected, recovery is extremely slow. Excess electrons do not participate in the photochemical step and do not react with oxygen, producing ROS (reactive oxygen species). Since they are highly reactive, ROS cause irreparable oxidative cell damage. As a strategy, plants produce accessory pigments (such as carotenoids) that have a photoprotective function in addition to participating in the absorption and transfer of electrons to the chlorophyll. This increased content of pigments are visible to WS plants, which had an increase in chlorophyll and mainly in carotenoid content in periods II, III and IV. Photoprotection provided by carotenoids involves xanthophyll compounds as violaxanthin, which are rapidly converted into zeaxanthin via antheraxanthin. Zeaxanthin has greater ability to dissipate energy in the form of heat and avoid photodamage in the photosynthetic apparatus (Demmig-Adams and Adams 1996; Kyzeridou et al. 2015; Lukatkin et al. 2017). In the Ubá mango tree, it was observed that the quantum yield of PSI (φR_0) was lower in plants exposed to radiation from the West Side (WS plants) with higher total carotenoid content (Car) in leaves. Probably, an increase in Car content is related to over-recovery of the quinone pool (Wilson et al. 2003) and may be a signal of the increased production of antioxidants (Cars, tocopherols, ascorbic acid, etc.) because it increases the probability of ROS formation when the quinone pool is reduced (Allen and Ort 2001; Lukatkin et al. 2017). Thus, there was a lower flow of electrons to reduce the final PSI receptors. This may be one of the different strategies of optimization of the photosynthetic apparatus of Ubá mango tree to acclimatize to the combined stress of high light and temperature. The standard of electron transport in PSII of Ubá mango tree played an important role in the PSI photoprotection. Tikkanen et al. (2014), working with *Arabidopsis*, reported that PSII photoinhibition is able to protect PSI, which means that PSII is the final regulator of the electron transfer chain in photosynthesis, providing protection mechanisms. These authors suggested that the dissipation of non-photochemical energy, phosphorylation of the antenna complex of PSII and the control of the speed of electron transfer by the intersystem are ways to protect PSI, suggestions that were confirmed for Ubá mango tree by results presented in this paper.

Influence of the photochemical performance in Uba mango leaves on postharvest fruit quality

In this study, ripe WS fruits had better flavor compared to ES fruits. Fruits harvested ripe in both treatments showed a significant increase in the TSS/TA ratio compared to fruits harvested at physiological maturity (unripe). The difference in flavor could be a result of photoinhibition occurring in the leaves of WS plants. The lower TR_0/RC and ET_0/RC values found in leaves during the fruit growth phase and TR_0/RC, ET_0/RC, RE_0/RC, ΨE_0, φE_0, φR_0 and PI_{TOTAL} during the fruit ripening stage in WS plants support this suggestion. It is also worth mentioning that these plants showed higher chlorophyll content (Chl) and density of photosynthetically active reaction centers per cross section (RC/CS_0) during these two phases, suggesting that Ubá mango tree has adaptation strategies of PSII and PSI to light and thermal stress. Léchaudel et al. (2010) found higher TSS content in mango fruits (*Mangifera indica* cv. 'Cogshall') exposed to the sun compared to fruits located under the shade of the canopy. The authors found that the photochemical performance of PSII was lower in the fruit peel exposed to the sun, suggesting that fruits are also affected by photoinhibition.

In relation to β-carotene content, fruits harvested unripe showed similar β-carotene content during ripening in both treatments. Sweeter WS fruits presented lower β-carotene content. According to Fanciullino et al. (2014), the availability of carbohydrates does not directly determine the synthesis of carotenoids in fruits. These relationships have not yet been modeled and need further investigation.

In addition to the higher flavor quality, Ubá mango is the variety that, compared to others, contains bioactive compounds with antioxidant action, such as ascorbic acid and β-carotene. Our results demonstrate the influence of solar radiance on the β-carotene content as observed in Table 1, where it is possible to verify that the high radiance condition influenced the carotenoid content, as observed in ES fruits, which presented higher β-carotene content (44.35 mg/100 g) when harvested ripe.

Abiotic stresses increase the production of reactive oxygen species and consequently induce the formation of antioxidants as protective systems (Léchaudel et al. 2010, 2013). Kyzeridou et al. (2015) observed that fruit of Rosaceae and Apocynaceae family contained lower total carotenoid content than leaves, and the relative cycle of electron flux around PSI was higher in fruit than in leaves.

Given the above, it is suggested that the formation of antioxidants and TSS in Ubá mango fruits is controlled not only by the harvest point, but also by environmental conditions.

In conclusion, our study clearly demonstrates that variations in chlorophyll *a* fluorescence parameters are accurate markers of the occurrence of photoinhibition in Ubá mango tree. Plants grown under light conditions predominantly on the West Side (WS) had lower overall photochemical performance, especially during the fruit ripening phase and after pruning, as well as higher chlorophyll and total carotenoid contents in leaves and fruits, with lower β-carotene and higher TSS content. Shade during the morning and excessive light and temperature after 11 a.m. led mango trees to produce more chlorophyll and carotenoids in leaves to quench excess energy absorbed by PSII and to minimize photoinhibitory damage to PSI. Photoprotection and repair of the photosynthetic apparatus after photoinhibition occur at different stages of energy conversion (Lukatkin et al. 2017). However, in our work, in mango trees under exposure to high irradiance and temperature, the extension of the photodamage did not exceed the repair processes.

In summary, mango plants submitted in the field to the combination of high light and heat exhibited very different photosynthetic and physiological responses (photochemistry and fruit quality). However, in both cultivation conditions, they presented an efficient mechanism of protection against combined stress: a) plants cultivated on the west side (WS) presented better photochemical performance in periods with the greatest need of photoassimilates, i.e., in period I—fruit growth phase (before fruit reaches the point of physiological maturity) and period III—after fruit harvest (1 week after fruit harvest), (b) tolerance of RC was higher in WS plants compared to ES plants; (c) the quantum yield of PSI (φR_0) was lower in WS plants but the total carotenoid content in leaves was higher, although sweeter WS fruits presented lower β-carotene content. The results obtained in this study have shown that there is considerable phenotypic plasticity in the Ubá cultivar, which can be exploited in regions with great relief variations and the combination of increased irradiance and high temperature.

Author contribution statement LF-S conducted the experiment, data analysis and wrote the first draft. LF-S, CZG and EP performed experiments. LF-S, CZG and DMS interpreted data and wrote the manuscript. DMS designed the studies, directed the experiment, and gave the final approval of the manuscript to be published. All authors commented on the results and the manuscript.

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References

Adir N, Zer H, Shochat S, Ohad I (2003) Photoinhibition—a historical perspective. Photosynth Res 76:343–370

Allen DJ, Ort DR (2001) impacts of chilling temperatures on photosynthesis in warm-climate plants. Trends Plant Sci 6:36–42

Chen LS, Cheng L (2009) Photosystem 2 is more tolerant to high temperature in apple (*Malus domestica* Borkh.) leaves than in fruit peel. Photosynthetica 47:112–120

Chuyong GB, Acidri T (2017) Light and moisture levels affect growth and physiological parameters differently in *Faidherbia albida* (Delile) A. Chev. seedlings. Acta Physiol Plant 39:117

Czyczyło-Mysza I, Myśków B (2017) Analysis of the impact of drought on selected morphological, biochemical and physiological traits of rye inbred lines. Acta Physiol Plant 39:87

Demmig-Adams B, Adams W (1996) The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends Plant Sci 1:21–26

Fanciullino AL, Bidel LPR, Urban L (2014) Carotenoid responses to environmental stimuli: integrating redox and carbon controls into a fruit model. Plant Cell Environ 37:273–289

Force L, Critchley C, Van Rensen JJS (2003) New fluorescence parameters for monitoring photosynthesis in plants. Photosynth Res 78:17–33

Gama VN, Cunha JT, Lima IM, Bacarin MA, Silva DM (2013) Photosynthetic characteristics and quality of five passion fruit varieties under field conditions. Acta Physiol Plant 35:941–948

Gomes MTG, Luz AC, Santos MR, Batitucci MCP, Silva DM, Falqueto AR (2012) Drought tolerance of passion fruit plants assessed by the OJIP chlorophyll a fluorescence transient. Sci Hortic 142:49–56

Huang W, Yang Y-J, Zhang SB (2017) Specific roles of cyclic electron flow around photosystem I in photosynthetic regulation in immature and mature leaves. J Plant Physiol 209:76–83

Kyzeridou A, Stamatakis K, Petropoulou Y (2015) The non-foliar hypoxic photosynthetic syndrome: evidence for enhanced pools and functionality of xanthophyll cycle components and active cyclic electron flow in fruit chlorenchyma. Planta 241:1051–1059

Léchaudel M, Urban L, Joas J (2010) Chlorophyll fluorescence, a nondestructive method to assess maturity of mango fruits (cv. "Cogshall") without growth conditions bias. J Agric Food Chem 58:7532–7538

Léchaudel M, Lopez-Lauri F, Vidal V et al (2013) Response of the physiological parameters of mango fruit (transpiration, water relations and antioxidant system) to its light and temperature environment. J Plant Physiol 170:567–576

Lichtenthaler HK, Buschmann C (2001) Chlorophylls and carotenoids: measurement and characterization by UV–Vis. Curr Protoc Food Anal Chem 3:1–8

Lukatkin AS, Tyutyaev EV, Sharkaeva ES, Lukatkin AA, da Silva JAT (2017) Mild abiotic stresses have different effects on chlorophyll fluorescence parameters in leaves of young woody and herbaceous invasive plants. Acta Physiol Plant 39:20

Mlinarić S, AntunovićDunić J, Štolfa I et al (2016) High irradiation and increased temperature induce different strategies for competent photosynthesis in young and mature fig leaves. S Afr J Bot 103:25–31

Mlinarić S, Dunić JA, Babojelić MS, Cesar V, Lepeduš H (2017) Differential accumulation of photosynthetic proteins regulates diurnal photochemical adjustments of PSII in common fig (*Ficus carica* L.) leaves. J Plant Physiol 209:1–10

Murchie EH, Ali A, Herman T (2015) Photoprotection as a trait for rice yield improvement: status and Prospects. Rice 8:31

O'Sullivan OS, Heskel MA, Reich PB, Tjoelker MG, Weerasinghe LK, Zhu APL, Egerton JJG, Bloomfield KJ, Creek D, Bahar NHA, Griffin KL, Hurry V, Meir P, Turnbull MH, Atkin OK (2017) Thermal limits of leaf metabolism across biomes. Glob Chang Biol 23:209–223

Oukarroum A, Madidi ES, Schansker G, Strasser RJ (2007) Probing the responses of barley cultivars (*Hordeum vulgare* L.) by chlorophyll a fluorescence OLKJIP under drought stress and re-watering. Environ Exp Bot 60:438–446

Park JH, Jung S (2017) Perturbations of carotenoid and tetrapyrrole biosynthetic pathways result in differential alterations in chloroplast function and plastid signaling. Biochem Biophys Res Commun 482:672–677

Rakić T, Gajić G, Lazarević M, Stevanović B (2015) Effects of different light intensities, CO_2 concentrations, temperatures and drought stress on photosynthetic activity in two paleoendemic resurrection plant species *Ramonda serbica* and *R. nathaliae*. Environ Exp Bot 109:63–72

Rodríguez-López NF, Cavatte PC, Silva PEM, Martins SCV, Morais LE, Medina EF, Damatta FM (2013) Physiological and biochemical abilities of robusta coffee leaves for acclimation to cope with temporal changes in light availability. Physiol Plant 149:45–55

Rosalie R, Joas J, Deytieux-Belleau C, Vulcain E, Payet B, Dufossé L, Léchaudel M (2015) Antioxidant and enzymatic responses to oxidative stress induced by pre-harvest water supply reduction and ripening on mango (*Mangifera indica* L. cv. "Cogshall") in relation to carotenoid content. J Plant Physiol 184:68–78

Sérino S, Gomez L, Costagliola G, Gautier H (2009) HPLC assay of tomato carotenoids: validation of a rapid microextraction technique. J Agri Food Chem 57:8753–8760

Stirbet A, Riznichenko GY, Rubin AB, Govindjee (2014) Modeling chlorophyll a fluorescence transient: relation to photosynthesis. Biochemistry 79:291–323

Strasser BJ, Strasser RJ (1995) Measuring fast fluorescence transients to address environmental questions: the JIP-test. In: Mathis P (ed) Photosynthesis: from light to biosphere. Kluwer Academic Publishers, Dordrecht, pp 977–980

Strasser RJ, Srivastava M, Tsimilli-Michael M (2000) The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: Yunus M, Pathre U, Mohanty P (eds) Probing photosynthesis: mechanisms, regulation and adaption. Taylor & Francis, London, pp 445–483

Strasser RJ, Tsimilli-Michael M, Srivastava A (2004) Analysis of the chlorophyll a fluorescence transient. In: Papageorgiou GC (ed) Chlorophyll a fluorescence: a signature of photosynthesis-advances in photosynthesis and respiration. Springer, Rotterdam, pp 321–362

Strasser RJ, Tsimilli-Michael M, Qiang S, Goltsev V (2010) Simultaneous in vivo recording of prompt and delayed fluorescence and 820-nm reflection changes during drying and after rehydration of the resurrection plant *Haberlea rhodopensis*. Biochim Biophys Acta 1797:1313–1326

Tikkanen M, Mekala NR, Aro EM (2014) Photosystem II photoinhibition-repair cycle protects Photosystem I from irreversible damage. Biochim Biophys Acta 1837:210–215

Van Wittenberghe S, Alonso L, Verrelst J et al (2015) Bidirectional sun-induced chlorophyll fluorescence emission is influenced by leaf structure and light scattering properties—a bottom-up approach. Remote Sens Environ 158:169–179

Wayne P, Bazzaz FA (1993) Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. Ecology 74:1500–1515

Wilson KE, Krol M, Hüner NPA (2003) Temperature-induced greening of *Chlorella vulgaris*. The role of the cellular energy

balance and zeaxanthin-dependent nonphotochemical quenching. Planta 217:616–627

Xue W, Lindner S, Dubbert M, Otieno D, Ko J, Muraoka H, Werner C, Tenhunen J (2017) Supplement understanding of the relative importance of biophysical factors in determination of photosynthetic capacity and photosynthetic productivity in rice ecosystems. Agric For Meteorol 232:550–565

Yashoda HM, Prabha TN, Tharanathan RN (2006) Mango ripening: changes in cell wall constituents in relation to textural softening. J Sci Food Agric 86:713–721

Yusuf MA, Kumar D, Rajwanshi R, Strasser RJ, Tsimilli-Michael M, Sarin NB (2010) Overexpression of γ-tocopherol methyl transferase gene in transgenic *Brassica juncea* plants alleviates abiotic stress: physiological and chlorophyll *a* fluorescence measurements. Biochim Biophys Acta 1797:1428–1438

Zlatev Z (2009) Drought-induced changes in chlorophyll fluorescence of young wheat plants. Biotechnology 23:438–441