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Nocturnal low irradiance pulses improve fruit yield and lycopene concentration in tomato

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ABSTRACT

Light is one of the most important factors modulating processes and sequences in plants life, like fruit ripening and the concentrations of water and lipid soluble antioxidants. The aim of this work was to evaluate the most effective frequency of low irradiance light pulses (LP) during the night and to analyze its effect on plant and fruit growth, as well as on modifications of concentrations of soluble sugar, amino acids, antioxidants and organic acids. LP of 15 min each were applied over the plants in a temperature controlled greenhouse after fruit set till they turned to mature red, with a frequency of 2 and 4 h. LP induced no changes in the typical maturation indexes such as soluble solid, total acidity, pH or firmness; meanwhile there was an 18% increase in fruit yield when plants were exposed to 15 min LP every 2 h during the night. Furthermore, by analyzing the tomato cluster receiving this LP treatment separately, the biomass of the fruit was found to have increased by 28% compared with the same cluster in control plants. In coincidence with this, fruit treated with a frequency of 2 and 4 h LP showed an increase in lycopene concentration, concomitantly with a rise in the proportion of red mature fruit harvested from the whole plant. On the other hand, there was a drop in the concentration of soluble sugars and free amino acids, possibly conducing to a decrease in water soluble antioxidants (ascorbic acid and glutathione) and citric and malic acids concentration. Overall, these results showed that nocturnal LP treatments improved fruit yield in tomato plants with higher amounts of lycopene, which indicate earlier fruit ripening.
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1. Introduction

Fruit growth and ripening are complex issues for plants. As plants develop, light plays a key role in carotenoid accumulation in tomato (Giovannoni, 2004), which is a phytochrome-mediated effect (Alba et al., 2000). During fruit maturation, several processes, such as pigment synthesis (Bramley, 2002; Alba et al., 2005), cell wall metabolism (Vicente et al., 2007), carbohydrate metabolism (Carrari et al., 2006) and antioxidants synthesis (Jimenez et al., 2002) are interconnected.

Plants perceive the interruption of dark periods when they receive a brief red light treatment modifying flowering (Salisbury and Bonner, 1956) or germination (Benech-Arnold et al., 2000). Furthermore, plants exposed to a light pulse (LP) before dawn alter their circadian rhythm which leads to changes in growth, enzyme activity, photosynthesis and other physiological processes (McClung, 2006 and references therein). In addition, treatments with LP extend postharvest life of spinach leaves stored in darkness improving their antioxidant concentration (Gergoff et al., 2013). In spite of this, the effect of nocturnal LP treatment in tomato fruit and the consequences for their ripening such as changes in lycopene concentration and in other quality parameters have not been addressed.

A previous work has demonstrated that LED can improve tomato quality, however, the treatments were done with different LED and for long periods of time. Those authors found a rise in glucose and ascorbic acid (AA) when applying blue and white LED treatments (Xu et al., 2012). On the other hand, as demonstrated by Massot

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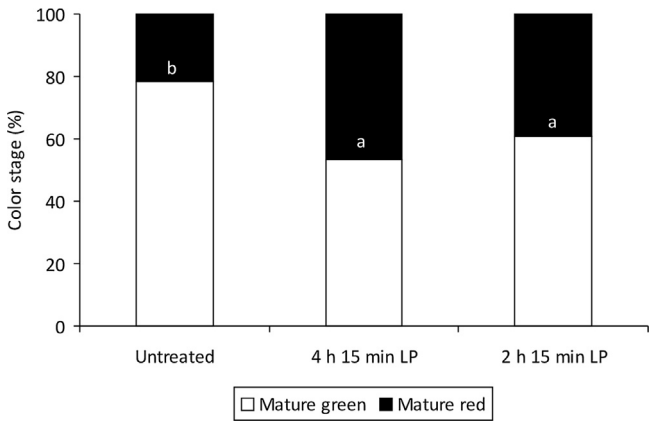

Fig. 1. Percentage of mature green and mature red tomato fruit in untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Results were analyzed by ANOVA ($P \leq 0.05$) to refuse the null hypothesis and multiple test range (LSD test) was performed to detect the differences among means. Letters denote statistical differences.

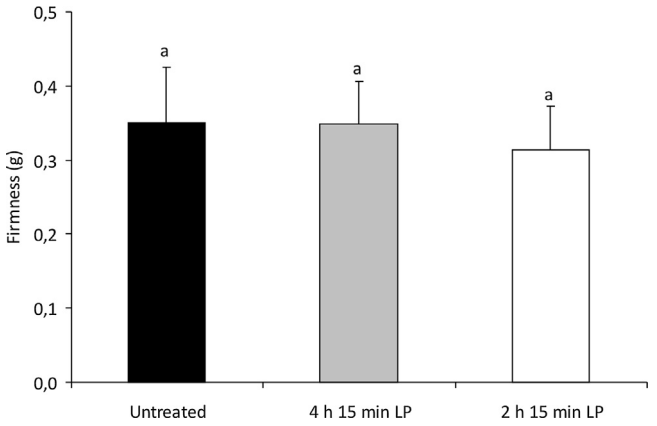

Fig. 2. Firmness of mature red fruit in untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Results were analyzed by ANOVA ($P \leq 0.05$) to refuse the null hypothesis and multiple test range (LSD test) was performed to detect the differences among means. Error bars represent standard deviation and letters denote statistical differences.

et al. (2012), light produces a higher effect in AA content in leaves than in tomato fruit, when plants are shaded for a long time. Both light intensity and quality have a strong relation to AA content and synthesis in leaves (Bartoli et al., 2006, 2009) and determinate plant growth (Fan et al., 2013). In model organisms, light has proved to regulate the expression of L-galactono-1,4-Lactone Dehydrogenase (GLDH) mRNA, the last enzyme in the AA synthesis pathway (Tanaka et al., 2015). Also, there are many changes in the GLDH and AA concentrations along one day, in a cycle regulated by irradiance rather than by circadian rhythm (Tamaoki et al., 2003).

Tomato fruit is a remarkable source of vitamin C (AA and dehydroascorbic acid) and carotenoids for human diet (García-Closas et al., 2004) and it is the most important fruit worldwide (FAO, 2013). The aim of this work was to determine the effect of nocturnal application of short and low irradiance LP on the ripening of the fruit, its antioxidant concentration and plant growth.

2. Materials and methods

2.1. Plant material and treatments

Tomato plants (*Solanum lycopersicum* cv Elpida) were cultured in 10 L pots inside a greenhouse of the Institute of Plant Physiology (CCT CONICET La Plata—UNLP) during four consecutive years (2011–2014) from 1st September till the middle of December, when the fruit were harvested. The temperature at different heights (0.0, 0.5, 1.0 and 2.0 m) and photosynthetic photon flux density (PPFD) were controlled and measured during the period of plant growth with a Licor LI-1400 data logger (equipped with a 1400–101 air temperature sensor and a LI-190SA quantum sensor) every half hour. Temperature and PPFD data are shown in supplementary Fig. 1. Ten plants were analyzed for each treatment and experiment. The LP treatment consisted of 15 min of 30 $\mu mol\, m^{-2}\, s^{-1}$ PPFD every 2 or 4 h during the night (From 6 pm to 6 am). The light source consisted in 20 W fluorescent tubes (OSRAM®) placed at an approximate distance of 15–20 cm from the fruit. LP were applied directly to the first inflorescence after fruit set (around 1st November) until harvest (around 15th December), when fruit turned to red stage (at least 90% of surface red). After harvest, fruit were immediately taken to the laboratory for the analytical determinations and extra samples were frozen in liquid nitrogen and stored at −80 °C until used.

2.2. Fruit weight, plant yield and chlorophyll concentration

After harvest, fruit weight and yield per plant and per inflorescence were recorded. Ten replicates were used for each of the four years of tomato cultivation. Apart from the fresh and dry fruit yield, plant height, dry stem and dry leaves were measured. Leaf chlorophyll concentration was estimated with a SPAD-502 Chlorophyll meter (Minolta, Japan) and results were expressed in Spad Units.

2.3. Total soluble solids, titratable acidity, pH and color

Twenty g of fruit tissue were processed with mortar and pestle and a few drops of the juice were placed in a refractometer to determinate total soluble solids (TSS) (Milwaukee MA871, Rocky Mount, USA) expressing results as °BRIX. Then 100 mL of distilled water were added to the juice. pH was potentiometrically measured and total titrable acidity (TTA) was determined titrimetrically with a 0.1 N solution of NaOH until pH 8.2 was reached (AOAC, 1980). Results were expressed as grams of citric acid per 1000 g of fresh fruit weight.

Fruit were classified under the USDA ripening stages, as described by Tu et al. (2000).

2.4. Firmness

Fruit firmness was determined with a texture analyzer (T.A., Exponent lite Texture Analyzer TA.XT.PLUS from Stable Micro Systems™ Goldalming, Surrey, UK). T.A. was equipped with a 25 mm diameter flat probe. The fruit was deformed for a distance of 0.5 mm at a speed of 0.25 mm/s. and a 5.9 g trigger force. Twenty fruits were analyzed for each treatment and harvest season. Results are expressed in force g, representing the maximum force developed during the test.

2.5. Concentrations of free amino acids and total and reducing sugars in fruit

The concentration of total free amino acids was determined according to Rosen (1957). Standard curve was made with glutamic acid at 570 nm in a UV–vis spectrophotometer (Shimadzu UV-160A, Shimadzu Corporation). Concentrations of free and reducing sugars were determined using the Somogyi–Nelson method with modifications according to Nelson (1944) and Somogyi (1952). The measurements were carried out in the UV–vis spectrophotometer at 520 nm. Standard curve was developed with sucrose.

2.6. Lycopene concentration

Frozen tomato fruit tissue was ground with mortar and pestle and 100 mg of the resulting powder was extracted with 5 mL of hexane:acetone:ethanol (2:1:1). The sample was vortexed and then 1 mL of water was added. The upper phase was carefully extracted and absorbance was determined at 503 nm. Results were calculated by using $\varepsilon = 172{,}000\ L\ mol^{-1}\ cm^{-1}$ (Taber et al., 2008) and expressed as μg of lycopene per gram of dry weight. Measurements were performed in triplicate.

2.7. AA and glutathione (GSH) concentration and corresponding redox state

The concentration of AA and its oxidised form, dehydroascorbate (DHA), was determined by HPLC according to Bartoli et al. (2006) with minimal modifications. The redox state of AA was calculated as: % DHA = [(DHA content) (AA content + DHA content)$^{-1}$] × 100.

The concentration of total GSH and oxidised glutathione (glutathione disulfide—GSSG) was determined according to Griffith (1980). The redox state of GSH was calculated as: % GSSG = [(GSSG content) (GSH content + GSSG content)$^{-1}$] × 100.

2.8. Concentration of citric and malic acid

Citric and malic acids were extracted from fruit in a 6% v/v ortofosforic acid solution with frozen mortar and pestle and centrifuged at 16,000 *g* for 10 min. Supernatant was separated for citric and malic acid determination by HPLC according to Romero Rodriguez et al. (1992) with minimal modifications. Results were expressed as mmol of citric or malic acid g $^{-1}$ of dry weight.

2.9. Statistical analysis

Data are presented as the average of the results obtained from four-independent experiments (seasons 2011, 2012, 2014 and 2015) with a minimum of 6 replicates each and analyzed by means of ANOVA. The means were compared by the LSD test at a significance level of 0.05.

3. Results

3.1. Fruit yield and plant biomass

The applications of 15 min LP every 2 h increased the fruit yield per plant by 18%. On the other hand, when the same LP treatments were applied every 4 h, there was no effect if compared to the untreated plants (Table 1). However, if the first cluster of the plant (where the LP treatments were applied) was analyzed separately, there was an increase of 21% and 28% of fruit yield for 15 min LP every 4 and 2 h, respectively.

The architecture of the plants changed with a great modification in the number of leaves per plant and height when plants were exposed to nocturnal LP for both frequencies (Table 1). Surprisingly, total leaf dry weight, stem dry weight, internode distance and chlorophyll concentration were not affected by any of the treatments when compared to the untreated plants.

3.2. Fruit quality and ripening parameters

After assessing quality parameters in fruit exposed to nocturnal LP, no changes in the acidity, soluble solids or pH were found (Table 2). However, the proportion of fruit which turned from green to red color was significantly higher: 46.5% and 39.3% of the tomatoes treated with 15 min LP every 4 and 2 h, respectively, got to the mature stage, in comparison to only 21.4% of untreated fruit (middle of December) (Fig. 1).

Table 2
Acidity, soluble solids and pH in mature red fruits of untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Letters denote statistical differences (ANOVA, $P \leq 0.05$).

	Untreated	4 h 15 min LP	2 h 15 min LP
Acidity (g kg^{-1} FW)	3.87 ± 0.35 a	4.09 ± 0.37 a	4.56 ± 0.55 a
Soluble solids (°BRIX)	4.84 ± 0.31 a	4.42 ± 0.47 a	4.57 ± 0.20 a
pH	4.32 ± 0.08 a	4.33 ± 0.03 a	4.29 ± 0.06 a

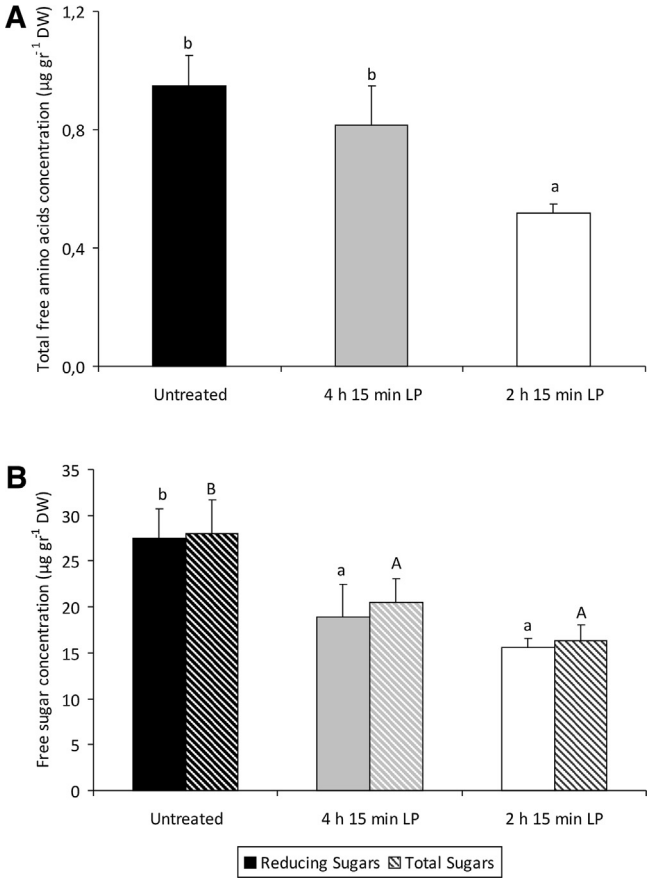

Fig. 3. The concentrations of total amino acids (A) and total and reducing sugars (B) in mature red fruit in untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Results were analyzed by ANOVA ($P \leq 0.05$) to refuse the null hypothesis and multiple test range (LSD test) was performed to detect the differences among means. Error bars represent standard deviation and letters denote statistical differences.

Another important parameter to evaluate fruit quality is firmness. In this case, LP at different frequencies produced no changes in the firmness of the fruit (Fig. 2).

Other parameters that explain the process of maturation are sugar and amino acid concentration. The treatment with 15 min LP every 2 h produced a significant reduction in the amount of total amino acids, but no differences were observed when LP were applied every 4 h (Fig. 3A). Considering the concentration of total and reducing sugars, there was a clear decreasing tendency when LP were applied (Fig. 3B) while total soluble solids did not show any difference due to the treatments (Table 2).

3.3. Concentration of antioxidants and organic acids in fruit

A significant increase in the concentration of lycopene was observed in mature red tomatoes exposed to LP pulses every 2 or 4 h during the night (Fig. 4).

Table 1
Plant and fruit yield parameters of mature red fruit in untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Results were analyzed by ANOVA ($P \leq 0.05$) to refuse the null hypothesis and multiple test range (LSD test) was performed to detect the differences among means. Data are presented as mean ± standard deviation and letters denote statistical differences.

	Untreated	4 h 15 min LP	2 h 15 min LP
Fruit yield per plant (g)	391 ± 24 a	408 ± 25 (4%) a	461 ± 16 (18%) b
Fruit weight per treated cluster (g)	274 ± 19 a	332 ± 28 (21%) b	350 ± 23 (28%) b
Plant height (cm)	67 ± 10 a	91 ± 13 b	102 ± 20 b
Leaf number	9.9 ± 1.3 a	13.7 ± 1.7 b	16.2 ± 2.9 b
Internode distance (cm)	6.8 ± 0.7 a	6.4 ± 0.4 a	6.1 ± 0.6 a
Leaf dry weight (g)	13.42 ± 0.78 a	13.81 ± 1.36 a	14.49 ± 1.32 a
Stem dry weight (g)	10.23 ± 1.66 a	10.41 ± 1.69 a	10.62 ± 1.71 a
Chlorophyll content (Spad Units)	23.9 ± 1.5 a	26.0 ± 0.4 a	25.4 ± 4.6 a

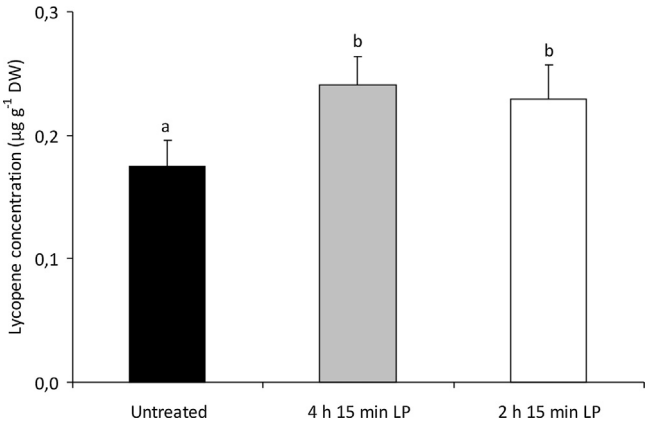

Fig. 4. Lycopene concentration in mature red fruit in untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Results were analyzed by ANOVA ($P \leq 0.05$) to refuse the null hypothesis and multiple test range (LSD test) was performed to detect the differences among means. Error bars represent standard deviation and letters denote statistical differences.

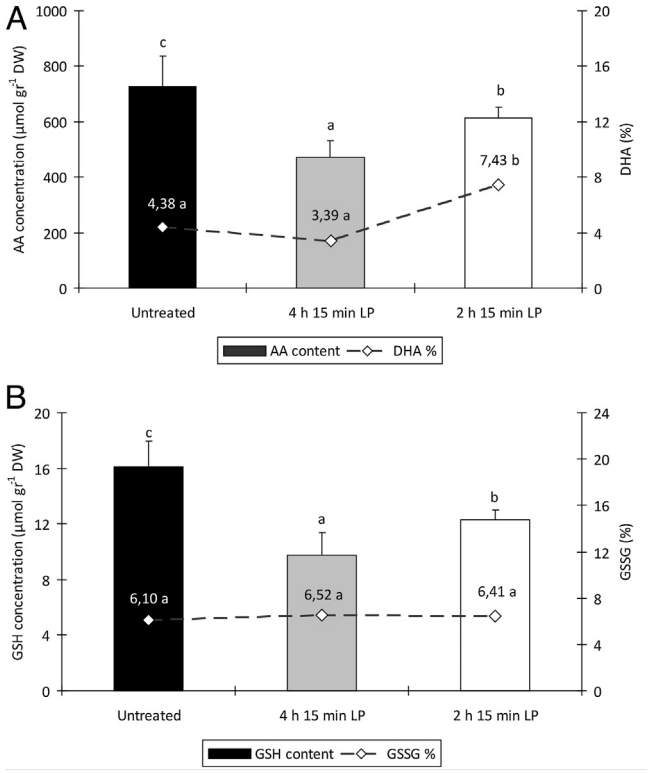

Fig. 5. Concentrations of AA (A) and GSH (B) and their corresponding oxidised proportions in mature red fruit in untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Results were analyzed by ANOVA ($P \leq 0.05$) to refuse the null hypothesis and multiple test range (LSD test) was performed to detect the differences among means. Error bars represent standard deviation and letters denote statistical differences.

Focusing on hydro-soluble antioxidants, AA accumulation decreased with 15 min LP every 4 h, and showed intermediate values when pulses were applied every 2 h, compared to the untreated fruit. The oxidation state of AA did not change with 15 min LP every 4 h, but it increased when the frequency was raised to every 2 h LP (Fig. 5A). The same pattern was followed by GSH, but with no changes in the oxidised form (Fig. 5B).

Following the same tendency, citric acid concentration resembled the AA and GSH pattern (Fig. 6A). The treatment with 15 min LP every 4 h caused a drop of the concentration of citric acid and the treatment with 15 min LP every 2 h produced intermediate values of acid content. On the other hand, malic acid accumulation decreased with the intermediate treatment, but, after the highest frequency treatment, it reached a value similar to the untreated fruit (Fig. 6B).

4. Discussion

4.1. Nocturnal LP treatments affect fruit yield

Fan et al. (2013) have determined that diurnal light strongly influences the growth and leaf development of tomato plants, concluding that the highest the light intensity, the lowest leaf area and height were found. Other experiments demonstrated that fruit yield and fruit size could be improved by 13% by the application of different color LED for 2 h after sunset, without modifying the content of chlorophyll (Xu et al., 2012). These results match those obtained in the present work, but apart from that, it also demonstrated that the application of some LP during the night increased the fruit yield per plant even further.

The effect of LP treatment was limited to the treated cluster so it was responsible for the differences in plant yield. This result suggests the absence of a systemic signal affecting non-treated fruit, an aspect that must be considered for the use of nocturnal LP in commercial tomato planting. The modification in fruit yield was not associated with changes in the biomass of green tissues. However, LP treatment modifies the architecture of the plant, which may lead to an improved use of incident light and tomato production. This physiological aspect deserves further study.

4.2. Nocturnal LP treatments modifies tomato ripening

Nocturnal LP treatments increase the concentration of lycopene which coincides with the proportion of fruit that turned to mature red due to this treatment. Lycopene is the most abundant carotenoid in mature tomato and it has been demonstrated that the synthesis of this antioxidant strongly depends on light (Liu et al., 2009; Obande et al., 2011). In this case, the sole applica-

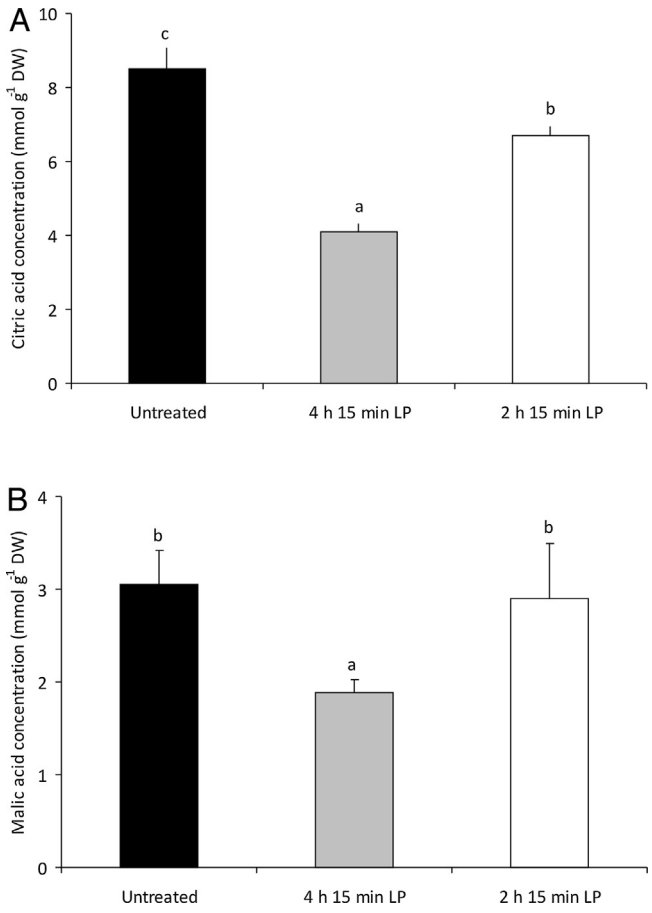

Fig. 6. Concentrations of citric (A) and malic (B) acids in mature red fruit in untreated plants and in plants treated with 4 h LP and 2 h LP during the night. Results were analyzed by ANOVA ($P \leq 0.05$) to refuse the null hypothesis and multiple test range (LSD test) was performed to detect the differences among means. Error bars represent standard deviation and letters denote statistical differences.

tion of white light at low irradiance produced a significant effect on fruit color and thus in lycopene concentration evidencing that LP applications reduce ripening time for tomato (i.e. the time to get a red stage). Interestingly, the results presented here suggest that nocturnal LP treatments reduce ripening time but do not affect other quality parameters, especially remarkable is the fact that fruit conserve firmness, an important attribute for tomato commercialization. In addition, these results indicate that lycopene synthesis is independent from other physiological processes, such as cell wall metabolism, as they are differentially affected by nocturnal LP treatments on tomato fruit.

4.3. *The effect of LP treatment on fruit metabolites*

Changes in the concentration of sugars and amino acids constitute important attributes during tomato maturation. Sugar concentration typically increases during the passage from green to red stage, and then decrease again, with concomitant changes in the sugars that are present such as glucose and fructose (Davies and Kempton, 1975). Concentration of sugars has been proved to be regulated by the sink-source relation, determining as a consequence an improvement of yield and fruit size of tomato (Ho, 1996). According to the present study, nocturnal LP could be producing some changes in fruit yield due to the redistribution of the same amount of sugars among a larger sink, provoking a dilution in the amino acids concentration and soluble sugars provided by a limited photosynthetic source.

As mentioned before, tomato fruit are a great source of water soluble and lipid soluble antioxidants, such as AA (Massot et al., 2012) and carotenoids (Liu et al., 2009), respectively. The decrease in the AA concentration could be a consequence of the reduction of the soluble sugars concentration in the fruit. AA synthesis strongly depends on the amounts of free sugars to activate the pathway, such as sucrose, glucose or fructose (Davey et al., 2000). Incident light over sink tissues affects AA concentration on edible organs such as tomato fruit and potato tubers, depending on the photosynthetic tissues as a source of photo-assimilates (Li et al., 2009, 2010; Tedone et al., 2004). These assimilates can be redistributed over the whole plant through the phloem system (Tedone et al., 2004; Franceschi and Tarlyn, 2002). However, Gautier et al. (2009) suggest that the concentration of AA in fruit is no limited by the source tissue, and it especially depends on irradiance when it is applied directly over fruit (Massot et al., 2012).

LP treatments decrease AA and GSH concentrations. A similar effect on both antioxidants might be due to their interconnection in the Foyer and Halliwell cycle (Foyer and Halliwell, 1976).

Citric and malic acid concentrations showed a trend of changes similar to the observed for the other metabolites when LP treatments were applied. These modifications may be the result of alterations in mitochondrial metabolism, involved in the synthesis of both organic acids and in plants in particular, in the synthesis of AA (Bartoli et al., 2000).

5. Conclusions

Overall, these results show that low irradiance LP applied during the night have an effect on plant and fruit growth and ripening, especially in plant height, number of leaves, fruit yield, color and concentration of lycopene. LP treatment reduces the concentration of some metabolites (v.g. free sugars, amino acids, AA and others) but does not modify other parameters of fruit quality such as firmness.

Light has a strong influence on plants on a wide range of processes such as photosynthesis (Galtier et al., 1995), photomorphogenesis and photoperiodism (Weller and Kendrick, 2014) and ripening (Giovannoni, 2004). Although it has been demonstrated that light affects vitamin C content (Gatzek et al., 2002; Tabata et al., 2002; Bartoli et al., 2009; Zushi et al., 2014), in the case of fruit ripening, LED (Xu et al., 2012) and UV-C (Liu et al., 2009) light has been used to improve yield and fruit quality, respectively. There was no data so far about the effects of white light (i.e. LP at low irradiance) during the night on tomato plants and fruit. This finding could be used as a tool which would imply low cost and clean technology with easy application over the crop. In addition, nocturnal LP treatments may be a useful experimental approach to unravel the physiological processes determining the desirable attributes of tomatoes for human consumption.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.scienta.2016.03.001.

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