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Stomatal aperture and physicochemical qualities in yellow pitahaya (*Hylocereus megalanthus* Bauer) fruits in response to day/night rhythm in pre and postharvest

Apertura estomática y calidad fisicoquímica en frutos de pitahaya amarilla (*Hylocereus megalanthus* Bauer) en respuesta al ritmo día/noche en cultivo y poscosecha

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Ripe pitahaya fruits in crop nearby Fusagasuga (Cundinamarca, Colombia).

Photo: G. Fischer

ABSTRACT

Yellow pitahaya is a tropical fruit with economic potential due to its physicochemical, organoleptic and nutritional properties. Given the CAM (crassula acid metabolism) of pitahaya, it is necessary to study the stomatal aperture and acidic behaviour in the cladode and fruit in field and postharvest in order to understand the physiology, crop management, and postharvest processes of yellow pitahaya, particularly in response to the day/night rhythm. Stomatal behaviour was characterised in a 4-year-old pitahaya crop (Silvania, Colombia), under ambient conditions of 19°C, 12/12 hours day/night, and additionally, total titratable acidity (TTA), total soluble solids (TSS) and maturity ratio (MR) were determined in the fruits. Subsequently, fruits harvested in physiological maturity (90% green, 10% yellow) were stored at 13°C and 80% relative humidity for 16 days, and the effect of three lighting treatments (continuous light, continuous darkness and light/dark change: 12/12 h) was evaluated, determining stomatal behaviour, TTA, TSS, MR, firmness, respiration and weight loss. In the field, the cladodes showed a behaviour characteristic of CAM plants, but the fruits did not. In storage, fruits subjected to the light/dark change showed significant increases in respiration intensity and cumulative weight loss. Postharvest treatments did not show significant differences in firmness, TTA, TSS and fruit maturity ratio. Based on the results, it is indicated that storage under alternating light and dark conditions decreases the postharvest shelf life of pitahaya fruit.

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Additional key words: dragon fruit; stomatal opening; CAM metabolism; alternating light/dark; respiration; storage.

RESUMEN

La pitahaya amarilla es un fruto tropical que posee potencial económico debido a sus propiedades fisicoquímicas, organolépticas y nutricionales. Debido al metabolismo CAM (crassula acid metabolism) de la pitahaya es necesario estudiar la apertura estomática y el comportamiento de la acidez en cladodio y fruto en campo y poscosecha para entender mejor su fisiología, manejo de cultivo y poscosecha, dependiendo del ritmo día/noche. Se caracterizó el comportamiento estomático en un cultivo de pitahaya de 4 años de edad (Silvania, Colombia), bajo condiciones ambientes de 19°C, 12/12 horas día/noche, y se determinó la acidez total titulable (ATT), sólidos solubles totales (SST) y relación de madurez (RM) en frutos. Los frutos cosechados en madurez fisiológica (90% verde, 10% amarilla) se almacenaron a 13°C y 80% de humedad relativa durante 16 días. Se evaluó el efecto de tres tratamientos de iluminación (luz continua, oscuridad continua y cambio luz/oscuridad: 12/12 h), determinando el comportamiento estomático, la ATT, los SST, la RM, firmeza, respiración y pérdida de peso. En campo, los cladodios presentaron un comportamiento característico de las plantas CAM, pero no los frutos. En almacenamiento, frutos sometidos al cambio luz/oscuridad presentaron aumentos significativos de la intensidad respiratoria y pérdida acumulada de peso. Los tratamientos poscosecha no presentaron diferencias significativas para las variables firmeza, ATT, SST y relación de madurez de los frutos. Con base en los resultados se indica que el almacenamiento a condiciones de luz y oscuridad alternantes disminuye la vida útil del fruto de pitahaya en poscosecha.

Palabras clave adicionales: fruta del dragón; apertura estomática; metabolismo CAM; alternancia luz/oscuridad; almacenamiento.

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INTRODUCTION

The demand for functional, nutrient-rich, healthy and beneficial fruits is increasing along with improved standard of living (Li *et al*., 2024). Pitahaya, native to the Andean region (Morillo-Coronado *et al*., 2017) occupies an important niche in the international exotic fruit market, especially in the United States and Europe, and in the domestic markets of countries such as Colombia, Mexico, Costa Rica, Nicaragua, Guatemala, Ecuador and the Caribbean islands (Paull and Duarte, 2012), Malaysia, Vietnam and Brazil (Nunes *et al*., 2014). Moreover, new plantations exist in Australia, Israel and Reunion Island (Le Bellec *et al*., 2006). In Asia, pitahaya is commercially cultivated in China, Malaysia, Thailand, Vietnam, Bangladesh, Sri Lanka, and India (Mori *et al*., 2023).

Pitahaya is a perennial, succulent plant belonging to the Cactaceae family and characterised by its climbing and/or epiphytic habit. Although it is a plant adapted to desert environments (Chuck-Hernández *et al.*, 2016), pitahaya has evolved to adapt well to humid tropical areas of the American continent (Corredor, 2012).

In Colombia, pitahaya crops are well adapted to the conditions of the coffee-growing zone, at altitudes between 1,500 and 1,900 m a.s.l. (Fischer *et al.*, 2023) and temperatures between 18 and 21°C. However, Corredor (2012) also reports crops between 800 and 1,900 m a.s.l., with temperatures between 16°C (at night) and 25°C (during the day). In India, Mori *et al.* (2023) report cultivation at altitudes up to 1,700 m a.s.l. Paull and Duarte (2012) suggest that longer days may trigger flowering, some plantations artificial light to extend day length.

The scaly fruit of yellow pitahaya is a globose, ellipsoidal-to-ovoid berry with white flesh and numerous black seeds (Mercado-Silva *et al.*, 2018). It reaches maturity approximately 6 months after the flower bud is formed and has a fresh weight between 120 and 250 g (Le Bellec and Vaillant, 2011). It has a sweeter flesh than the red species (Paull and Duarte, 2012). In the epidermis of leaves, stems and fruits, stomata are located, formed by two guard cells, generally elongated, which enclose a pore through which plants absorb CO_2 and release O_2 (Taiz *et al.*, 2017). In pitahaya, leaves are reduced to spines and photosynthetic activity is predominantly carried out by the plant's modified succulent stems, called cladodes (Corredor, 2012; Sánchez *et al.*, 2013).

The importance of this fruit can be explained, in part, by its attractive qualities — exotic appearance, intense yellow or red colour and its sensory, nutraceutical characteristics and commercial value (Esquivel and Ayara, 2012; Verona-Ruiz *et al.*, 2020; Deori *et al*., 2024). Due to the trade policies of some producing and exporting in countries such as Colombia, Israel and Vietnam (Le Bellec and Vaillant, 2011), only two pitahaya species are commonly found in the market at present: yellow pitahaya (*Hylocereus megalanthus* Bauer, syn. *Selenicereus megalanthus*), a fruit with yellow skin, spines and white flesh; and red pitahaya (*Hylocereus* spp. Britt & Rose), a fruit with a red skin, no spines, and white or red flesh (Le Bellec and Vaillant, 2011).

In plants with C3 and C4 metabolism, stomata show a rhythmic behaviour, opening during the day and closing at night (Winter and Holtum, 2014). In CAM metabolism plants, such as pitahaya and other cacti, the opposite occurs, the maximum opening of the stomata takes place at night, especially at the beginning of night. At this time, CO_2 is absorbed and fixed, mediated by a carbonic anhydrase by PEP carboxylase, and stored as malic acid in the vacuoles of the fruit, which decreases its pH drastically. Meanwhile, in the daytime, CO_2 is released from the vacuole and subsequently decarboxylated to produce CO_2, which is then subsequently carboxylated by Rubisco in the chloroplast stroma through the Calvin-Benson cycle. Elevated levels of internal CO_2 stimulate stomatal closure in the daytime (Lambers and Oliveira, 2019). Sánchez *et al.* (2013) found a low stomatal density in pitahaya cladodes (11.28 stomata/mm^2), which was still 8 times higher than in fruits (1.43/mm^2), and observed in purple passion fruit, a C3 plant, 106.5 leaf stomata/mm^2 and 12.6/mm^2 on fruit surface.

Biological circadian rhythms, which include the closing and opening of stomata, are synchronised through environmental conditions such as light and temperature (Goodspeed *et al.*, 2013; Gil and Park, 2019). They behave as a vital biological clock that favours the maintenance of habitual growth, healthy development and fitness of the plant (Chaudhary *et al.*, 2023). Since many plants exhibit circadian patterns of abundant transcripts, the circadian clock plays an important role in regulating plant biochemistry, being regulated by numerous genes involved in metabolism (Sanchez and Kay, 2016). Fruit and vegetable cells, after they have been harvested, remain active and continue to sense light, so their biological clocks continue to function (Braam, 2013). This ability of harvested produce allows the plant to modify the levels of chemicals that protect it from being eaten by herbivores and may also increase its level of phytochemicals important for the health of consumers (Braam, 2013). This was the case in the study by Castillejo *et al*. (2023), who used night-time supplemental lighting with cool white, blue, green, red or far-red LEDs in broccoli florets storage at 5°C, increasing the bioactive compound sulforaphane significantly.

Nocturnal conditions with lower temperatures and higher relative humidity favour the maintenance of a water status that enables the toleration of situations of high heat and dry periods (Taiz *et al*., 2017; Rengel *et al*., 2023). In this regard, Davis *et al*. (2019) highlight the high water use efficiency (WUE) of CAM plants, which is a primary benefit in agriculture which boosts yields, including under water stress conditions, and makes this group of plants more resilient to climate change. Chuck-Hernandez *et al*. (2016) claim that, due to CAM metabolism, the WUE of pitahaya is five to ten times higher that of C3 plants. In addition, arid conditions with very hot sunshine can lead to sun strike on cladodes (Fischer *et al*., 2022) and flower bud drop in pitahayas, and, possibly, excess solar energy can cause photoinhibition (Flórez-Velasco *et al*., 2024), which is why in some countries with these conditions there are plantations with shading between 30 and 50% (Perween *et al*., 2018).

There are few studies of post-harvest stomatal behaviour, Johnson and Brun (1966) showed that stomata of banana (*Musa acuminata* L. var. Hort. Valery) are able to open and close for several weeks after harvest, while Guaquetá *et al*. (2007) observed a stomatal closure in guava at 3.5 h after harvest that occurred faster when the temperature was higher (25°C *vs.* 13°C).

During postharvest, changes in quality attributes such as texture, aroma, flavour and penetration resistance may occur in fruits as indicators of maturity (Pareek, 2016; Pott *et al*., 2020). In pitahaya, TTA is reduced during storage (Nerd *et al*., 1999). Respiration affects the postharvest life of fruits as there is an inverse relationship between respiration intensity and postharvest life of the fruit (Pareek, 2016). Postharvest weight loss is governed by the transpiration process and fruit respiration (Martínez-González *et al*., 2017).

Studies by Nerd *et al*. (1999) in red pitahaya fruits and by Siddiq and Nasir (2012) in yellow pitahaya indicate that these fruits have non-climacteric behaviour. However, Rodríguez *et al*. (2005) found a climacteric peak in yellow pitahaya, classifying it as a climacteric fruit, while Paull and Duarte (2012) mention that both yellow and red pitahaya are non-climacteric. In general, extending the shelf-life of harvested fruits is mainly done through controlling respiration rates (Saltveit, 2019; Umeohia and Olapade, 2024).

Multiple factors affect the quality of pitahaya fruits (Le Bellec and Vaillant, 2011) and there are no adequate technological packages for production and postharvest handling that allow this crop to be more competitive (Álvarez-Herrera *et al*., 2016). Therefore, the objective of this study was to determine whether periods of light and darkness, which govern the opening of stomata in pre-harvest, also affect stomatal behaviour and the physicochemical quality and respiration of fruit in postharvest, considering conditions of darkness, permanent light and alternating light/dark for 12 h. If light causes stomata closure in storage, artificial lighting could be an option to extend the postharvest life of these CAM fruits.

MATERIALS AND METHODS

Location and plant material

The study was carried out on a 4-year-old commercial crop of yellow pitahaya (*H. megalanthus* Bauer), located at 4°27‘ N and 74°22’ W, in the municipality of Silvania (Colombia), at an elevation of 1,900 m, with mean temperature of 19°C and rainfall of 1,400 mm per year^{-1}. The plant material consisted of cladodes and fruits at green-yellowish maturity (90% green and 10% yellow; Fig. 1), corresponding to the physiological maturity point (Dueñas *et al*., 2012), located in the middle third of the plant, of homogeneous size, without phytosanitary problems or evidence of physical damage.

Figure 1. Physiological maturity index of pitahaya fruits used in this study. Photo: G. Fischer.

The postharvest study was carried out in a storage chamber (13°C and 80% relative humidity) with cold light lamps (12 VDC 990X12X1 mm; 5630-72 LED) for 16 d in the postharvest laboratory of agricultural products at the Faculty of Agricultural Sciences, Universidad Nacional de Colombia, Bogota.

Experimental design and statistical analysis

In the field, a completely randomised design (CRD) was used with the time of day as a factor, while in post-harvest, a CRD was established with three lighting treatments in continuous cycles (24 h of darkness, 24 h of light, and 12 h of light + 12 h of darkness). Analysis of variance (ANOVA) and Tukey’s comparative tests ($P \leq 0.05$) were performed using SAS 9.1 software (SAS Institute, Cary, NC).

Stomatal behaviour and density

The stomatal behaviour of cladodes and fruits in plants was evaluated every 3 h for a period of 72 h (15 experimental units in the field and 3 in postharvest). In addition, post-harvest measurements were carried out for 16 d, every 3rd d. The surface of the fruits and cladodes was printed using the enamel printing technique proposed by Brewer (1992). Recognition of stomata (open and closed) was carried out using the scale of Laurin *et al*. (2006), adapted to light microscopy. Stomatal density (number of stomata/mm^2) in fruits and cladodes was obtained by counting stomatal structures in a 1 mm^2 field with the support of a BM2000 binocular microscope (Nanjing Jiangnan Novel Optics, Ningbo, Zhejiang, China), a DCM510 adaptable digital camera (OCS Tec, Neuching, Germany) and ScopePhoto 3.0 software (UpdateStar, Berlin, Germany).

Physico-chemical analysis

Total soluble solids (TSS) and total titratable acidity (TTA) were evaluated every 6 h for 3 d in the field and postharvest, and every 3 d for 16 d in postharvest. TSS were measured in the field with a portable refractometer Brixco 3020 (Labexco, Bogota, Colombia) and in postharvest with a digital refractometer HI 96801 (Hanna Instruments, Woonsocket, RI) with a scale of 0-85% of each one. TTA was determined volumetrically by neutralisation of a 5 g sample of fruit pulp or cladode with a 0.1 N concentrated NaOH solution and phenolphthalein as pH indicator (AOAC, 1990). The results were expressed in percentage of citric acid as indicated by Herrera (2010) (Eq. 1).

$$TTA(\%\ citric\ acid) = \frac{100{*}A{*}B{*}C}{D} \qquad (1)$$

where, *A* was volume (mL) of NaOH used, *B* normality of NaOH (0.1 N), *C* equivalent weight of citric acid (0.097 g meq^{-1}) and *D* weight of sample (g).

The ratio of TSS to TTA determined the maturity ratio (MR) in fruits. Weight loss was evaluated every 6 h for 72 h and then every 3rd day for 16 d, taking into account the difference in weight between the initial day and the time of sampling (Eq. 2).

$$\begin{array}{c}\%\\ weigth\\ loss\end{array} = \frac{100{*}Initial\ weight\text{-}final\ weight}{Initial\ weight} \qquad (2)$$

Penetration resistance was measured in the laboratory, every 6 h for 3 d and every 3 d for 16 d, in shelled fruit, using a digital penetrometer LS1 (Ametek, Berwyn, PA), with a 0.5 cm diameter probe at a point on the equatorial axis of each fruit.

In the same period of time, post-harvest respiratory intensity (RI, mg CO_2 kg^{-1} h^{-1}) was measured by quantifying the CO_2 emission of pitahaya fruits preserved in 2 L airtight chambers, using infrared CO_2-BTA sensors (Vernier Software & Technology, Beaverton, OR) coupled to the LabQuest data acquisition system (Vernier Software & Technology, Beaverton, OR). The variable was calculated using the formula proposed by Garcia (2015) (Eq. 3).

$$RI = \boldsymbol{m}{*}(Vc - Vf - 47{,}522) * 3.6 * 1.842 * \frac{1}{wf} \qquad (3)$$

where, *m* was slope determined with the LabQuest system (ppm CO^2 s^{-1}), *Vc* volume of the chamber (mL), *Vf* volume of the fruits (mL), *Wf* weight of the fruits (g). The constant 47.522 corresponds to the volume of the sensor entering the chamber and 1.842 is the density of CO_2 in mg cm^{-3}.

RESULTS AND DISCUSSION

Stomatal behaviour

In the field, significant differences ($P \leq 0.05$) were found between the times of day when the stomatal aperture of cladodes was assessed (Fig. 2). The highest stomatal opening was observed in the evening hours (between 21:00 and 03:00 h) with an average of 67.4%, in contrast to daylight hours (between 9:00 and 15:00 h) where an average of 8.8% of stomata were open. The fruits did not show a rhythmic stomatal behaviour depending on the time of day (Fig. 2).

The rhythmic opening and closing of stomata in cladodes allow us to observe the CAM behaviour of the pitahaya plant, with greater opening at night (Sánchez *et al*., 2013; Taiz *et al*., 2017). The fact that the stomatal aperture in fruits did not show significant differences during the hours evaluated would suggest that the fruits, in this study, unlike the cladodes, do not conform to CAM-type stomatal metabolism. However, Sánchez *et al*. (2013) found that yellow pitahaya fruits in the field still show CAM rhythmic stomatal behaviour, although this is less marked than in cladodes. These authors measured a correlation of R^2=-0.27 between solar radiation and open stomata in fruits which, as mentioned above, was much higher in cladodes (R^2= -0.48).

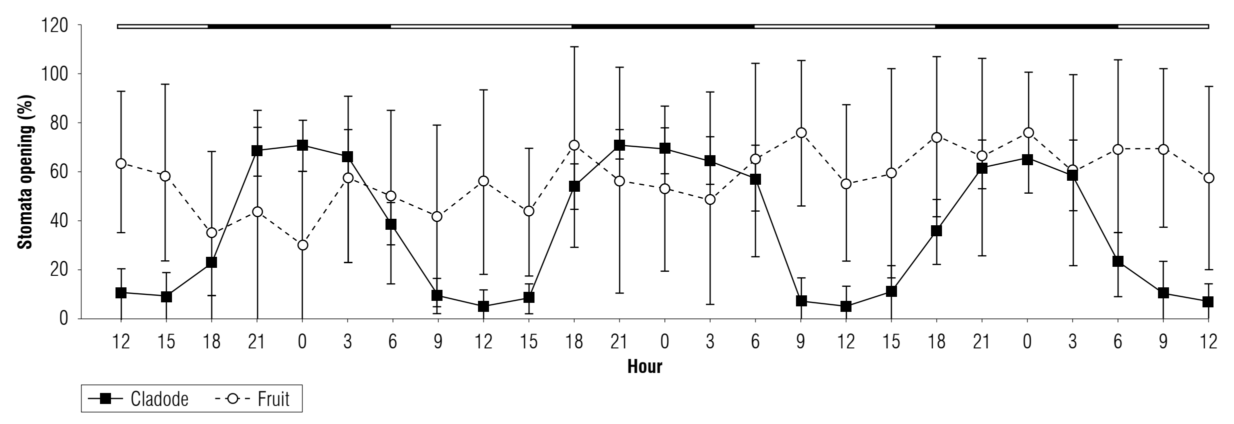

Figure 2. Percentage of stomata opening in cladodes and fruits of pitahaya during 3 days under field conditions. The upper box indicates alternation between hours of darkness (black) and light (white). Sampling was done every 3 hours. Vertical bars indicate standard deviation.

In C3 banana and guava plants, Guaquetá *et al*. (2007) observed the same trend between intact leaves and fruits. These results suggest that in the daytime there was a higher percentage of open stomata in leaves than in fruits, and the stomatal behaviour of the two organs correlated well with the intensity of incident solar radiation, while stomata in carambola fruits were continuously open.

Overall, little to no coincidence of pitahaya fruit stomata opening with foliar (cladode) can be observed. This reflects the conclusion of Yahia *et al*. (2019), that for the fruit organ, there are no clear reports of marked acid fluctuations between day and night, nor a constant net CO_2 assimilation in this organ. However, the fruits showed evident photochemical activity.

During storage, it was observed that the stomatal aperture of the fruits was independent of the time of day (Fig. 3). The independence of fruit stomatal aperture from time of day agrees with the study by Nerd *et al*. (1999), where fruits of *H. undatus* and *H. polyrhizus* did not show CAM metabolism, which had been observed in the intact cladodes of the plant. Similarly, in detached fruits, stomata tend to be less responsive to environmental factors than intact fruits (van Meeteren and Aliniaeifard, 2016).

However, significant differences were recorded between light treatments, at 13 and 16 days after harvest (DAH), where the percentage of open stomata was significantly higher ($P \leq 0.05$) in fruit subjected to light-dark alternation. In comparison, the stomata of *Brassica oleracea* cabbage (C3 plant), stored at 1°C and 95% RH, in darkness or continuous light, kept their stomata open under light, but closed in darkness (Noichinda *et al*., 2007).

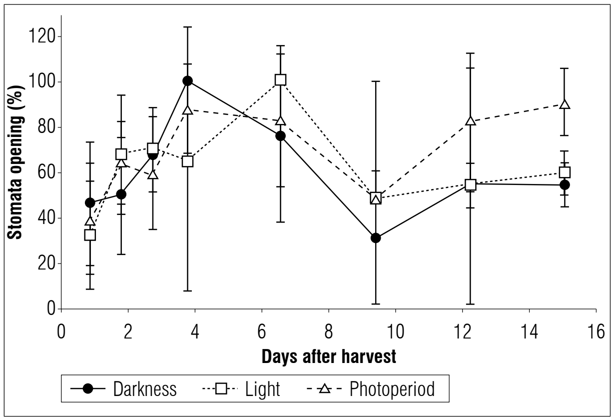

Figure 3. Percentage of stomatal aperture in pitahaya fruits during 16 days of storage at 13°C and different lighting conditions (continuous darkness ●, continuous light □, 12 h light and 12 h darkness per day Δ). Sampling at days 1, 2, 3, 4 and then every 3 days. Vertical bars indicate standard deviation.

The results obtained on stomatal aperture up to 16 DAH indicate, to some extent, that alternating light/dark storage promotes stomatal metabolism in fruit. It is possible, as the authors surmise, that the fruit and their stomata would maintain a certain circadian rhythm related to the light/dark cycle when they were intact on the plant. Hassidim *et al*. (2017) observed, in *Arabidopsis thaliana* kept under permanent light, an adjustment in gas exchange by leaves through the circadian clock so that stomata 'instinctively' opened more during daylight hours than at night (de Leone *et al*., 2020) confirming that the circadian clock is one of the important regulators of stomata opening in plants without water stress (Hotta *et al*., 2007).

Casal (2008) states that the measurement of photoperiod depends on the coincidence between light and circadian rhythm involving stability and instability effects of the CONSTANS gene, related to this process and controlled by light. Presumably, and following the floral induction theory of Taiz *et al*. (2017), from 13 DAH onwards, sufficient day/night cycles had occurred for a greater stomatal opening to occur, which also activates an elevated fruit metabolism, as seen later in the results of the physicochemical and respiration analysis of the fruit.

Physico-chemical analysis

Total titratable acidity (TTA)

The TTA in the fruit was higher than in the cladodes, indeed, more than twice as high in most measurements. However, during the first night, and to a lesser extent on the third night, there was a significant increase in acidity in the cladodes which coincided with the greater opening of the stomata on those nights (Fig. 3). Lambers and Oliveira (2019), who characterise CAM plants by their assimilation of CO_2 during the night, when their stomata are open, which allows the accumulation of organic acids in the vacuole, subsequently moving to the Calvin cycle during the day. The TTA of the fruits did not show statistical differences between day and night values, only a tendency for acidity to increase between 18:00 and 0:00 h was observed in the second and third night of sampling (Fig. 4), which confirms the greater reaction of the cladodes than the fruits to CAM metabolism. Fruit TTA values were found to be in the range of twice those measured by Sotomayor *et al*. (2019), with 0.14% TTA in ripe yellow pitahayas and 0.12% TTA observed by Vázquez-Castillo *et al.* (2016) taking into account that our study worked with physiologically ripe fruits (90% green and 10% yellow), and pitahaya acidity decreases during the ripening process in cultivation (Sotomayor *et al*., 2019).

In storage, there were no significant differences for TTA between treatments, with the percentage of citric acid ranging from 0.13 to 0.38 (Fig. 5), similar to the value of 0.15 reported by Lima *et al*. (2013) in yellow pitahaya. A general trend of decreasing fruit acidity was observed, possibly because during the ripening process, organic acids are used as a substrate for respiration (Vallarino and Osorio, 2019), as was also observed by Rodriguez *et al.* (2005) in yellow pitaya. Peaks of TTA increase were presented at 4 d for fruits with photoperiod and at 7 d for fruits in darkness and in continuous light.

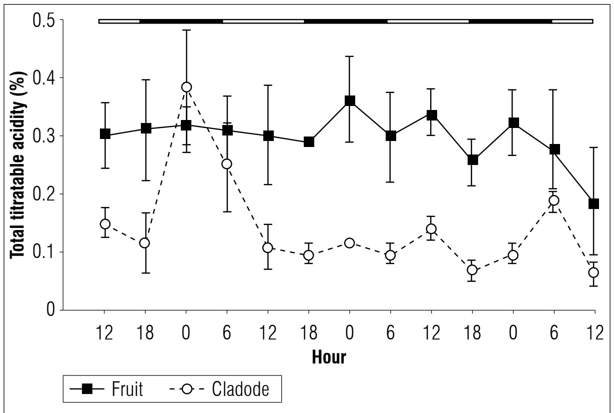

Figure 4. Total titratable acidity of fruits and cladodes of yellow pitahaya (*Hylocereus megalanthus*) in the field during day (light box) and night (dark boxes). Sampling every 6 hours, for 3 days. Vertical bars indicate standard deviation.

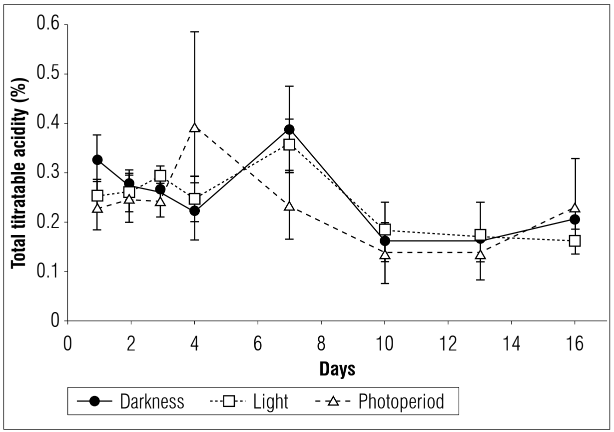

Figure 5. Percentage of total titratable acidity in pitahaya fruits during 16 days of storage at 13°C and different lighting conditions (continuous darkness ●, continuous light □, 12 h light and 12 h darkness per day Δ). Sampling at days 1, 2, 3, 4 and then every 3 days. Vertical bars indicate standard deviation.

Total soluble solids (TSS)

The TSS content in fruit during field measurements (average 13.4° Brix) did not show significant differences depending on the time of day and, consequently, the maturity ratio (average TSS/ATT 47.1) also remained constant. It should be noted that the main changes in TSS content occur as the fruit forms and ripens (Pareek, 2016), while in our study we only included 3 d of measurements.

Fernández *et al*. (2015) illuminated red pitahaya (*H. undatus*) plants in the field for 6 h at night (between 21:00 and 3:00 h) and also found no change in the TSS content; however, the productivity (kg fruits harvested/month) of the plants increased by 300%, a result in agreement with Jiang *et al*. (2016), who classified the red pitahaya 'Shih Hou Cyuan' (*H. undatus* × *H. polyrhizus*) as a long-day plant due to the increase in the induction of flower buds when night-time interruption by lighting was applied (between 9:00 and 3:00 am).

During storage, the TSS also showed no significant differences between the light treatments and the values ranged from 14.96 to 18.56. The fruits of *Hylocereus* sp. *in situ* presented similar values of 14.29 (Cañar *et al*., 2014) and 17-18° Brix (Le Bellec *et al*., 2006; Mejía *et al*., 2013). On the other hand, Caetano *et al*. (2011) reported that TSS in *H. megalanthus* range between 11.9 and 17.8° Brix. Additionally, Nerd *et al.* (1999) showed that TSS do not vary significantly during storage because the greatest accumulation of sugars in the fruit occurs in the final phase of development in the plant, where this behaviour in exchange is related to the decrease in the starch and mucilage content of the pulp. Likewise, as in intact fruits, the variation in the maturity ratio (TSS/TTA) in postharvest was not significant for any of the treatments evaluated.

Weight loss

During the 1st d of storage, the accumulated weight loss did not present significant differences ($P>0.05$). However, after 7 d significant differences were observed ($P\leq0.05$) in fruits subjected to light and dark cycles, with the greatest final weight loss (17.34% at 16 d) (Fig. 6). This result coincides with the greater loss of fresh mass in *Brassica oleracea* when its stomata were open during the application of light in storage, losing more water due to elevated transpiration through open stomata (Noichinda *et al*., 2007).

Centurión *et al*. (1999) found weight losses of 14% in red pitahaya fruits, stored (in darkness) at 20°C for 11 d, while Wills and Golding (2016) determined that a weight loss greater than 5% is sufficient to affect the quality of stored fruits. The decrease in fresh mass of the harvested organs is due to the processes of transpiration and respiration (Holcroft, 2015). Studying the water loss of banana fruit, Khanal *et al*. (2022) found that 44% of transpiration was stomatal and 56% cuticular. In yellow pitahaya, Dueñas *et al*. (2009) attribute the weight loss to respiration, which confirms the greater weight reduction in the light/dark treatment (Fig. 6), in which greater respiration and stomatal opening were found at 16 DAH (Fig. 3 and 7), which accelerated the loss of water and product quality.

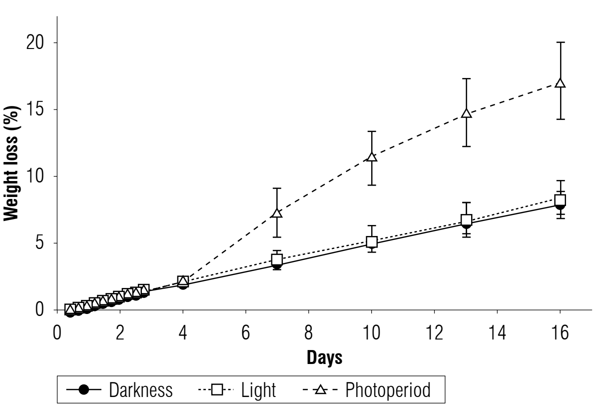

Figure 6. Percentage of accumulated weight loss of pitahaya fruits during 16 days of storage at 13°C and different lighting conditions (continuous darkness ●, continuous light □, 12 h of light and 12 h of darkness per day Δ). Sampling was done on days 1, 2, 3, 4 and then every 3 days. Vertical bars indicate standard deviation.

Respiration

The respiratory intensity of the fruit during storage did not show significant differences with respect to the time of day, but it did between the treatments, as in the alternation of light and darkness, the highest respiratory rate was obtained at 16 days ($P\leq0.05$) with 22.45 mg CO_2 kg^{-1} h^{-1} (Fig. 7). These results indicate that alternating light and dark conditions stimulate respiratory metabolism, which generally decreases the postharvest life of fruits (Pareek, 2016).

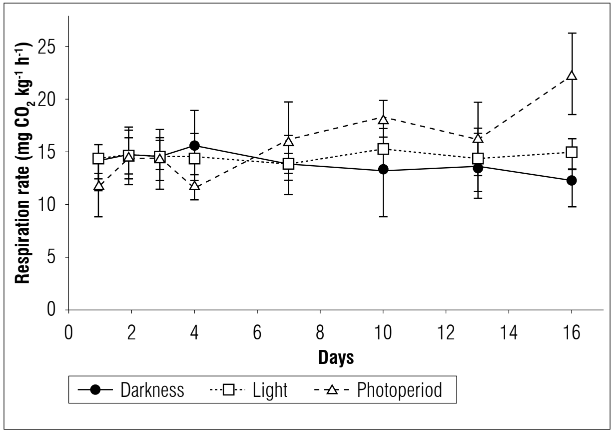

Figure 7. Respiration rate of pitahaya fruits during 16 days of storage at 13°C and different lighting conditions (continuous darkness ●, continuous light □, 12 h of light and 12 h of darkness per day ∆). Sampling was carried out on days 1, 2, 3, 4 and then every 3 days. Vertical bars indicate standard deviation.

The release of CO_2 from the fruits in photoperiod was higher during the last stages of the experiment (from 7 DAH) (9.96 to 22.45 mg CO_2 kg^{-1} h^{-1}) while in light and darkness, it ranged from 12.45 to 15.83 and 12.95 to 16.11 mg CO_2 kg^{-1} h^{-1}, respectively (Fig. 7). These results are similar to those reported by Gallo (1996), with 20-80 mg CO^2 kg^{-1} h^{-1} in yellow pitahaya and lower than the concentrations measured by Osuna *et al*. (2011) in early ripening red pitahaya fruits stored at 20°C (41 to 43 mg CO^2 kg^{-1} h^{-1}). Rodríguez *et al*. (2005) indicate that lower temperatures reduce the metabolic processes of pitahaya. Herrera (2012) and Saltveit (2019) state that non-climacteric fruits, such as the yellow pitahaya in this case, show a slight reduction in respiration after harvest, as observed in fruits stored in darkness, but, on the contrary, this is not the case in pitahayas stored in alternating light and darkness, where respiration rates increased (Fig. 7). However, the hypothesis that artificial light during storage would cause the stomata to close in these fruits of a CAM plant, which would be an option to extend the post-harvest life of pitahayas, has not been fulfilled.

Firmness

There was no significant effect of the treatments on the firmness of the fruits, which ranged between 31.4 and 68.6 N. van To *et al*. (2002) observed that the firmness of mature *H. undatus* fruits was considerably reduced at 20°C during 14 d of storage, contrary to what was found in our experiment, where the storage conditions of 13°C and 80% RH did not enable a considerable reduction in firmness, also considering that the yellow pitahayas were barely at physiological maturity. In yellow pitahaya, Dueñas *et al*. (2012) associated the activity of the xylanase enzyme with the softening of the rind and suggested an important participation of xylanase in this process. They measured the enzymatic activity of polygalacturonase, cellulase and xylanase and found greater activity of the latter, in parallel with the softening of the fruits. However, in a previous study Rodríguez *et al*. (2006) had determined the possibles participation of polygalacturonase in the softening of pitahaya, while in red pitaya Centurión *et al*. (1999) attributed this process to the activity of pectin methylesterase. In many fruits, softening is an important factor during their ripening process (Anwar *et al*., 2019).

During ripening, progressive depolymerization, loss of cell structure and solubilization of cell wall components contribute to fruit softening and consequent textural alterations, while, in general, non-enzymatic and enzymatic factors may contribute to softening (Pareek, 2016). Nerd *et al*. (1999) reported that storage of *H. undatus* and *H. polyrhizus* fruits at 14°C enabled their marketing qualities to be preserved for up to two weeks, while Rodríguez *et al*. (2005) observed that *H. megalanthus* fruits stored at 8°C had a longer post-harvest life than those stored at 19°C. Botton *et al*. (2019) describe that the lower temperatures decrease the rate of ethylene biosynthesis, a hormone classified as inducing loss of firmness.

CONCLUSION

In cultivation, the cladodes of pitahaya exhibit a stomatal behaviour typical of CAM plants, while intact fruits do not adjust to said stomatal metabolism. Alternating light and darkness in postharvest causes significant increases in stomatal opening, respiration and weight loss of the fruit; indicating that the photoperiod may not be the best condition for the storage of these fruits. According to the results of the present study, storage in conditions of permanent darkness may have advantages depending on the commercial destination. This is because, although in conditions of continuous light similar results were obtained to conditions of darkness, the first of these conditions would generate a higher energy cost. Therefore, conditions of darkness or permanent light potentially extend the shelf life of yellow pitahaya fruits. The present work constitutes a basis for establishing storage protocols for the plant species under study to maintain the quality of the fruits.

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