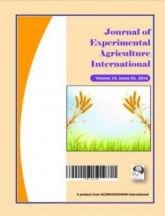

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The Role of Ethylene on Banana Fruit Ripening Via Sugar and Starch Metabolism

Sarah Nadja Araújo Fonseca[1], Willian Batista-Silva[2*], Edson Hiydu Mizobutsi[1], Gláucia Michelle Cosme Silva[3], Juceliandy Mendes da Silva Pinheiro[1], Mariana Oliveira de Jesus[1] and Gisele Polete Mizobutsi[1]

[1]Departamento Ciências Agrárias, Universidade Estadual de Montes Claros, Janaúba, MG, Brazil.
[2]Departamento de Biologia Vegetal, Universidade Federal de Viçosa, 36570-900, Viçosa, Minas Gerais, Brazil.
[3]Departamento de Produção Vegetal, Universidade Estadual do Norte Fluminense Darcy Ribeiro, 28035-200, Campos dos Goytacazes, RJ, Brazil.

Authors' contributions

This work was carried out in collaboration between all authors. Authors SNAF, GPM and WBS designed the study, performed the statistical analysis, wrote the first draft of the manuscript. Authors EHM, GMCS, JMSP, SNAF, JMSP and MOJ managed the analyses of the study. All authors read and approved the final manuscript.

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ABSTRACT

Banana as a climacteric fruit has a relatively short shelf-life period and thus, technologies that decrease the metabolism and the triggering of the maturation process are extremely necessary on its postharvest conservation. However, the consequences of these technologies on quality attributes are unknown. Therefore, we evaluate the effects of 1-Methylcyclopropene associated with low density polyethylene bags on physical and chemical attributes in the postharvest of banana fruits. Bananas were treated with different concentration of 1-Methylcyclopropene as 0, 50, 100, 150 and 200 ŋL.L^{-1} under refrigeration and harvest in five different times after treatment. Further, fruits treated with 50 ŋL.L-¹ showed a more advanced stage of ripening after the 25 days of storage.

**Corresponding author: E-mail: williambatistadasilva@gmail.com;*

Altogether, our results suggest 1-MCP is an effective treatment to control sugar and starch metabolism in banana and its efficiency is directly dependent of storage temperature. Additionally we identify interestingly correlation with skin color changes with sugars and starch content, which can indicate its potentiality of the fitted equations for prediction of central metabolism of bananas non-destructively using 'hue angle and chrome' value.

Keywords: Postharvest; banana quality; 1-MCP; sugar metabolism; starch.

1. INTRODUCTION

Banana (*Musa* sp.) is an important commercial food crop exported to many countries. Banana is considered as a climacteric fruits, exhibiting a short shelf-life [1]. According to Golding *et al.* [2], during the maturation, there is a low basal rate of ethylene production called as a System 1, followed by System 2, which this second one is characterized by autocatalytic climacteric rise in ethylene production. Under normal condition, ethylene binds to receptor- membrane proteins, triggering responses associated with maturation [3,4]. This phytohormone is directly associated with several ripening process changes during the burst from autocatalytic stimulation [5]. In this vein, banana ripening, according to Medina-Suárez *et al.* [6] and Ghosh *et al.* [7], is characterized by a significant up- and down-regulation of transcripts that encode enzymes involved in ethylene biosynthesis, cell respiration, starch metabolism as well as sugar metabolism and several other key metabolic events on the primary and secondary metabolism, such as chlorophyll breakdown and carotenoid accumulation (Katz et al., 2004). Hence, it is generally accepted that continued production and action of ethylene are required for integration of these biochemical events [2].

Notably, the fruit`s quality is related to the maintenance of the normal characteristics of the product, such as texture, color, flavor and aroma, the way the food is produced to the consumer for the longest possible time. However, these characteristics are directly depending on metabolic activity which is several factors-responsive. Thus, technologies that modulate the metabolism and inhibit the senescence process at the same moment are needed.

The use of ethylene inhibitors in banana can delay the maturation process, consequently, increasing the postharvest life of the fruit. In the same vein, the volatile ethylene non-toxic antagonists such as 1-methylcyclopropene (1-MCP) has provided a useful tool for elucidating the role of ethylene in ripening climacteric fruit [8,2,9,10,11]. Recently, 1-MCP has been extensively used on climacteric and non-climacteric fruits for delaying fruit ripening and control fruit quality in tomato [12], melon [13], plum [14], mango [15]; [16], strawberry [17], papaya [9,18], and bananas [2,19]. Although various studies have focused on the 1-MCP effect on the storage of banana fruit [20,21], still in our knowledge, few works have been done associating the effect of 1-MCP combined with refrigeration and packaging on metabolic adjustment as well as changes in the color of the fruits. Furthermore, still remain unclear the correlation pattern of these parameters when the ethylene action is inhibited and how long they remain ethylene-dependent.

Hence, the objective of the present study was to evaluate the effect of 1-methylcyclopropene associated with low density polyethylene packaging in the preservation and maintenance of postharvest quality as well as its effects on the metabolism and correlation pattern of chemical, physical and metabolic attributes in banana 'Prata Gorutuba' (Musa spp. AAB 'Prata Anã' clone: Gorutuba) stored under refrigeration.

2. MATERIALS AND METHODS

2.1 Fruit Material

Bananas bunches (containing 4 individual fruits) cv. Prata Gorutuba (*Musa* AAB 'Prata Anã') were kindly provided by the Itapicuru Company, located in Minas Gerais State, Southeastern Brazil. Mature fruit showing totally green skin (maturity stage 2, see Supplementary Fig. S1) were harvested, washed, carefully selected, and transported in a refrigerated truck at 15°C during 4h to the laboratory before performing analyzes.

2.2 Solution Preparation and Fruit Treatment

The fruits were placed in hermetic plastic boxes (0.3 m^3) and then submitted to 0, 50, 100, 150 e 200 $\eta L.L^{-1}$ of 1-methylcyclopropene (1-MCP)

(SmartFresh®) in the form of wettable-powder, containing 0, 14% i.a. of 1- methylcyclopropene. After complete dissolution, the banana's fruits were exposed during 8 hours to the gas (1-MCP), in room temperature (RT) 25±1ºC. After treatments, the fruits were packed in to Low Density Polyethylene (LDPE) plastic bags (25 µm), and then stored in cooling chamber at 14.5 ± 1ºC and relative humidity air (RH) 95% ± 5 % during 25 days after treatment. Finally, after this storage time, the banana's bunches were removed from the packages and kept at RT for 5 days, and analyzes were taken daily until the last day.

2.3 Physical Quality Attributes

The firmness was performed using a penetrometer (Brookfield model CT3) with 4mm diameter. The evaluation made in two equidistant regions, on opposite sides, of the equatorial region of the fruits. The firmness was measured as the maximum penetration force expressed in Newton (N). The skin color of the fruit was performed using a Color Flex 45/0, stdzMode: 45/0. To determine the chromaticity values (L∗ – lightness, and h° – hue angle) were calculated using the chromaticity values a∗ and b∗ according to McGuire [22].

2.4 Determination of Chemical Quality Parameters

Around ten gram (10 g) of banana from each replicate were crushed and homogenized with 100 ml boiled distilled water (previously adjusted to pH 8.3). The pH was measured by using pH meter Crison MicropH 2001 (Crison Instruments SA, Barcelona, Spain). The mixture was titrated with 0.10 M NaOH to pH 8.3 and the result was expressed as mg malic acid per 100 g sample. The total soluble sugar content (SSC) were determined according to Madamba [23] as previously described by Bico et al., [24].

2.5 Physiological Parameters

The soluble sugars were determined by the anthrone method Dubois *et al.* [25]. The quantification of starch was carried out according to the method described by Yemm and Willis [26] and dosages were made by the anthrone method Dubois et al. [25]. The starch was obtained by spectrophotometry, with reading wavelengths 510 nm, according to the method described by Nelson [27].

2.6 Experimental Design and Statistical Analyzes

The experiment was performed in a completely randomized design (CRD), with five replicates. Statistical analyzes were performed using the GENES software [28]. The averages of the treatments were compared by the Tukey's test ($P \leq 0.05$). Pearson's correlations were also calculated. Analyzes were performed using Sigma Stat software v.2.0 (SPSS Inc., Chicago, IL, USA) and GraphPad prism 6 (GraphPad Prism version 6 for Windows, GraphPad Software, La Jolla, California, USA).

3. RESULTS

3.1 Effect of 1-MCP in Physical Quality Parameters during Banana Ripening

As shown in Fig. S1, the 1-MCP could delay the ripening of banana fruit and in complement, the physical quality parameters follows the same visual response (Fig. 1). Among the treatment, $50\eta L.L^{-1}$ 1-MCP treatment had the similar effect with a normal ripening, which after 3 days there was not more significantly difference in comparison with $0\eta L.L^{-1}$ 1-MCP (See in Fig. 1 and Supplemental Table S1). However, in higher concentrations the firmness in the control fruit dropped sharply from of 30.59N on the 1st day to 4.03 N on the 5th day after remove from the refrigeration (Fig. 1A). Interestingly, the L value the 1-MCP treatment has not shown drastically changes during fruit ripening, except in 3rd day where, the L value was reduced in 100, 150 and $200\eta L.L^{-1}$ 1-MCP (60.97, 58.96 and 63.04 respectively, see in Fig. 1B and supplemental Table S1). The change of the peel color was expressed in hue angle (*h*º) values. As is shown in Fig. 1C, the peel color of banana fruit in all treatments turned more yellow through the period of storage (Supplemental Figs. S1 and S2). Banana treated with 1-MCP showed a significantly higher level of hue angle values compared to that of other treatments. This effect was considered dose response, the higher the concentration of 1-MCP, the greater the delay in the peel color changes (Fig. 1C and Supplemental Fig. S1). At the same time, the Chroma (Fig. 1D), a similar results from the previous observed with hue angle, showing a higher color intensity (Chroma), mainly after 5th day of storage at 25ºC with reduced values to 1-MCP treatments (Supplemental Table S1).

3.2 Effect of 1-MCP in Chemical Quality Parameters during Banana Ripening

As shown in Fig. 2A, the pH values had significant reduced during fruit ripening and these effects were retard by with increased concentrations of 1-MCP. The lowest values on the 4th day after treatment and storage (4.42, 4.43, 4.46 and 4.57) were detected in the control and fruits submitted to the lowest concentrations of 1-MCP (0, 50, 100 and 150ηL. L-1, respectively). These effects are in a close relationship with malic acids content in the (Fig. 2B). During fruit ripening fruit, the 1-MCP significantly has affected the malic acid, which has kept enhanced the values in fruits treated with 100, 150 and 200ηL. L-1 (Fig. 2B and Supplemental Table S2). As shown in Fig. 2C, the SSC (ºbrix) increased during fruit ripening in all treatments. A significant extension in ripening time was obtained for all concentrations of 1-MCP with the increase in time to ripen over untreated fruit. The 1-MCP treatment has suppressed significantly the SSC content over fruit ripening as compared with control (Fig. 2C). The rate of sugar content evolution is drastically affected in 5th day after treatment and storage, which 200ηL.L^{-1} 1-MCP has suppressed ~50% of SSC in the fruit juice. The malic content changes has influenced the brix/acid ratio (Fig. 2D), showing to be due mainly to a higher TA in 1-MCP treated fruit rather than a lower level of SSC, which malic acid degradation over ripening is reduced in 1-MCP treatment.

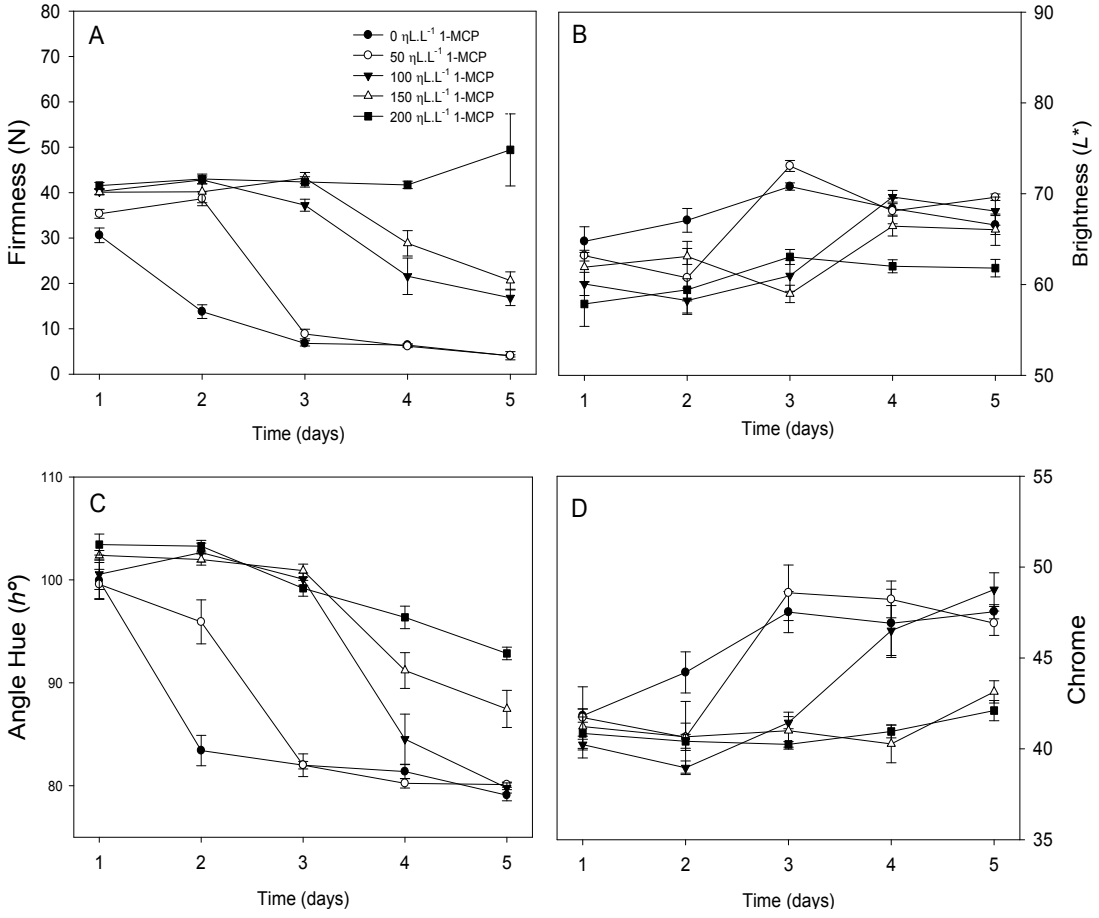

Fig. 1. Physical quality attributes in banana cv. Prata Gorutuba (*Musa* AAB 'Prata Anã') under different concentrations of 1-MCP during 5 times of storage in room temperature.

A: Firmness, B: Brightness, C: Angle hue and D: Chrome. Each value is the mean for four replicates, and vertical bars indicate the standard errors (n = 5)

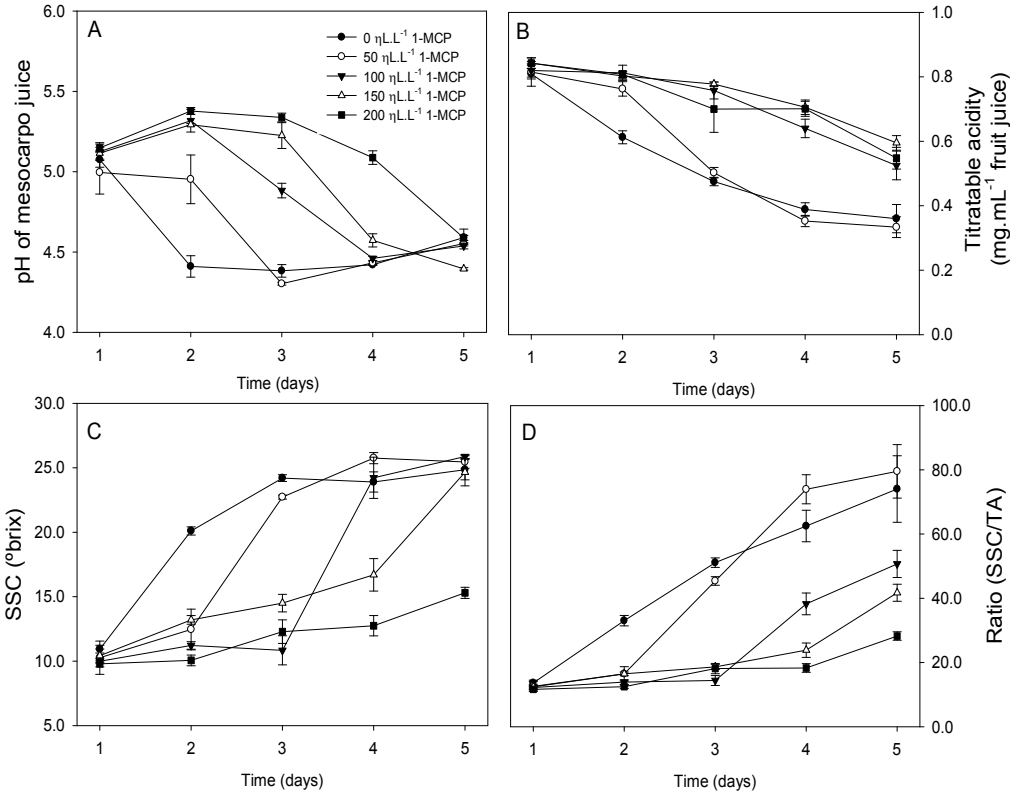

Fig. 2. Chemical traits of quality in banana cv. Prata Gorutuba (*Musa* AAB 'Prata Anã') under different concentrations of 1-MCP during 5 times of storage in room temperature.

A: pH of mesocarp juice, B: Titratable acidity, C: SSC and D: SSC/TA. Each value is the mean for four replicates, and vertical bars indicate the standard errors (n = 5)

3.3 Effect of 1-MCP in Physiological Quality Parameters during Banana Ripening

The ripening are a complex process genetically programmed, culminating in a dramatic changes, mainly in color, texture, flavor and soluble solids and volatile aroma [29]. In order to characterize better the 1-MCP after refrigerating storage on physiological traits, we measured the sugars, starch contents as well as the ratio sugar/starch (Fig. 3). As shown in Fig. 3 the non-reducing sugar has been found in larger quantities and lower concentration to reducing-sugars (Fig. 3A and B). However, both have increased in quantity during fruit ripening, reaching the higher levels at 5th in control fruits. Additionally, the sugar content has increased during ripening fruit, concomitantly with the evolution of SSC. The 1-MCP treatment has delayed the accumulation of sugars and starch degradation (Fig. 3). As shown on Fig. 3C, fruits treated with 200 ŋ.L.L-¹ 1-MCP have had reductions in the total sugar content of 25% in the 5th day after treatment and lower temperature storage in comparison with untreated fruits at the same time. Therefore, the 1-MCP combined with lower temperature storage can significant influence on the ripening process of bananas mainly controlling the sugar content in bananafruits. As shown in Fig. 3D, the starch content is decreased during fruit ripening, as expected, however the 1-MCP has a directly influence in starch catabolism during ripening process, suggesting the connection directly with enzymes involved with degradation of this compound. The treatment with 200 ŋL.L-¹ has reduced 2-fold when compared with control (untreated fruits). Additionally, the variation in the sugars and starch content correlated strongly with some physical properties of the fruit, such as SSC, skin color parameter and the malic acids (Fig. 5). Interestingly, starch has negatively correlated with SSC (-0.92), the ratio SSC/TA (-0.89), L* (-0.81) and Chrome (-0.90) (Fig. 5).

This expected negative correlation shows the importance of the degradation of the reserves (starch) for increasing the sugars content of sugars and increase in the content of soluble solids of the fruits.

3.4 Multivariate Analysis

All measured variables were used to perform the analysis of the principal components (PCA). Furthermore, the PCA was performed to explore more deeply the contribution of changes 1-MCP treatment followed by lower temperature storage in the metabolite composition as well as physical parameters across fruit developmental stages by score plot and loading plot (Fig.4). Through the PCA, this fingerprint analyzes showed that indeed the dominant source of variation in the combined dataset is the differential contribution of the metabolite composition across fruits ripening in 1-MCP treatment. The first component (PC1) explained 89.6% of the variation and the second component (PC2) only 9.7%, which showed no distinguish between the 1-MCP treatment and time after storage. Therefore, our attention was turned to the PC1 (Fig.4A). Our results were separated in three groups whose were also confirmed by Euclidean distances. In the group I, include the time over fruit ripening, which low concentrations of 1-MCP such as 0 and 50 in ripe fruit (T4 and T5) characterized by low influences of 1-MCP and fruit complete ripe (See Fig. 4A – orange circle) while the group II, include the blue circle group and it is composed by intermediate fruit ripe and mixed with higher 1-MCP such as 100 and 150nL.L^{-1}, showing a mix of effect by 1-MCP treatment and time of storage. Finally, the group III composed by unripe fruit under storage independently of 1-MCP treatment and 1-MCP, mainly by higher 1-MCP concentrations influences (Fig.4A). In a complementary manner, we also performed the loading plot, intending to analyze the variables that contributed to the separation of the groups. Ripe fruits (Group I) was separated mainly by non-reducing sugars (Fructose and Glucose), total sugars content as well as the ratio SSC/TA, which are associated with fruit quality (Fig.4B). This results shows that50nL.L-1 in T5 (5 days after storage) does not have any influences in avoid starch catabolism and control of fruit ripening, showing results similar with control. The group II was mainly separated by color and soluble solids contents and by reducing-sugars. In the last case, the group III interestingly was separated by starch, firmness and Angle hue. Both of these variables are directly controlled by 1-MCP concentrations and stage of fruit ripening process (See in Fig. 4B).

4. DISCUSSION

The 1-MCP as an inhibitor of ethylene perception has been investigated in a large number of researches as an agent maintaining the quality as well as to investigate the role of ethylene in ripening and senescence of many fruits and vegetables [8], including bananas [30,31] . These responses are also investigated alone, or in association with different agents such as chitosan [32], and hormones [31] as well as atmospheric modification [33]. However, according with Blankenship and Dole [34] the 1-MCP treatment depend on numerous factors and are dependent on plant material. In banana, with at least 5 and 50 nL.L^{-1} there is no effect on unripe bananas, while 500 nL.L^{-1} delayed the ripening process [30]. In addition, few works have associate 1-MCP treatment and low density polyethylene packaging aiming extend the shelf life and maintain the fruit quality as well as its effects in the sugars and starch metabolism in banana fruits, once 1-MCP has a strong completive ability with ethylene receptors and suppress the respiration and climacteric peck in fruit [34;30,35] .

This research becomes pertinent, since is already known that one of the factors that most affects the responses to 1-MCP is the active concentration and the treatment exposure time, additionally, the relation between concentrations exposing time are directly interdependent [36] . In our study, the 1-MCP treatment associated with low density polyethylene packaging in the banana fruit preservation may delay the ripening process via significantly changes in physical (See in Fig. 1 and Supplemental Table S1), chemical (See in Fig. 2 and Supplemental Table S2) and physiological traits (See in Fig. 3 and Supplemental Table S3). In addition, delaying fruit firmness, skin color and controlling the cellular pH by increasing of malic acid which are directly associated with reparation rate. Consequently, the ratio SSC/TA is altered which is easily separated by PCA analysis in three independent group according fruit age and 1-MCP treatments (Fig. 4). Furthermore, the sugar contents both, non-reducing and reducing-sugar is as expected suppressed by 1-MCP treatment, which can be explained partially by starch degradation and respiration rate (Fig. 3D). Starch degradation is delayed over fruit ripening by 1-

MCP treatment driving a few alterations in sugars and soluble solids contents. Therefore, reducing in sugar/starch ration in treated fruit was reduced in comparison with untreated fruits (Fig. 3E). Overall, our data indicate that the conversion of starch to sugars is in good agreement with fruit softening and ethylene production during banana ripening.

The influences of 1-MCP treatment in respiration rate and ethylene production is already well documented by [19,30). Therefore, the reduction in respiration rate is possibly the result of reduction in several essential respiratory steps such as, glycolysis and TCA, as well as phosphorylating chain (OXPHOS), decreasing the ATP production and starting the anaerobic pathway, resulting in lower SSC due to the slower hydrolysis of carbohydrates (Starch to sugars) [37,38]. Our results show that 1-MCP and low density polyethylene packaging might be a viable alternative to extend the post-harvest life of banana and function as a controlling agent of the nutritional levels. In agreement with those found by (Purgatto et al., [39]) which banana fruit ripening is characterized by textural softening,

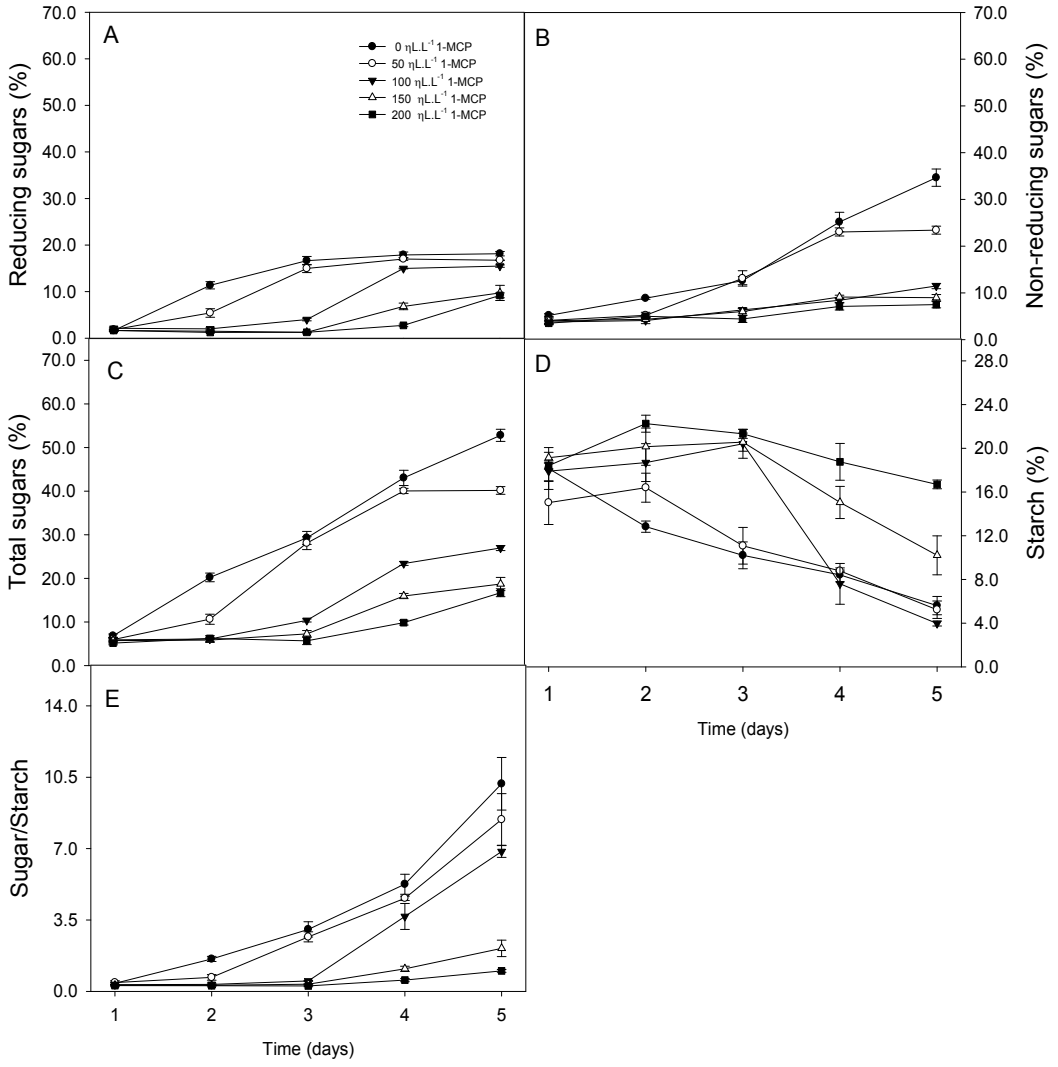

Fig. 3. Physiological traits of quality in banana cv. Prata Gorutuba (*Musa* AAB 'Prata Anã') under different concentrations of 1-MCP during 5 times of storage in room temperature

A: Reducing sugars content, B: Non-reducing sugars content, C: Total sugar content D Starch content and E: Sugar/Starch ratio. Each value is the mean for four replicates, and vertical bars indicate the standard errors (n = 5)

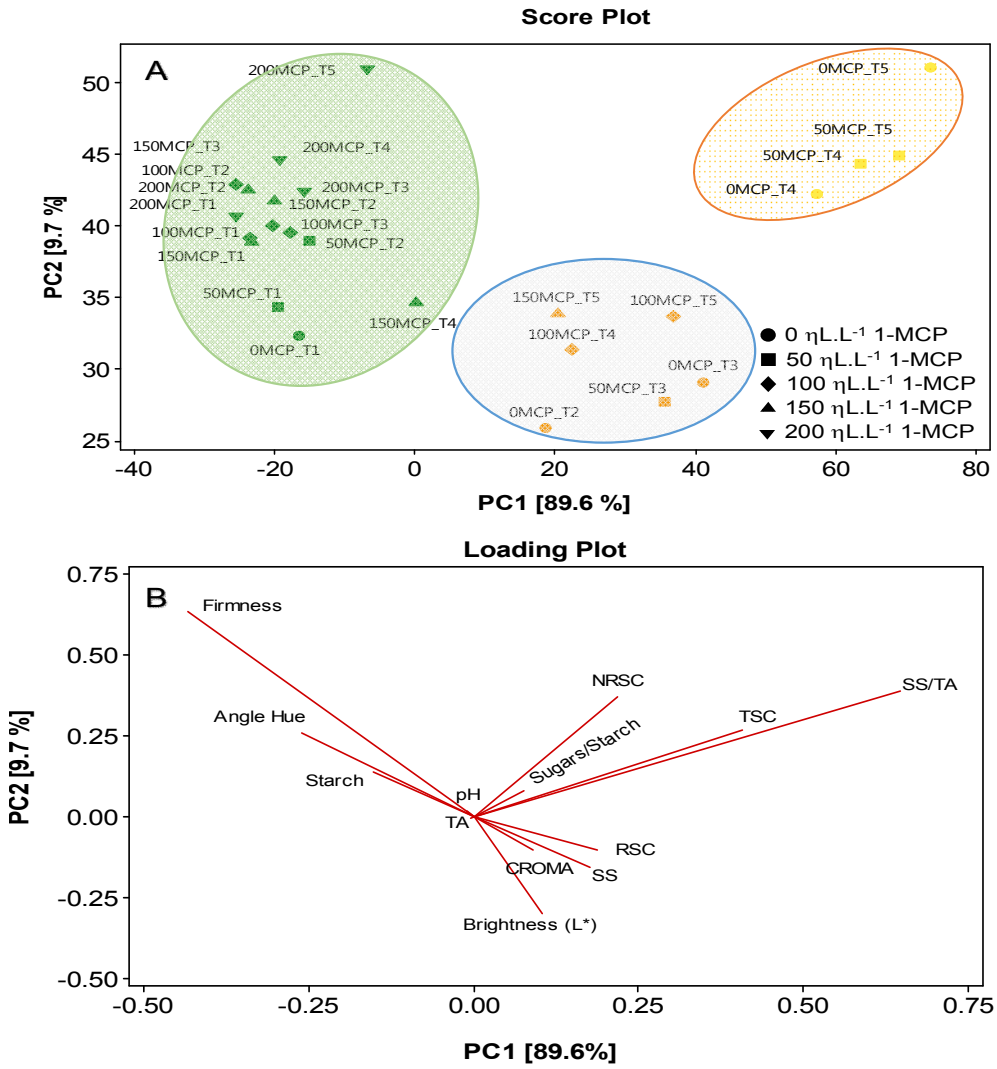

Fig. 4. Principal component analysis. (A) Score plot derived data of 1-MCP treatment under different days after treatment [0 days (T1), 1 day (T1), 2 days (T2), 3 days (T3), 4 days (T4) and 5 days (T5). The large circles represent the three clusters formed by the Euclidean distance method. (B) In loading plot the direction and length of the lines are directly proportional to variables importance in separating groups.

PC1, principal component 1; PC2, principalcomponent 2. Abbreviations: Hidrogenionic potential (pH), NRSC (Non-reducing sugarcontent), Total sugar content (TSC), Reducing sugar content (RSC), Soluble solids content/ Titratable acidity ratio (SS/TA), Soluble solids content (SS), Titratable acidity (TA)

sugar content, acidity and color changes. In addition, Ziliotto et al. [40] have shown in transcriptome profiling of ripening nectarine treated with 1-MCP has in comparison with untreated fruit after 24h, 106 targets differentially genes were expressed and 30% of their targets correspond to gene involved in primary metabolism related with ethylene and other phytohormones as well as some gene involved in softening, skin color development and sugar metabolism. Interestingly, in our results, angle hue (°*h*) is an important skin-color parameters to identify the sugar content in banana fruit, hence they shows a higher and positive correlation with starch content and been an important variable that has contributed to separate groups in PCA analysis (See in Fig. 4A and Fig. 5).

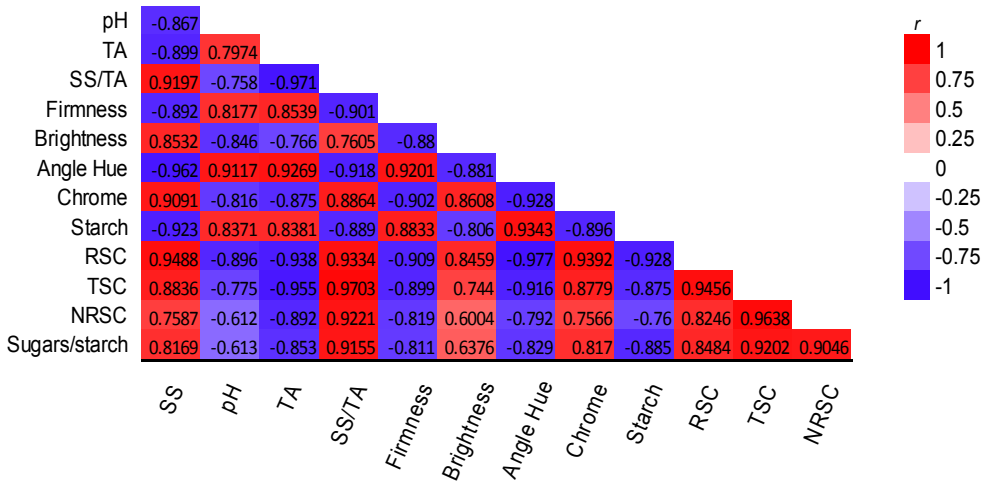

Fig. 5. Correlation matrix based on Pearson coefficients derived from physical, chemical and physiological trails data from banana cv. Prata Gorutuba (*Musa* AAB 'Prata Anã') under different concentrations of 1-MCP during 5 times of storage in room temperature. Correlation coefficients are presented in colors, and the significant ones are indicated in bold (P) based on p-value corrected by FDR correction (Bonferroni-Hochberg).

Abbreviations: Hidrogenionic potential (pH), NRSC (Non-reducing sugar content), Total sugar content (TSC), Reducing sugar content (RSC), Soluble solids content/Titratable acidity ratio (SS/TA), Soluble solids content (SS), Titratable acidity (TA)

Faced to physical variables changes, such as Firmness, *L*, h°* and chrome, the firmness reduced during maturation for all treatments, however the fruit softening was reduced following the increase in the 1-MCP concentrations, resulting in a smaller loss of firmness after removal of the refrigerated chamber. According with Ali et al. [41], the fruit softening occurs due to deterioration of structural and non-structural carbohydrates such as, cell wall and-or starch oxidation, resulting in an increase in the sugars content. In banana fruit softening were reported by a coordinated degradation of pectic, hemicellulosic polysaccharides in the cell wall and starch [42] . In banana, several gene is are involved in starch-to-sugars conversions during ripening process has been reported, including the amylases such as *MAmy*, *Ma-bms*, *Maisa* and *MaDEBs* [43,44,45,46]). Recently, Xiao et al. [47] has shown a complex actions of numerous enzymes related to starch breakdown at transcriptional and translational levels and proved that MabHLH6 may act as a positive regulator of this process via activation of a series of starch degradation-related genes. Taken together, our study suggests that 1-MCP treatment can be involved regulating somehow the starch-degradation gene and acting mediating partially transcription factors responsive to ethylene. In the same way, according with Zewter et al. [21], bananas treated with 1-MCP kept in a package of non-perforated polyethylene, showed an increase in total sugars, provided by conversion of starch to sugar, as with the advancement of ripening a decline occurs after reaching a certain peak when the fruits enter the senescence phase. In summary, the treatment 100, 150 and 200 ŋL.L-¹ de 1-MCP in bananas 'Prata Gorutuba' for 8 hours delay the ripening in approximately 25 days, when packed in PEDB and stored under refrigeration (14.5°C), without changes in their physical and chemical characteristics. In complement, our results suggest 1-MCP treatment effectively prolongs the quality attributes not compromising the normal ripening after removal of package and kept in room temperature (25ºC), accumulating sugars by starch degradation. Furthermore, the correlation pattern of physical and chemical attributes demonstrates thus the dependence of ethylene action and of the interplay between these events despite mechanism to be distinct and act in different area in the fruit.

5. CONCLUSION

As conclusion, our results suggest that, 1-MCP is an effective treatment to control sugar and starch metabolism in banana and its efficiency is

directly dependent of storage temperature. In addition, we identified a straight correlation with skin color changes and carbohydrates content, which can indicate its potentiality of the fitted equations for prediction of central metabolism of bananas non-destructively using 'hue angle and chrome' value.

HIGHLIGHTS

- 1-MCP is an effective treatment to control sugar and starch metabolism in banana.
- Skin color changes is an important predictive variable to identify changes in the central metabolism in banana fruits.
- Ethylene action is an interplay of physical and chemical changes in banana fruit.

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COMPETING INTERESTS

Authors have declared that no competing interests exist

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