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Minimum O_2 levels during storage to inhibit aerobic respiration and prolong the postharvest life of 'Tommy Atkins' mangoes produced in different growing seasons

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ABSTRACT

The definition of the minimum O_2 levels required to maximally inhibit fruit aerobic respiration is essential to efficiently delay ripening and senescence during long-distance transportation. The aim of this study was to determine the minimum O_2 levels required to maximally inhibit the aerobic respiration and prolong the postharvest life of 'Tommy Atkins' mangoes produced during the summer, winter and spring growing seasons in the São Francisco Valley (SFV), Brazil. For the identification of the minimum O_2 levels, mangoes were stored for 42 days at 9 °C and 90–95% RH. The change from aerobic to anaerobic metabolism was weekly determined based on the levels of O_2, CO_2 and ethanol production inside hermetically closed containers containing fruit samples. The minimum O_2 levels required to maintain aerobic respiration of mangoes produced in the summer, winter and spring changed from 0.25 to 13.75 kPa, 0.80 to 2.30 kPa and 1.42 to 17.40 kPa, respectively, as the storage duration increased. In order to validate the minimum O_2 levels to maintain fruit aerobic respiration and quality, 'Tommy Atkins' mangoes produced in the SFV were harvested at the commercial maturity in the winter growing season in 2022 and were stored under dynamic controlled atmosphere (DCA) conditions with the minimum O_2 levels determined with fruit produced in the same growing season in the previous year, 2021. Fruit stored under DCA were compared to fruit stored in refrigerated atmosphere (RA) for 60 days at 9 °C and 90–95% RH. The minimum O_2 levels used in the DCA effectively inhibited fruit ripening, controlled black flesh and reduced rot incidence during 60 days of cold storage and 60 + 7 days of shelf life.

1. Introduction

Mango (*Mangifera indica* L.) is one of the most produced and consumed tropical fruit worldwide due to its pleasant flavor, aroma and excellent nutritional composition. Brazil is the seventh largest mango producer in the world, with most of production located in the Northeast region, known as the São Francisco Valley (SFV), which is responsible for about 87% of the total exported mango in the country (Singh and Zaharah, 2015; FAOSTAT, 2021).

Among the most important cultivars, Tommy Atkins represents about 75% of the total cultivated area in Brazil, which has been widely produced due to its high acceptance in the global market, high productivity, and intense color, as well as satisfactory postharvest shelf-life conservation (Singh and Zaharah, 2015). However, as a climacteric fruit with high respiration rate and perishability, mango ripens quickly after harvest, limiting its commercialization in distant markets (Singh and Zaharah, 2015; Evans et al., 2017).

Majority of the Brazilian mangoes are exported in refrigerated

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containers that reduce fruit metabolic activity and ripening (Teixeira et al., 2018). However, low temperatures alone are not enough to delay mango ripening during long-term shipping, making it difficult to access markets that require transit by sea for more than 15 days (Bender et al., 2021). Under such conditions, the use of controlled (CA) or modified (MA) atmospheres associated with refrigerated containers is an alternative to further inhibit fruit ripening processes and guarantee high quality of mangoes exported to distant markets (Teixeira et al., 2018; Bender et al., 2021).

Studies have shown that CA conditions are effective on delaying ripening changes in 'Kent' (Trinidad et al., 1997; Bender and Brecht, 2000a), 'Tommy Atkins' (Lizada and Ochagavia, 1997; Bender and Brecht, 2000a), 'Haden' (Bender et al., 2000b), 'Palmer' (Teixeira and Durigan, 2011; Teixeira et al., 2018), 'Shelly' (Ntsoane et al., 2019) and 'Keitt' (Hailu, 2016) mangoes. However, these studies have been carried out with fruit produced in very specific seasons and edaphoclimatic conditions. In the Brazilian SFV, mangoes are produced under semi-arid irrigated conditions throughout the year, which results in fruit with different quality and storage potentials (Ortega and Sobel, 2010; Vilvert et al., 2021; Freitas et al., 2022).

In general, the recommended atmospheric partial pressure for mangoes ranges from 5 kPa to 10 kPa of O_2 and 0 kPa to 10 kPa of CO_2, depending on the genotype and growing conditions (Yahia, 2009; Valdez-Fragoso and Mújica-Paz, 2016). However, the CA technique does not allow constant monitoring of fruit metabolism to dynamically establish the minimum partial pressure of O_2, and for safety, O_2 is maintained at a level well above the minimum limit tolerated by the fruit, which does not allow the maximum reduction of metabolism and, consequently, the maximum potential of CA in preserving fruit quality. Similarly, although MA packages (MAPs) have been shown to delay ripening changes in mangoes (Brecht et al., 2017; Vilvert et al., 2022), determining the minimum O_2 levels that ensure fruit aerobic respiration will help selecting the most efficient MAP to maintain postharvest quality of different cultivars, harvested at different growing seasons and maturity stages. Using the lowest possible O_2 levels without triggering anaerobic respiration is important to reach the maximum inhibition of the aerobic respiration, and consequently fruit ripening changes such as softening, chlorophyll degradation and loss of organic acids (Yang and Hoffman, 1984; Singh and Zaharah, 2015). Thus, it is essential to determine these O_2 levels in order to extend the postharvest life of mangoes harvested at different seasons and shipped to distant markets.

Although mango production in the SFV takes place during the whole year, there are two main harvests during the winter and summer growing seasons, which have been shown to result in different fruit quality (Ortega and Sobel, 2010; Simões et al., 2021; Vilvert et al., 2021; Freitas et al., 2022), and possibly contrasting storage potentials.

The aim of this study was to determine the minimum O_2 levels required to maximally inhibit the aerobic respiration and prolong the postharvest life of 'Tommy Atkins' mangoes produced during the summer, winter and spring growing seasons in the SFV, Brazil.

2. Material and methods

2.1. Plant material and experimental conditions

'Tommy Atkins' mangoes (*Mangifera indica* L.) were produced in a commercial orchard located in the SFV, in Petrolina, PE, Brazil (latitude 9°03′04.6′'S, longitude 40°17′46.5′'W). Medium-sized fruit (0.475 a 0.550 g) were harvested in the summer (March 2021), winter (September 2021) and spring (August 2022) growing seasons at physiological maturity, characterized by full shoulders at the stem end and a predominant light green skin color (National Mango Board, 2010). The commercial orchards used in the study were subjected to the same management practices in all growing seasons, according to technical recommendations. The meteorological data observed from full bloom to harvest are shown in the Supplementary

After harvest, the fruit were taken to the Postharvest Laboratory at EMBRAPA, Petrolina, PE, Brazil, and were washed and homogenized based on size, color, uniformity, weight and absence of disease and injuries. The mangoes were then packed in cardboard boxes and stored at 9 °C (± 0.5 °C) and 90–95% RH for 42 days to simulate the commercial conditions of long maritime transport. The experiment was composed of four replications with 21 fruit per replication. Each four replications were subjected to physicochemical analysis every week for six weeks, as described below, resulting in the evaluation of 84 fruit per week and 504 fruit in each growing season.

2.2. Definition of minimum O_2 levels to maintain aerobic respiration

At harvest and every seven days of storage, each sample of 21 fruit was placed in a 20 L hermetically sealed polyethylene chamber, equipped with rubber septa and a mini fan attached to the lid for air homogenization. Inside each chamber, two sachets of 20 g of potassium permanganate (99%) were added to absorb the ethylene produced by the fruit.

After closing the chambers, the internal O_2 was gradually reduced due to fruit respiration. After 16 h of closing the chambers, the O_2 partial pressure (pO_2), CO_2 partial pressure (pCO_2) and ethanol concentration were monitored every hour until the identification of ethanol in the atmosphere, indicative of a change from aerobic to anaerobic respiration. All analyzes were performed weekly during storage with different fruit samples. The minimum values of O_2 and CO_2 at the exact moment of transition from aerobic to anaerobic respiration were estimated with a linear regression.

2.2.1. Determination of O_2, CO_2, respiratory quotient and ethanol

The pO_2 and pCO_2 were determined with a PA 7.0 gas analyzer (WITT-Gasetechnik GmbH & Co KG, Germany). Ethanol concentration was quantified using a Dräger X-am 5000 portable gas analyzer (Dräger, Germany); results were expressed in μL L^{-1}. The respiration rate was evaluated by the production of CO_2 during the first two hours in which the fruit remained closed in the 20 L chambers. CO_2 production rate was expressed in mg kg^{-1} h^{-1}. The respiratory quotient (RQ) was calculated through the ratio between the CO_2 production and the O_2 consumption inside the chambers.

2.2.2. Atmosphere with CO_2 absorption

The minimum pO_2 at the beginning of ethanol synthesis by the fruit was also determined under CO_2 absorption conditions, with the insertion of two sachets of 100 g of calcium hydroxide inside each chamber. Under these conditions, pO_2 and ethanol production were monitored as mentioned above. The atmosphere condition with CO_2 absorption was established after the analysis of the chambers without CO_2 absorption.

2.3. Validation of the minimum O_2 levels under dynamic controlled atmosphere (DCA) conditions

Medium-sized (0.475 a 0.550 g) 'Tommy Atkins' mangoes produced in the winter growing season in 2022 were harvested at the commercial maturity. After harvest, fruit were washed and homogenized based on size, color, uniformity, weight and absence of disease and injuries. The fruit were then stored at 9 °C (± 0.5 °C) and 90–95% RH for 60 days under refrigerated atmosphere (RA) or dynamic controlled atmosphere (DCA) conditions. Each storage condition was composed by four replications with 24 fruit per replication. Fruit stored under RA were placed in plastic trays, whereas fruit stored under DCA were placed inside 20 L hermetically sealed polyethylene chambers. Each sample had 150 g of potassium permanganate (99%) and 100 g of calcium hydroxide to absorb ethylene and CO_2, respectively.

The DCA was established and maintained with a continuous humidified flow system at 500 mL min^{-1}. Compressed air was the source O_2 (21%) and high purity (99.99%) gas cylinder (White Martins gases

Industriais Ltda, Brasil) was the source of N_2. Both gasses were mixed to obtain the O_2 levels required for DCA storage. The supply and composition of gasses inside the chambers were monitored twice a day throughout storage, using the gas analyzers mentioned above (Fig. 1). At the beginning of DCA storage, safe O_2 level was established at 1.3 kPa, which was determined as the average (1.2 kPa) plus 10% (0.1 kPa) of the minimum O_2 value observed at harvest in fruit produced in the same growing season in the previous year, 2021. This approach was used to ensure aerobic respiration in all fruit samples, because it takes into account the 10% variability among samples observed in the previous study described above. During storage, O_2 was maintained at the lowest safe level due to lower and beneficial ethanol production, which was maintained below the recommended value of 500 μL L^{-1} (Weber et al., 2020; Thewes et al., 2021). Fruit analyses were accomplished at 0, 15, 30, 45 and 60 days of storage and after seven days of shelf life at 25 °C (± 0.5 °C) and 90–95% RH, as described below.

2.4. Fruit quality analyses

2.4.1. Respiration rate

The respiration rate was evaluated by the production of CO_2 during the first two hours in which the fruit remained closed in the 20 L chambers. The measurement was performed with a gas analyzer. CO_2 production rate was expressed in mg kg^{-1} h^{-1}.

2.4.2. Skin and pulp color

Skin and pulp color were determined in the equatorial region of each fruit with a Minolta colorimeter model CR-400 (Konica Minolta, Japan). Color values were determined according to Mcguire (1992) and were expressed as °hue, where 0° represents red, 90° represents yellowish green, 180° represents turquoise blue and 270° represents violet.

2.4.3. Pulp firmness

Pulp firmness was determined with a digital texture analyzer model TA.XTplus (Stable Micro Systems, UK), equipped with a 6 mm diameter stainless steel probe and a penetration distance of 10 mm. After peeling, two measurements were taken in the equatorial region of each fruit to determine the average firmness (N).

2.4.4. Black flesh and rot incidence

Black flesh and rot incidences were determined by multiplying the number of diseased fruit by 100 and dividing by the total number of fruit in each replication. The results were expressed in percentage.

2.4.5. Soluble solids content (SSC)

Soluble solids content (SSC) was determined with a digital refractometer model PAL-1 (Atago, Japan), with automatic temperature compensation. Measurements were performed with 1 mL of fruit juice, and data were expressed as a percentage.

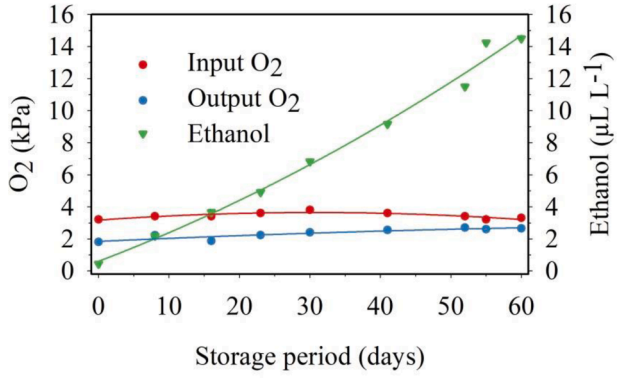

Fig. 1. Input and output O_2 levels and ethanol concentration in DCA chambers used to store 'Tommy Atkins' mangoes for 60 days at 9 °C (± 0.5 °C). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

2.4.6. Titratable acidity (TA)

Titratable acidity (TA) was determined in 1 mL of the same mango juice used for SSC analysis, diluted in 50 mL of distilled water, which was then titrated with a 0.1 N NaOH solution until pH 8.1. The titration was performed with an automatic digital titrator model Titrino Plus 848 (Metrohm, Switzerland). The results were expressed as percentage of citric acid in the juice.

2.4.7. SSC/TA ratio

SSC/TA ratio was calculated in each sample by dividing the SSC value by its respective TA value.

2.5. Statistical analysis

The study about the definition of minimum O_2 levels to maintain fruit aerobic respiration followed a completely randomized design and the data obtained in each growing season were analyzed separately. Data from physicochemical analyses were submitted to one-way ANOVA, and the means in each storage week were compared by Tukey's test ($p \leq 0.05$). The study to validate the minimum O_2 levels under DCA conditions to maintain fruit quality followed a completely randomized, in a split-plot arrangement, with the two atmospheric conditions in the plot and the five storage times in the subplot. Atmospheres were compared in each storage time using the F test. Data were represented by means and standard deviations. Arc sin transformation of percentage data was performed before application of ANOVA. All statistical analyses were conducted using the ExpDes.pt R package.

3. Results

3.1. Definition of minimum O_2 levels to maintain aerobic respiration

'Tommy Atkins' mangoes produced in the three growing seasons had the same pattern of reducing O_2 consumption, as well as increasing CO_2 production and RQ during storage (Supplementary Fig. 1). After 2 h of closing the chambers, the internal pO_2 was 18.7–20.0 kPa, 18.9–19.5 kPa and 19.70–20.23 kPa, while the internal pCO_2 was 1.8–3.2 kPa, 2.0–2.7 kPa and 1.23–1.65 kPa for fruit harvested in the summer, winter and spring growing seasons, respectively (Supplementary Fig. 2). In the same 2 h period, ethanol was not detected inside the chambers (Fig. 2A, 2B, 2C). In all growing seasons, less ripened fruit at the first weeks of storage required longer time inside the sealed chamber to reach ethanol production, compared to more ripened fruit at later weeks of storage (Fig. 2A, 2B, 2C).

The lowest O_2 levels required to maintain aerobic respiration were 0.25, 0.32 and 2.45 kPa, at the 3rd, 2nd, and 1st weeks of storage, for summer produced fruit, as well as 1.69, 1.57 and 1.42 kPa, at the 4th, 3rd, and 2nd weeks of storage, for spring produced fruit, respectively (Fig. 3A, 3C). In the last weeks of storage, the minimum O_2 levels increased to 13.75 kPa and 17.40 kPa in the summer and spring produced fruit, respectively (Fig. 3A, 3C). For winter produced fruit, the pO_2 and pCO_2 at the transition from aerobic to anaerobic respiration remained relatively constant throughout the six weeks of storage. In this period, the minimum pO_2 were 1.22 kPa, 1.18 kPa, 2.30 kPa, 2.30 kPa, 1.79 kPa and 0.80 kPa over the six weeks of storage, respectively (Fig. 3B). The pCO_2 at the minimum rate of aerobic respiration had an opposite behavior to that observed for pO_2.

The pO_2 and ethanol concentration in the environment with CO_2 absorption showed similar behavior to that observed without CO_2 absorption in the three harvests (Data not shown). According to the physicochemical quality analyses, skin and pulp colors changed from green and white to yellow, pulp firmness decreased, and soluble solids

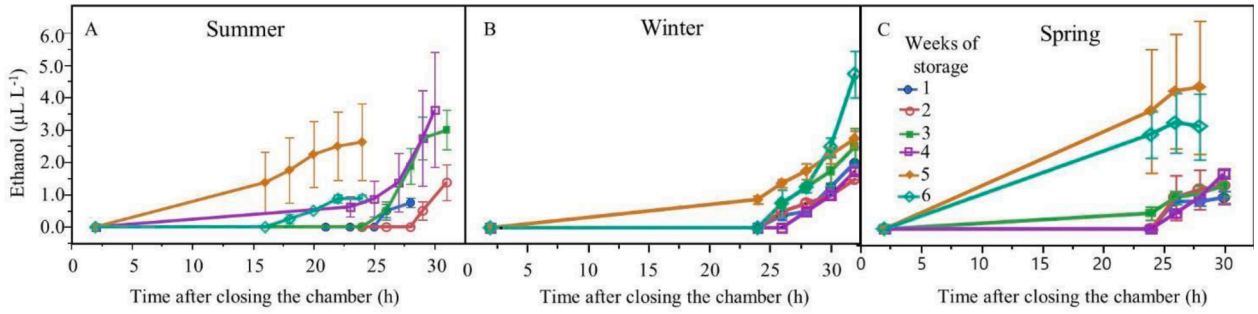

Fig. 2. Ethanol concentration inside hermetically sealed chambers with 'Tommy Atkins' mangoes produced in the summer (A) winter (B) and spring (C) growing seasons and stored for six weeks at 9 °C. Values are represented as mean ± standard error ($n = 4$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

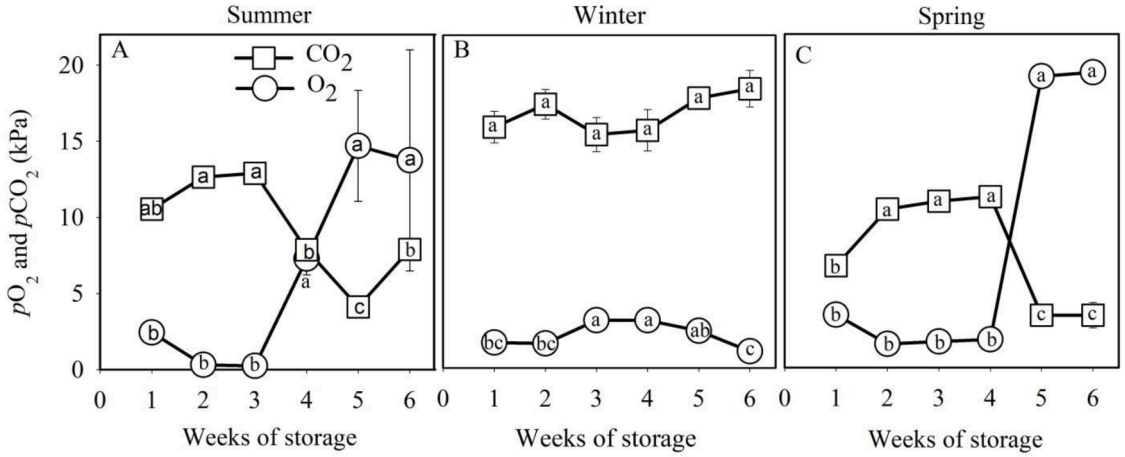

Fig. 3. Partial pressures of O_2 and CO_2 at the transition from the aerobic to anaerobic respiration of 'Tommy Atkins' mangoes produced in the summer (A), winter (B) and spring (C) growing seasons in 2021 and stored at 9 °C for six weeks. Values are represented as mean ± standard error ($n = 4$). O_2 and CO_2 partial pressures were identified at the beginning of ethanol production in the fruit. Mean O_2 or CO_2 values followed by the same letter are statistically equal at each growing season according to the Tukey test (5%).

Table 1
Physicochemical quality of 'Tommy Atkins' mangoes produced in the summer, winter and spring growing seasons in 2021 and stored at 9 °C for six weeks.

Quality trait	Storage time (weeks) 1	2	3	4	5	6
	Summer growing season					
Skin°hue	114.29^{a*}	113.38^{a}	113.03^{a}	111.55^{ab}	107.00^{bc}	105.58^{c}
Pulp°hue	103.90^{a}	101.94^{ab}	100.26^{ab}	99.84^{ab}	98.20^{b}	98.74^{b}
Pulp firmness (N)	67.49^{a}	59.63^{ab}	52.86^{ab}	58.05^{ab}	45.58^{b}	48.89^{b}
SSC (%)	7.68^{c}	9.85^{b}	11.43^{ab}	12.18^{a}	12.40^{a}	12.23^{a}
TA (g 100^{-1})	0.94^{a}	0.93^{a}	0.96^{a}	0.78^{a}	0.92^{a}	0.89^{a}
SSC/TA	8.33^{c}	10.76^{bc}	11.95^{b}	15.72^{a}	13.71^{ab}	13.77^{ab}
	Winter growing season					
Skin°hue	114.24^{a}	108.74^{ab}	106.12^{b}	106.57^{b}	107.01^{b}	107.04^{b}
Pulp°hue	102.73^{a}	100.59^{ab}	98.53^{bc}	99.23^{bc}	97.43^{c}	99.40^{bc}
Pulp firmness (N)	65.85^{a}	58.96^{ab}	54.82^{abc}	49.42^{bc}	49.80^{bc}	45.76^{c}
SSC (%)	8.25^{d}	11.05^{c}	12.85^{b}	13.80^{ab}	14.13^{ab}	14.93^{a}
TA (g 100^{-1})	0.98^{a}	0.87^{b}	0.81^{bc}	0.78^{bc}	0.74^{c}	0.60^{d}
SSC/TA	8.43^{e}	12.78^{d}	15.97^{c}	17.76^{bc}	19.17^{b}	24.88^{a}
	Spring growing season					
Skin°hue	107.13^{ab}	112.98^{a}	110.45^{ab}	107.740^{b}	105.37^{b}	109.50^{ab}
Pulp°hue	96.05^{a}	96.24^{a}	96.26^{a}	95.60^{a}	96.07^{a}	96.34^{a}
Pulp firmness (N)	58.70^{a}	58.39^{a}	55.00^{ab}	49.73^{ab}	49.39^{ab}	47.28^{b}
SSC (%)	6.45^{b}	9.98^{a}	10.65^{a}	10.76^{a}	10.53^{a}	11.53^{a}
TA (g 100^{-1})	1.29^{a}	0.98^{a}	1.03^{a}	1.00^{a}	1.07^{a}	0.72^{b}
SSC/TA	5.02^{a}	10.13^{b}	10.47^{b}	10.71^{b}	10.52^{b}	16.17^{a}

*Means followed by the same letter in each row are statistically equal according to the Tukey's test ($p \leq 0,05$).

content (SSC) increased during storage of mangoes produced in all three growing seasons (Table 1). Titratable acidity (TA) was not affected by storage time in summer produced fruit, but it decreased during storage in winter and spring produced fruit (Table 1). The SSC/TA ratio increased 65%, 195% and 222% from the 1st to the 6th week of storage in mangoes produced in the summer, winter and spring growing seasons, respectively (Table 1).

3.2. Validation of the minimum O_2 levels under dynamic controlled atmosphere (DCA) conditions

Mango respiration rate was higher in RA, compared to DCA, only at 60 days of cold storage (Fig. 4A). During storage, exposure to shelf life condition (7 days at 25 °C) resulted in higher respiration rate of RA stored fruit, compared to DCA stored fruit (Fig. 4A, 4B). Skin and pulp hue values were maintained higher under DCA than under RA throughout cold storage and shelf life conditions (Fig. 4C, 4D, 4E, 4F). Fruit softening rate during cold storage was higher under RA than under DCA (Fig. 4G). At 45 and 60 days of cold storage, RA stored fruit showed lower pulp firmness than DCA stored fruit (Fig. 4G). Shelf life conditions resulted in softening of both AR and DCA stored fruit (Fig. 4H). After shelf life, fruit kept under DCA showed higher pulp firmness than fruit stored under RA only at 30 + 7 and 45 + 7 days, but not at 15 + 7 and 60 + 7 days (Fig. 4H).

The soluble solids content showed a higher increase, as well as higher values, in RA stored fruit than in DCA stored fruit during cold storage (Fig. 5A). After shelf life, there was no statistical difference for soluble solids content between RA and DCA stored fruit at 15 + 7, 30 + 7, 45 + 7 days (Fig. 5B). At 60 + 7 days of shelf life, DCA stored fruit showed higher soluble solids content than RA stored fruit (Fig. 5B). The

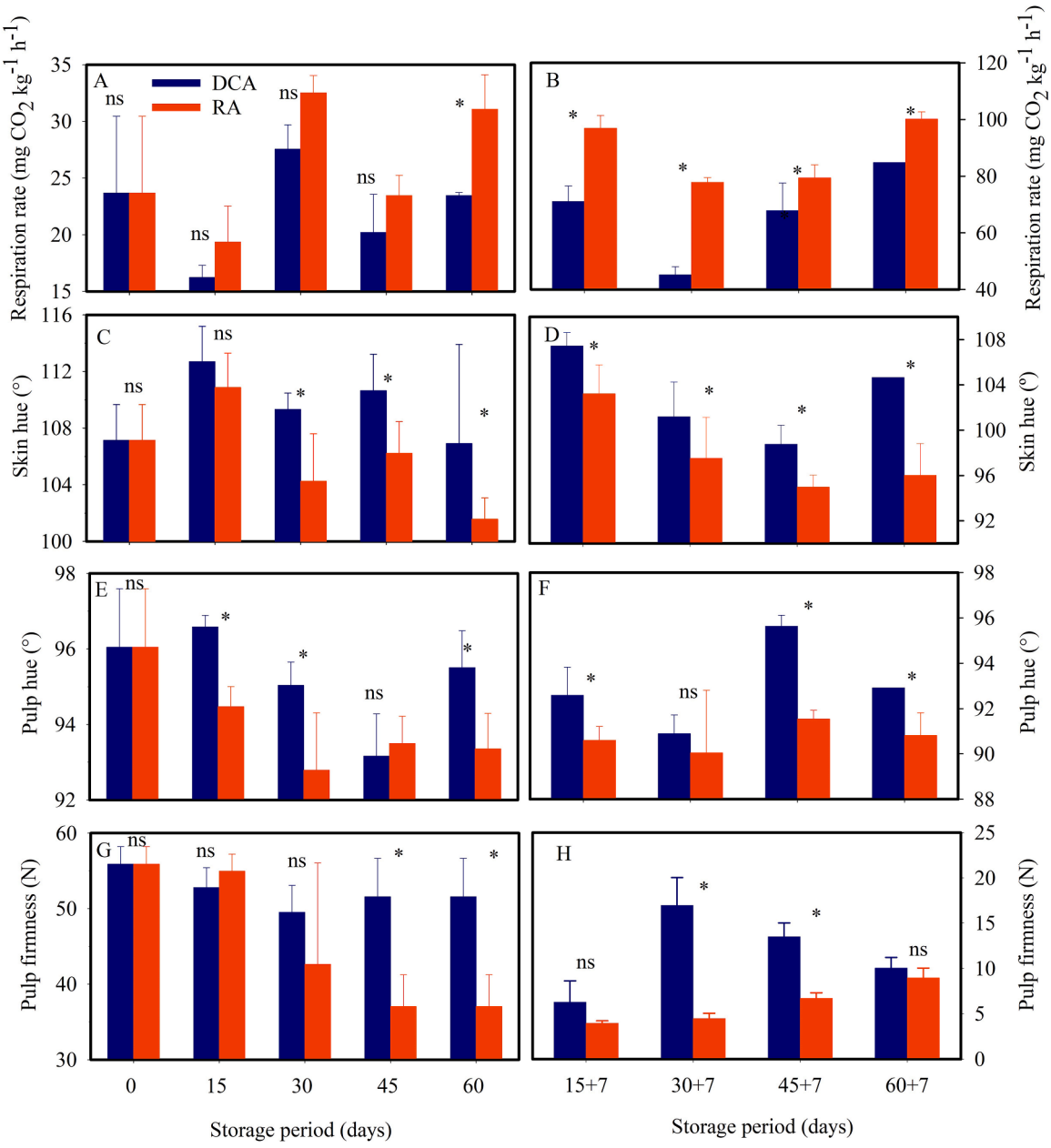

Fig. 4. Respiration rate (A and B), skin hue (C and D), pulp hue (E and F), and pulp firmness (G and H) of 'Tommy Atkins' mangoes produced in the winter growing season in 2022 and stored under dynamic controlled atmosphere (DCA) and refrigerated atmosphere (RA) for 60 days at 9 °C (A, C, E, G) plus 7 days of shelf life at 25 °C (B, D, F, H). Means followed by ns (non-significant) are statistically equal, according to the F test. Means followed by asterisk (*) are statistically different according to the F test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

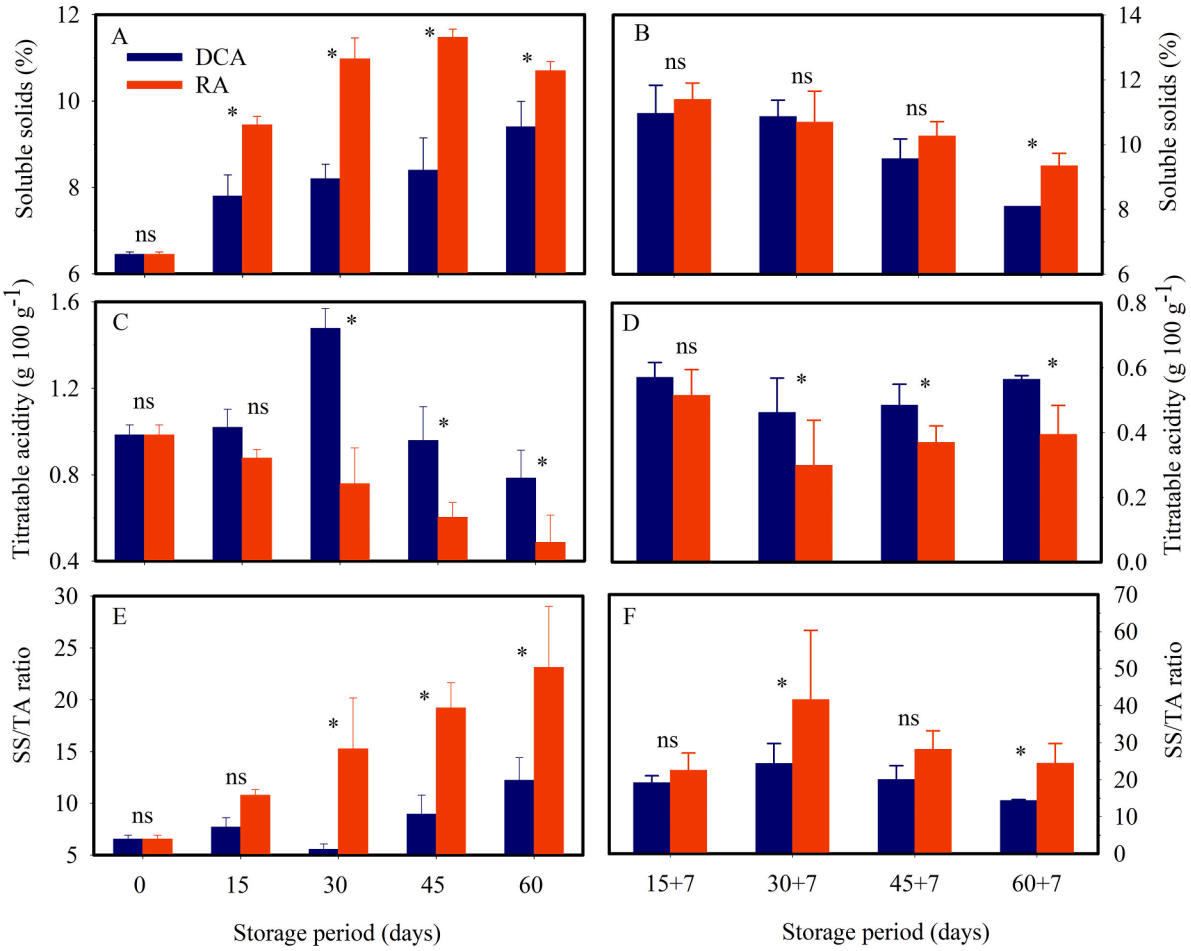

Fig. 5. Soluble solids (A and B), titratable acidity (A and B) and SS/AT ratio (A and B) of 'Tommy Atkins' mangoes produced in the winter growing season in 2022 and stored under dynamic controlled atmosphere (DCA) and refrigerated atmosphere (RA) for 60 days at 9 °C (A, C, E) plus 7 days of shelf life at 25 °C (B, D, F). Means followed by ns (non-significant) are statistically equal, according to the F test. Means followed by asterisk (*) are statistically different according to the F test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

titratable acidity was maintained higher in DCA stored fruit, compared to RA stored fruit at 30, 45 and 60 days of cold storage and after seven days of shelf life (Fig. 5C, 5D). The SSC/AT ratio increased throughout cold storage more markedly in RA stored fruit than in DCA stored fruit (Fig. 5E, 5F). Higher SSC/TA ratios were observed in RA stored fruit at 30, 45 and 60 days of cold storage, compared to DCA stored fruit (Fig. 5E). After shelf life, no statistical differences were found between RA and DCA stored fruit for SSC/TA ratio at 15 + 7 and 45 + 7 days of storage plus shelf life, but higher SSC/TA ratios were observed in RA stored fruit at 30 + 7 and 60 + 7 days of storage plus shelf life, compared to DCA stored fruit (Fig. 5F).

Mangoes kept under DCA were free of black flesh throughout cold storage and shelf life conditions, whereas mangoes kept under RA showed about 50% and 75% black flesh incidence after 60 days of cold storage and 60 + 7 days of shelf life conditions, respectively (Fig. 6A, 6B). Rot incidence was observed after 45 days under RA, and after 60 days under DCA storage. At 60 days of cold storage and 60 + 7 days of shelf life conditions, DCA showed lower rot incidence than RA (Fig. 6C, 6D).

4. Discussion

4.1. Definition of minimum O_2 levels required to maintain aerobic respiration

Respiration rate is an important indicator of fruit metabolic activity, which can be used to optimize storage conditions. In our study, respiration rate of 'Tommy Atkins' mangoes harvested in three growing seasons and stored at 9 °C showed a decrease in O_2 consumption and an increase in CO_2 production during storage, increasing also the respiratory quotient (RQ). Throughout fruit ripening, the cells and tissues become disorganized, causing blockages in the tissue that reduces the O_2 permeability (Amarante and Banks, 2000; Lima et al., 2010). Under these conditions, a gradual increase in CO_2 production was observed during storage, characterizing a standard behavior of climacteric fruit respiration (Evans et al., 2017). Similar respiration rates have been observed in 'Keitt' and 'Tommy Atkins' mangoes stored at 8 °C (Bender et al., 2021).

The RQ represents the ratio between the volume of CO_2 produced and the volume of O_2 consumed by a living tissue (Saltveit, 2019). Depending on the metabolic substrates, RQ values normally vary from RQ = 1 (sugar), RQ < 1 (lipids), and RQ > 1.0 (organic acids). (Fonseca et al., 2002). According to our results, the RQ was about 1.0 at the beginning and increased up to 1.8 and 1.5 at the end of storage for mangoes produced in the summer and winter growing seasons,

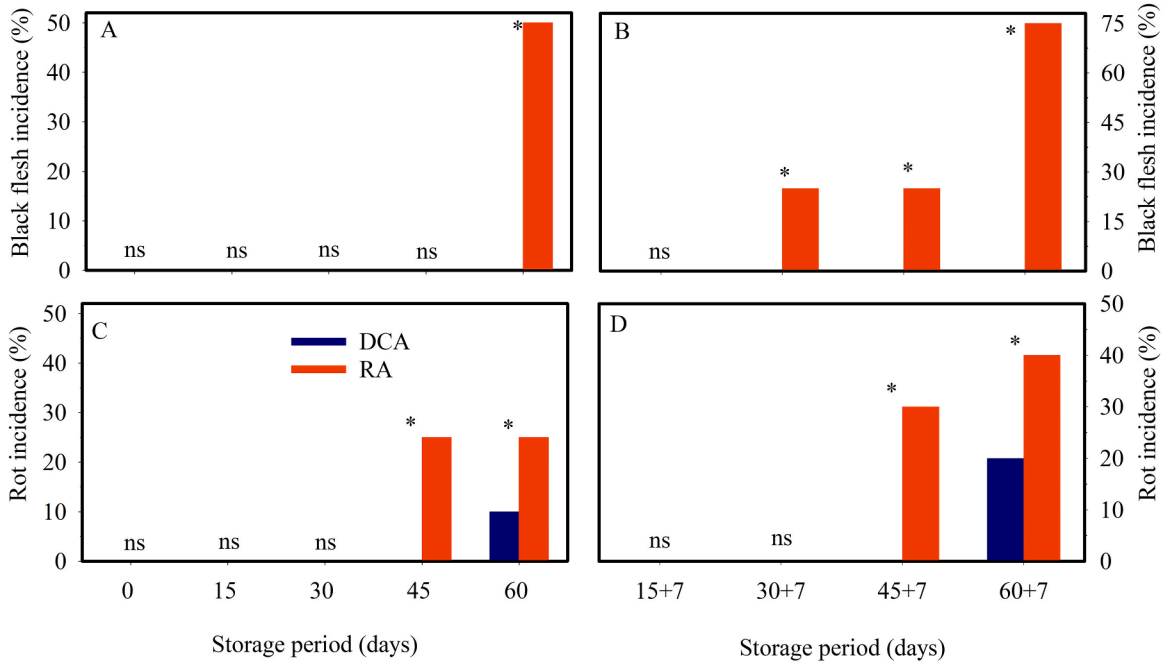

Fig. 6. Black flesh incidence (A and B) and rot incidence (C and D) in 'Tommy Atkins' mangoes produced in the winter growing season in 2022 and stored under dynamic controlled atmosphere (DCA) and refrigerated atmosphere (RA) for 60 days at 9 °C (A and C) plus 7 days of shelf life at 25 °C (B and D). Means followed by ns (non-significant) are statistically equal, according to the F test. Means followed by asterisk (*) are statistically different according to the F test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

respectively. In fruit produced in the spring growing season, the QR was 1.08 in the sixth week of storage. These results suggest a change in the source of carbon used for fruit respiration during storage (Saltveit, 2019).

In the summer, the production of ethanol was late for the fruit stored for one, two and three weeks, and the peak started approximately 26–29 h after the closing of the chambers. On the other hand, fruit stored for longer periods, especially four, five and six weeks, anticipated ethanol production to 16–23 h after closing of the chambers. Controlled (CA) and modified (MA) atmosphere technologies are based on reducing pO_2 and increasing pCO_2 in the storage atmosphere to inhibit ripening and maintain fruit quality during storage (Kader, 2003). However, decreasing O_2 levels in the storage environment will eventually lead to anaerobic respiration in the fruit, resulting in acetaldehyde and ethanol production (Saltveit, 2019). Therefore, analyzing fruit ethanol production in response to decreasing O_2 levels in the sealed chambers was an efficient approach to determine the level of O_2 that results in the change from aerobic to anaerobic respiration.

The pO_2 and pCO_2 at the transition from aerobic to anaerobic respiration in the summer and spring produced fruit show that mangoes at early stages of storage (up to 3 weeks) were more tolerant to low pO_2 ($\leq$3,5 kPa). On the other hand, the pO_2 at the transition from aerobic to anaerobic respiration in the winter produced fruit was about $\leq$ 2.3 kPa throughout storage. These results indicate that 'Tommy Atkins' mango can be stored at 9 °C for up to six weeks under atmospheres with pO_2 of 2.3 kPa, without anaerobic respiration. The different requirements in pO_2 during storage between harvests may be linked to the environmental conditions in which the fruit were produced in the SFV.

CA storage using fixed pO_2 and pCO_2 has been studied in many mango cultivars, including 'Kent' (Trinidad et al., 1997; Bender and Brecht, 2000a), 'Tommy Aktins' (Lizada and Ochagavia, 1997; Bender and Brecht, 2000a; Bender et al., 2021), 'Manila' (Ortega-Zaleta and Yahia, 2000), 'Haden' (Bender et al., 2000b), ' Palmer' (Teixeira and Durigan, 2011; Teixeira et al., 2018), and 'Shelly' (Ntsoane et al., 2019). More recently, studies using dynamic controlled atmosphere (DCA) through chlorophyll fluorescence in 'Chok Anan' mango has been published (Ikwan et al., 2021), but this technology induces low O_2 stress at the beginning of storage. Similarly, studies have been accomplished with MAPs to maintain postharvest quality of mangoes (Fonseca et al., 2002; Brecht et al., 2017; Vilvert et al., 2022). All these studies used pO_2 that possibly did not favor the maximum maintenance of fruit quality by maintaining high partial pressure of O_2 during storage, which can lead to a loss of quality due to excessive respiration or inducing ethanol production. In our study, 'Tommy Atkins' mangoes produced in the summer and kept in cold storage for 2 and 3 weeks showed that the transition from aerobic to anaerobic respiration takes place at pO_2 below 0.5 kPa. However, at later weeks of storage, the same fruit produced ethanol at much higher pO_2 possibly due to anaerobic respiration or accelerated metabolism in response to ripening and senescence (Porat and Fallik, 2008). Indeed, previous studies have shown that mango ripening leads to higher ethanol production, accumulating high levels in the post-climacteric phase (Bender et al., 2000a, 2000b). In addition, several studies have also shown beneficial effects of ethanol in delaying ripening/senescence in broccoli (Asoda et al., 2009), melons (Jin et al., 2013), and apples (Weber et al., 2020). Ethanol is also involved in the desirable synthesis of aromatic compounds in apples (Wrigth et al., 2015; Thewes et al., 2021), which could improve mango consumer quality.

Although studies have shown that CO_2 can also affect fruit respiration, our results have shown that the levels of CO_2 accumulated until the shift from aerobic to anaerobic respiration had no effect on ethanol synthesis in the fruit. The behavior of the fruit stored with CO_2 absorption was equal to the fruit stored without CO_2 absorption. These conditions were evaluated to determine possible commercial conditions for marine transport of mangoes over long distances with the use of ideal pO_2 and pCO_2, or only of O_2 with CO_2 absorption.

'Tommy Atkins' mangoes produced in all three growing seasons showed a decrease in skin green color during storage, represented by lower hue angle values, which is one of the most important changes leading to desirable quality attributes for consumption (Evans et al., 2017). According to Kader (2003) and Brecht et al. (2017), mangoes that will be consumed by nearby markets can be harvested with light green

color, but the fruit will be more sensitive to mechanical damage and rot incidence, presenting lower postharvest longevity.

Pulp color is an important quality index used to determine mango developmental stage, which changes in response to chlorophyll degradation and carotenoids and flavonoids synthesis (Singh and Zaharah, 2013; Nordey et al., 2014). According to our results, mangoes produced in all three growing seasons reached the end of storage with pulp color varying from cream to less intense yellow, indicating desirable fruit ripening during cold storage at 9 °C (Brecht et al., 2017). Such low temperature was efficient in reducing skin and pulp color changes, considering the small differences between color values at harvest and after six weeks of storage. Indeed, Bender et al. (2021) also verified small changes in the development of skin and pulp color of 'Tommy Atkins' and 'Keitt' mangoes stored at 5 and 8 °C.

Fruit softening after harvest takes place due to the increasing activity of cell wall degrading enzymes, as well as due to loss of cell turgor pressure (Singh and Zaharah, 2013; Lawson et al., 2019). The main practical implication of these changes is that the loss of pulp firmness makes fruit distribution and marketing more difficult. 'Tommy Atakins' mango has been recommended to be harvested with pulp firmness at 129.50 N to improve postharvest life and reduce losses (Brecht et al., 2017). The same authors suggest that the minimum pulp firmness for mangoes exported from South America should be between 66 and 90 N at the packing house. In addition, fruit softening can be mitigated by appropriate handling procedures and conservation techniques such as the use of low temperatures associated with controlled or modified atmospheres (Brecht et al., 2017).

The increase in SSC during storage is due to the conversion of carbohydrate reserves, such as starch, into simple sugars, providing the sweet taste of the fruit (Singh et al., 2013; Khaliq et al., 2015; Xing et al., 2020). The decrease in TA during fruit storage occurs due to organic acid consumption in the respiratory metabolism, which intensifies during ripening (Maldonado et al., 2019). Consequently, the significant increase in the SSC/TA ratio observed in our study was due to the combined effects of TA reduction and SSS increase during storage.

4.2. Validation of the minimum O_2 levels under dynamic controlled atmosphere (DCA) conditions

In our study, the low pO_2 during DCA storage was efficient in inhibiting fruit respiration at 60 days of cold storage and after seven days of shelf life at 25 °C. At low pO_2, ethylene biosynthesis is reduced by inhibiting the activity of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase, both key enzymes in the ethylene synthesis pathway (Kader, 2003). Therefore, the lower respiration rate in DCA stored fruit is possibly the result of lower ethylene production, which is known to trigger the respiration rise in climacteric fruit, such as mangoes (Both et al., 2017). In addition, the greater production of ethanol in DCA stored fruit could also inhibit *ACC* oxidase and *ACC* synthase expression and activity, as reported in other studies (Asoda et al., 2009). In addition, Weber et al. (2020) have also shown that the application of 500 μL L^{-1} of ethanol during storage of 'Braeburn' apples triggered a reduction in ACC oxidase activity, ethylene production, respiration and membrane permeability, in addition to maintaining the fruit greener and reduce β-galactosity activity. However, these positive effects of ethanol on maintaining fruit quality have been reported to be concentration dependent (Pesis, 2005), suggesting that the maximum level of ethanol observed in DCA stored fruit (16 μL L^{-1}) was beneficial for mango quality maintenance during storage.

In our study, the low pO_2 was efficient in delaying mango skin and pulp color changes during DCA storage, compared to RA storage. Indeed, studies have reported that low pO_2 can decrease the expression of genes related to pigment changes in crop species (Ntsoane et al., 2019; Zhang et al., 2021). However, other studies have also shown that 'Tommy Atkins' and 'Palmer' mangoes stored under static CA conditions with pO_2 at 2% and 5%, respectively, resulted in anaerobic respiration, development of undesirable flavors, fruit discoloration, irregular maturation and greater susceptibility to rot (Singh and Zaharah, 2015; Teixeira et al., 2018). These different outcomes can be explained by the different growing conditions and fruit quality traits that possibly resulted in different minimum pO_2 required to maintain fruit aerobic respiration, as observed in our study with mangoes produced in different growing seasons.

The higher pulp firmness observed in DCA stored fruit, compared to RA stored fruit, was possibly due to the pO_2 effect on inhibiting ripening and cell wall degrading processes, as well as on triggering ethanol production. Ethanol has been shown to maintain pulp firmness in cherries (Bai et al., 2011) and melons (Liu et al., 2012), possibly by inhibiting ethylene synthesis that reduces the expression/activity of cell wall degrading enzymes (Goulao and Oliveira, 2008; Payasi et al., 2009). In that case, the low pO_2 efficiently maintained mango firmness, increasing fruit resistance to long distance markets, which is considered one of the most important limitations (Brecht et al., 2017).

Black flesh is a physiological disorder characterized by dark-brown and dry discoloration of the inner flesh in the fruit, which takes place after harvest and most frequently in cold stored fruit (Brecht, 2019; Mogollón et al., 2020). Although there is limited information about the mechanisms regulating black flesh development, the dark-brown symptoms suggest that oxidative processes could be involved in determining the incidence and severity of the disorder in the fruit (Li and Chen, 2017; Brecht, 2019; Mogollón et al., 2020; De Bang et al., 2021). Indeed, our study shows that the DCA conditions with low pO_2 efficiently controlled black flesh incidence in 'Tommy Atkins' mangoes stored at 9 °C for 60 days. In that case, such a low pO_2 condition could possibly inhibit oxidative processes required for black flesh symptoms development in the fruit.

The rot incidence during long term storage is one of the most important causes of fruit losses (Vilanova et al., 2014). In our study, fruit stored under DCA had lower rot incidence than fruit stored under RA, which was possibly due to the inhibitory effect of low pO_2 on ripening and pathogen development in the fruit. Indeed, studies have shown that low pO_2 reduces rot incidence in fruit species possibly by delaying ripening and triggering acetaldehyde and ethanol synthesis that inhibit pathogen development in the fruit (Pesis, 2005; Imahori et al., 2013).

Although SSC gradually increased in both storage conditions, the increase was more pronounced in RA than in DCA stored fruit. During fruit ripening, starch is hydrolyzed into sugars, mainly glucose, fructose and sucrose, which results in higher SSC and provides the desirable sweet taste. Therefore, our results suggest that starch breakdown into sugars was delayed in DCA stored fruit, compared to RA stored fruit. This effect possibly occurred due to the low pO_2 in DCA storage, which inhibited fruit ripening and delayed the metabolic processes involved in starch breakdown and sugars accumulation in the fruit (Singh and Zaharah, 2013).

The TA decreased during storage, but it was maintained higher in DCA than in RA stored fruit, mainly at later stages of storage. In that case, the lower pO_2 applied in DCA possibly reduced the activity of the tricarboxylic acid cycle, maintaining higher levels of organic acids in the fruit (Saquet, 2019). Consequently, the fruit flavor, represented by the balance between the content of sugars and organic acids quantified by the SS/TA ratio, increased more markedly in fruit stored under RA, compared to DCA, due to higher degradation of acids and starch hydrolysis (Singh and Zaharah, 2013; Saquet, 2018).

5. Conclusions

'Tommy Atkins' mangoes produced in the summer, winter and spring growing seasons required different minimum O_2 levels to maintain aerobic respiration ranging from 0.25 kPa to 13.75 kPa, 0.80 kPa to 2.30 kPa and 1.42 kPa to 17.40 kPa, respectively, as the duration of storage increased.

Storage of 'Tommy Atkins' mangoes under DCA using the minimum

O_2 levels identified in our study effectively inhibited fruit ripening, controlled black flesh and reduced rot incidence during 60 days of cold storage at 9 °C and 60 + 7 days of shelf life at 25 °C.

CRediT authorship contribution statement

Luana Ferreira dos Santos: Methodology, Formal analysis, Investigation, Data curation, Writing – review & editing. **João Claudio Vilvert:** Methodology, Formal analysis, Investigation, Data curation. **Tassiane Alves de Souza:** Methodology, Formal analysis, Investigation, Data curation. **Jasciane da Silva Alves:** Methodology, Formal analysis, Investigation, Data curation. **Tiffany da Silva Ribeiro:** Methodology, Formal analysis, Investigation, Data curation. **Daniel Alexandre Neuwald:** Methodology, Writing – review & editing. **Sergio Tonetto de Freitas:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

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