REVIEW ARTICLE

Factors associated with postharvest ripening heterogeneity of 'Hass' avocados (*Persea americana* Mill)

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Abstract – Introduction. 'Hass' is the main avocado cultivar commercialized worldwide. The extended flowering period, very low percentage of fruit set and inability to ripen on the tree renders the fruit heterogeneous and unpredictable during postharvest management. The "triggered" and "ready-to-eat" growing markets for 'Hass' avocados are affected by the variable postharvest ripening or ripening heterogeneity which creates severe logistical problems for marketers and inconsistent quality delivery to consumers. **Synthesis.** The dry matter content, the current avocado harvest index that correlates very well with oil content, has been extensively used to harvest 'Hass' avocados to comply with the minimum standards to guarantee consumer satisfaction. However, previous work and empirical experience demonstrate that dry matter does not correlate on a fruit-to-fruit basis with time to reach edible ripeness. Thus, avocados of very different ages are harvested from individual trees, resulting in heterogeneous postharvest ripening of fruit within a specific batch. Several preharvest factors related to environmental and growing conditions and crop management as well as postharvest technology strategies influence the observed variability of postharvest ripening. **Conclusion.** Modern approaches based on studying the composition of individual fruits displaying contrasting postharvest ripening behavior, combined with non-destructive phenotyping techniques, seem to offer practical solutions for the fresh supply chain of avocados to sort fruit based on their ripening capacity.

Keywords: avocado / *Persea americana* / fruit quality / ripening stage / preharvest management / secondary metabolites / non-destructive analysis

Résumé – Facteurs associés à l'hétérogénéité du mûrissement post-récolte des avocats (*Persea americana* Mill cv. Hass). Introduction. Le 'Hass' est la principale variété d'avocat commercialisée dans le monde. Sa période de floraison prolongée, son très faible pourcentage de nouaison et son incapacité à mûrir sur l'arbre en font un fruit hétérogène et imprévisible à gérer après récolte. Le marché croissant des avocats 'Hass' « déclenchés » et « prêts-à-manger » est affecté par la variabilité ou l'hétérogénéité du mûrissement post-récolte, ce qui crée de sérieux problèmes logistiques aux spécialistes du marketing et offre une prestation de qualité inégale aux consommateurs. **Synthèse.** La teneur en matière sèche, l'actuel indice de récolte des avocats qui correspond parfaitement à la teneur en huile du fruit, a été largement utilisé pour récolter les avocats 'Hass' en conformité avec les normes minimales de garantie de satisfaction des consommateurs. Toutefois, des travaux antérieurs et l'expérience empirique démontrent que la matière sèche ne correspond pas à un paramètre sur lequel se baser d'un fruit à l'autre pour estimer la durée jusqu'au fruit mûr prêt à manger. Ainsi, pour des fruits d'âge très différents récoltés arbre par arbre, il en résulte une hétérogénéité du mûrissement des fruits après récolte dans chaque lot. Plusieurs facteurs pré-récolte liés aux conditions agro-environnementales et à la gestion des cultures ainsi que des stratégies de traitement technologique post-récolte ont une influence

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sur la variabilité observée du mûrissement post-récolte. **Conclusion.** Les approches modernes fondées sur l'étude de la composition individuelle des fruits, permettant d'affichant les différences de comportement en phase de mûrissement après récolte, combinées à des techniques de phénotypage non destructives, semblent offrir des solutions pratiques à la filière d'avocats frais, par un tri des fruits en fonction de leur capacité à mûrir.

Mots clés : avocat / *Persea americana* / gestion pré-récolte / métabolites secondaires / qualité des fruits / stade de maturité / analyse non-destructive

1 Introduction

Avocado (*Persea americana* Mill) is an economically important tropical fruit, and the cultivar Hass dominates the international trade market [1, 2]. The world demand for 'Hass' avocados has opened up new consumer niches − the "triggered" and "ready-to-eat" markets. Due to these formats, countries that previously had a low demand for avocados have opened their doors to this fruit. This increase in demand is aided by the organoleptic, nutritional and functional attributes [3–5] found in avocados, including a high content of polyunsaturated fatty acids (PUFAs). A high dietary uptake of unsaturated fatty acids is associated with decreased risk of cardiovascular diseases [6, 7]. In addition, the high content of monounsaturated acids (MUFAs ~71%; mainly oleic acid) and high dietary fiber content (~6.8%) have been associated with positive effects on weight control and hyperlipidemia [8, 9]. The main drivers of avocado purchase in the USA according to a study reported by the Hass Advisory Board [10] are: "Being good for you, the nutritional benefits, taste, quality and the variety of use". In the USA there are investments in campaigns to promote avocado as a healthy fruit.

Historically, Mexico remains the major producer and exporter in the world. During the 2014–2015 season, Mexico exported 847,000 t to different destinations, followed by Peru with 179,044 t and Chile with 67,643 t. The main export destinations are Europe and the USA [11]. The 2014–2015 season for the worldwide market of avocados was outstanding, with an annual growth of 211% and 1.4 Mt of fruit commercialized. International trade has doubled in the span of 6 years without major price concessions irregardless of the depressed economic situation around the world. Consumption in the USA for the 2014–2015 season approached 3 kg per capita, and France, as the main avocado consumer in Europe, was about 1.5 kg per capita. The margins between retail prices and import prices were pretty high (0.53 Euros fruit^{-1}), and this differential has increased over the years by 0.19 Euros fruit^{-1} compared with the 2008−2009 season. Most of the fruit is commercialized "triggered" (ripened to a certain extent but not yet fully ripe and commercialized unpackaged) and "ready-to-eat" (sold in bags of two pieces) in Europe. These treatments have helped increase consumption even without the extensive promotions and campaigns that occur in the USA [10]. In terms of price, the "ready-to-eat" is very remunerative for distributors, with differences of prices higher than 30% in comparison with "triggered" loose fruits [11]. Even though the "triggered" and "ready-to-eat" markets are tempting and profitable, avocado physiology is complex and the pre- and postharvest history of the fruit results in heterogeneous ripening during post-harvest management. This leads to logistical problems for marketers, increased labor costs, and inconsistent quality delivery to consumers, with increased fruit losses [12, 13].

Avocado physiology is quite complex compared with other fruits. The avocado flowering period can last up to three months, thus a wide variability in age among fruits at harvest time is evidenced [14]. Avocados can remain on a tree for more than 12 months, which is far beyond the time needed to reach physiological maturity and ability to ripen [15]. Furthermore, avocado ripening only happens when the fruit is detached from the tree and postharvest ripening heterogeneity is only evidenced during postharvest management of the fruit. In this review, we will provide an overview of preharvest and postharvest factors that affect the observed ripening heterogeneity of 'Hass' avocados, and provide some perspectives for future work on this topic.

2 Avocado fruit development

Avocado growth is characterized by a single sigmoid curve [16], with the early period of growth characterized by cell division [17]. Avocado is quite unique compared with other fruits in that cell division in the mesocarp is not only restricted to the initial period of growth, but it continues during fruit development and in mature fruit attached to the tree [18]. This fruit presents a very extensive flowering period of 2 to 3 months, and it does not ripen on the tree [19]. Fruit can hang on a tree for more than 12 months, long after reaching physiological maturity. As a consequence, at harvest, fruits of very different ages are obtained [15]. This peculiar characteristic of fruit only ripening after removal from the tree has been linked to a flow of inhibitory compounds from the leaves to the fruit referred to as the "tree factor", that inhibits ripening on the tree [20, 21]. Some authors have suggested that C$_7$ sugars (mannoheptulose and perseitol) may control/trigger the ripening process, but other studies indicate that additional metabolites are involved [13, 22–25].

3 Avocado fruit ripening physiology

Avocado is a climacteric fruit and as such it is characterized by an increase in the respiration rate and ethylene production at the onset of ripening [26]. Compared with other climacteric fruits, avocado produces high amounts of ethylene (80−100 μL kg^{-1} h^{-1} at 20 °C) when ripening [27]. In contrast to other tropical fruits, avocados are also unique in that the main respiratory substrates are sugars of the C$_7$ type (*e.g.*, mannoheptulose and perseitol) instead of C$_6$ sugars

(*e.g.*, glucose, fructose, sucrose) [22–24, 28]. These C_7 sugars have been reported to be inhibitors of the ripening process on the tree [22–25] and also as the compounds responsible for the differences observed in the ripening rate of individual fruits. Landahl *et al.* [25] found higher amounts of mannoheptulose near the pedicel of the fruit and from this hypothesized C_7 sugars to be ripening inhibitors. Blakey *et al.* [12], working on individual avocados but limited in sample size, reported a correlation between the rate of individual fruit ripening and the content of mannoheptulose. However, Pedreschi *et al.* [13] analyzed the content of C_7 sugars and followed the individual ripening of a hundred fruits and found no correlation of C_7 sugars at harvest with the observed differences in the ripening rate. Other respiratory substrates may be fatty acids, although the evidence for this is contradictory. A minimal change during the postharvest period of the fatty acid composition and content was reported by Luza *et al.* [29] but in another study an increase in PUFAs was described during postharvest fruit ripening [30]. The increased oil concentration reported during storage and ripening is related to postharvest dehydration and increased lipid recovery due to changes in the avocado mesocarp at the structural level with an enhanced activity of cellulase and polygalacturonase, resulting in degradation of cell walls, the oil being more available for extraction [28, 31].

'Hass' avocados, depending on the regulations or agreements of each country, are harvested when the fruit reaches a certain amount of oil content in order to prevent immature fruit being commercialized. Oil content is the most widely used harvest index for avocados [32] and since oil content correlates very well with dry matter, the latter is generally used due to its simplicity to estimate the oil content [32]. For example, in Chile, the harvest season starts when the fruit reaches 23% dry matter equivalent to ≈9% oil content and at the different time periods of the season (*e.g.*, early, middle and late) are defined based on the estimated oil content (23−26%, > 26−30% and > 30% dry matter, respectively). Oil accumulates until harvest. Within a geographical location, late-season fruits have a much higher concentration of oil than early-season avocados, changing from 9% in the early season to 14% in the late season. Structural lipids are part of the cell membrane (phospholipids and glycolipids) and storage lipids (triglycerides) are located in the idioblasts [33]. The fatty acid profile is the result of the adaptation to the environment [34, 35] and fatty acid profiles have recently been proposed as biomarkers to distinguish avocados from different growing areas [36].

Ripening is a complex process that involves the active participation of different metabolic pathways such as cell wall-modifying enzymes and ethylene biosynthesis enzymes which require energy. Ripening processes are highly dependent on continuous protein synthesis to provide substrates/intermediates to key metabolic pathways such as ethylene biosynthesis and respiration [37]. The ripening process can be affected by many factors including: water movement, phytohormones, mineral nutrition, carbohydrates and ripening enzymes [38–42]. As a climacteric fruit, avocado ripening is characterized by an increase in the respiration rate accompanied by an increase in ethylene production. Avocado during ripening is characterized by fruit softening [43] due to cell wall dismantling (depolymerization and solubilization) carried out by cellulase, pectin methyl esterase (PME), polugalacturonase (PG), ß-galactosidase, xylanase and xylosidase, enzymes that work in concert or synergistically [44]. In addition, peel color changes in 'Hass' avocados from green to black and synthesis of flavor and aroma compounds take place [2, 3]. The three most abundant volatiles hexanal, (E)2 hexenal and 2,4 hexadienal decrease in concentration as the fruit ripens and acetaldehyde, methyl acetate, pentanal and ß-myrcene increased. These changes in volatile composition coincide with the fruit becoming creamier and less watery in texture [3].

4 Avocado ripening heterogeneity physiology

Avocado ripening physiology is more complicated than other fruits due to its extensive flowering period, low percentage of fruit set and inability to ripen on the tree. In addition to this fruit physiology complexity, environmental conditions and cultural practices contribute to the observed variable ripening [45, 46]. Within a location, differences in spread of ripening within a batch have been reported [12]. Early-season fruit takes longer to ripen during the postharvest period [34]. Both early- and middle-season fruits are more prone to have a pronounced ripening heterogeneity within a batch and/or consignment than late-season fruit [12, 47].

4.1 Blooming

In subtropical climates, full bloom in avocado generally starts at the end of winter and it extends from 3 to 8 weeks. The initiation and time of flowering is affected by different factors including temperature, water stress and application of gibberellins [19]. Temperature is the main factor involved in the transition from the vegetative to the reproductive phase, since subtropical avocados produce buds if subjected to temperate temperatures. Water stress does not induce blooming when temperatures are high, but increases the induction of blooming when temperatures are temperate. However, blooming can be delayed up to a month after water stress is finished [19]. It is important to emphasize that floral organs can increase the potential water loss surface of the tree by 90% [48]. Application of paclobutrazol (a gibberellin inhibitor) at the swollen bud stage resulted in a delay in the development of the vegetative shoot of 4 to 5 days compared with the control which resulted in an increased time before shoot growth competed with fruit set [49]. The factors that influence blooming in different ways will have an effect on the heterogeneity observed during ripening of the fruit [50].

An avocado tree can potentially generate two million flowers but only yields 200 to 300 fruits. This load adjustment is characteristic of this species and there are two periods of fruit drop, during the third and fourth weeks post-fruit set and in summer [19]. This is due to the strong competition between young fruits and the vegetative growth. Weekly removal of vegetative buds during blooming and fruit set significantly reduces the percentage of fruit fall. Nonetheless, fruit at harvest

come from different moments of fruit set, and these differences in fruit age at harvest will be evidenced as ripening heterogeneity during the postharvest period [51].

4.2 Climacteric

The climacteric phase of avocado is part of the ripening process. This phase is accompanied by a series of biochemical changes that include the auto catalytic production of ethylene and the increase in the respiration rate [34]. Early-season fruit (23−26% dry matter) on average takes longer to reach the climacteric stage compared with middle-season (> 26−30% dry matter) and late-season (> 30% dry matter) fruits [47].

The avocado ripening process is biphasic and includes a period of low respiration rate and very low levels of ethylene, and a second period characterized by the climacteric behavior. The climacteric phase leads to color, aroma and texture changes. All these events occur after harvest, because as long as they are attached to the tree there is ripening inhibition.

4.3 Phytohormones (endogenous and exogenous application)

The role of endogenous hormones in the regulation of avocado growth and ripening has been studied, but still requires further elucidation [46]. Abiotic stress stimulates the production of abscisic acid (ABA) and might have an impact on postharvest ripening. A relationship between changes in the endogenous levels of ABA and the onset of the rise in ethylene production was reported by Adato *et al.* [52]. ABA levels in recently harvested avocados were high and varied in different orchards and cultural conditions. ABA accumulation during ripening began one day after the rise in ethylene production and since ABA accumulation proceeded the color and softening changes, ABA was postulated to take part in the regulation process involved in later stages of ripening [52]. Postharvest ripening was stimulated by the infusion of ABA through the pedicel on recently harvested avocados to study if it was involved in ripening heterogeneity. However, no effect on ripening heterogeneity was observed, but only on the days to reach edible ripeness [12]. A study on 'Hass' avocado fruit of different seasons (early, middle and late) reported changes in relation to the ripening speed and heterogeneity following water infusion and ABA treatments [12]. Harvested fruit infused with ABA had significantly faster ripening but there was no effect on the heterogeneity. According to Blakey *et al.* [12], mature fruit with lower water content ripens faster, possibly because the fruit is more stressed and contains a higher endogenous ABA concentration. In addition, higher ABA biosynthesis stimulates the production of ethylene, that triggers ripening [34]. Water infusion thorough the pedicel immediately after harvest apparently reduced the ripening spread or heterogeneity in middle- and late-season fruits in the experiment carried out by Blakey *et al.* [12], but the results and conclusions were based on small sample sizes (n = 10). The authors suggested that water content at harvest influenced the variation in ripening, and that indirect non-destructive measurements of

water content (*e.g.*, dry matter through NIR) could be used to segregate fruit and thus reduce postharvest ripening heterogeneity. However, this statement has recently been challenged by Pedreschi *et al.* [13], who found no correlation between water content of individual fruits and time to reach edible ripeness in early- and middle-season fruits.

In addition to C_7 sugars as ripening inhibitors of the fruit while on the tree, endogenous levels of auxins in the fruit have been reported during the early seventies as the resistant factor in ripening of avocado [53, 54]. The application of exogenous auxins to the fruit stimulated ethylene production and accelerated ripening, but if auxins are infused into the fruit tissue by the vascular system, ethylene levels are limited and ripening is inhibited. Ethylene production during ripening may promote the activation of IAA oxidase, resulting in lower levels of auxin in the fruit tissue [49].

Ethylene regulation of ripening in avocado has also been related to the seed. Seedless fruit, both at ambient temperature and after cold storage, had a higher respiration rate and ethylene production than seeded fruit [55].

5 Preharvest factors involved in ripening heterogeneity

Several preharvest factors: genetics, location and microclimate, light availability, temperature, rain and irrigation, mineral nutrition and fertilization, growth regulators, and ripeness at harvest, have been directly or indirectly linked to the postharvest ripening heterogeneity observed for 'Hass' avocado [46].

5.1 Genetics

According to Blakey [34], different avocado cultivars have differing sensitivity to cold damage. However, to our knowledge, there are no studies reporting differences in ripening heterogeneity of different avocado cultivars.

5.2 Pruning

Avocado ripening is affected by its distribution within the tree. There exists a direct and proportional relationship between the height of the fruit in the tree and the time to reach edible ripeness, contributing to the postharvest ripening heterogeneity observed even within a tree. The highest part of the tree is exposed to more radiation, thus correct canopy management is important in order to harvest homogeneous fruits of high quality [46]. Differences of 15−20 °C in pulp temperature have been reported for sun-exposed avocados compared with non-sun-exposed fruit in five different cultivars including 'Hass' [56]. Sun-exposed fruit accumulated more dry matter than non-sun-exposed fruit but ripened more slowly and had a longer shelf life. This exposure to high temperatures during growth had similar effects to postharvest heat treatments on avocados [56], resulting in the induction of heat shock proteins.

Application of chilling stress to the avocado tree resulted in induction of ethylene and faster ripening [57].

Even though pruning is key to enable light entrance in the tree, care must be taken as to its timing. Excessive pruning close to or during fruit set can stimulate vegetative growth, with consequences on fruit load, firmness and eventual ripening [46].

5.3 Irrigation:water relations

Irrigation has numerous effects on the physiology and quality of fruit. Water deficit has been reported to be the most important factor involved in the variable ripening of avocado fruit [58]; probably due to the link between pre- or postharvest water stress and the accumulation of ABA [59, 60]. A study examined the effect of ABA or water infusion on ripening of 'Hass' avocados [12]. ABA infusion hastened ripening but had no effect on ripening heterogeneity, while water infusion reduced the variable ripening of middle and late season fruit.

Water availability and the transpiration rate are essential for calcium accumulation and this nutrient has been associated with fruit firmness [34]. However, in 'Hass' avocado no correlation was found between the fruit ripening time and total calcium content in the mesocarp at harvest [13]. Perhaps if calcium associated with the cell wall were analyzed a correlation with fruit firmness and the time to reach edible ripeness would be established. The soil moisture content at the time of harvest has been reported to affect the ripening rate of 'Hass' avocados, with postharvest ripening heterogeneity being more severe in inefficiently irrigated orchards during relatively dry seasons. Soil analysis of orchards displaying more variable ripening revealed a more irregular silt and clay content. This variation affects the water retention capacity and may be related to the observed ripening heterogeneity [61].

5.4 Nutrition

'Hass' avocado nutritional demand is generally low and the fertilization strategy employed in Chile is based mainly on soil application of nitrogen, boron and zinc [46]. The postharvest quality of the fruit is primarily affected by calcium, and secondly by nitrogen and boron [46]. Calcium is tightly linked to avocado fruit firmness and physiological disorders (*e.g.*, pulp and vascular browning), in addition to the load level and fruit distribution, that also influence firmness [62]. Different levels of calcium in the fruit have been associated with a delay in ripening due to an effect on respiration and retardation of the ethylene peak [46]. Calcium absorption and transport to the fruit is very limited since it is only absorbed by the new root caps and its transport is *via* xylem vessels by passive flow impulse through evapotranspiration of the leaves. Thus, xylem vessels feed the fruits during the first stages of development and if calcium availability is low, the calcium content of the fruit will be low [62]. In addition, tree vigor influences the availability of calcium in the fruit. As the tree vigor increases, the calcium content of the fruit decreases, with some differences observed between cultivars [62].

The use of different rootstocks has been associated with diverse outcomes in terms of calcium content in avocado fruit. Trees of the avocado cv. Fuerte on Guatemalan rootstocks tend to display higher levels of calcium in leaves than the Mexican rootstocks. Higher levels of calcium in leaves imply that when the fruit becomes the main sink of the plant, the fruit will end up with more calcium accumulation [46]. Studies related to individual fruit calcium content and ripening rate are limited. To our knowledge, no correlation between total calcium in avocado pulp at harvest and days to reach edible ripeness has been reported [13]. Studies which focus on calcium associated with the cell wall are not available. Thus, cell wall calcium differences within fruits and different orchards due to differences in fertilization and cultural practices might be one more factor associated with the observed postharvest ripening heterogeneity.

Nitrogen, the second most important mineral in avocado nutrition, plays a fundamental role at the structural level. An excess of nitrogen fertilization induces the activation of cytokinins that inhibit the production of ethylene and ABA. The inhibition of these phytohormones related to ripening causes an imbalance between the vegetative growth and fruit together with a delay in ripening, and may induce physiological disorders such as pulp browning. On the other hand, nitrogen deficit leads to premature foliar senescence, that results in small fruit and susceptibility to sunburn [62, 63]. Mesocarp avocado tissue nitrogen levels lower than 1% in January (approximately 4 to 5 months after fruit set and 4 to 5 months before harvest) are used in South Africa as a good indicator of the potential quality of the fruit during the postharvest period [64, 65].

Ninety-five percent of total boron is present in the cell wall and it is associated with cell wall structure. In Chilean orchards, this nutrient is commonly found in insufficient quantities [46]. A deficit of boron has been associated with faster ripening of avocados after harvest [66, 67] and similarly to the cell wall-associated calcium, boron differences might be one more factor contributing to the observed ripening heterogeneity.

5.5 Growth regulators

Growth regulators are commonly used to control vegetative growth and to improve the fruit growth in relation to the leaves. Plant growth regulator strategies to increase 'Hass' avocado yield and size have been tested in multi-year experiments [68]. Gibberellic acid (GA3) at a dose of 25 mg L^{-1} applied at the cauliflower stage of inflorescence development or at the end of June or beginning of July increased total yield and fruit size.

The high levels of gibberellins in the plant tissue that result in heavy growth during the vegetative growth phase are controlled by gibberellin inhibitors such as paclobutrazol and uniconazol [49]. The use of Uniconazol-P (Sunny®) in commercial 'Hass' avocado orchards is common practice to control vegetative growth and increase size fruit and yield [69], but might cause unbalanced calcium and other nutrient assimilation and distribution displaying a role in the observed postharvest ripening heterogeneity. The direct effect of the exogenous application of plant growth regulators on avocado postharvest ripening heterogeneity has not been documented so far.

5.6 Comprehensive studies

As far as we have been able to ascertain, only one study carried a very complete analysis of more than 90 preharvest factors related to environmental and growing conditions and cultural practices for 'Hass' avocados grown in Chile [46]. A total of 42 different orchards from very contrasting locations were sampled. In general, orchards located on the coast had a shorter postharvest life in terms of firmness than the ones located on the hills. A multifactorial analysis was needed to explain the variations during postharvest ripening (*e.g.*, loss of firmness and thus postharvest storage life, incidence of disorders, etc.) with at 9−10 preharvest factors needed to rank an orchard as good or bad quality producing fruit in terms of storage capacity and development of physiological disorders. Days from flowering to harvest, total flesh calcium content, N/Ca^{2+}, altitude, dry matter, the Ca^{2+}/K ratio, and medium temperature were classified as the main factors determining the postharvest performance of the fruit. It is important to note that "dry matter" only ranked as number five, supporting previous statements that dry matter alone cannot be used to predict and control postharvest ripening heterogeneity [13].

6 Postharvest factors involved in ripening heterogeneity

6.1 Temperature

To extend the shelf life and/or the periods of commercialization of 'Hass' avocado, the fruit is stored at temperatures within the 5−7 °C for early- and middle-season fruit and 4.0−5.5 °C for late-season fruit with a limited storage life of 4−6 weeks [70]. Improvements in storage methods have recently been reported to extend the shelf life of 'Hass' avocados [70–72]. However, regarding heterogeneity it appears that regular cold storage is best. After cold storage at 5 °C for 30 days, 'Hass' avocado batches from different growers at two maturity stages (early and middle with 23% and 26% DM, respectively) presented a lower ripening heterogeneity compared with controlled atmosphere (4 kPa O_2 and 6 kPa CO_2 at 5 °C) and 1-MCP-treated batches [73]. Even though cold storage alone reduces the ripening heterogeneity, for export countries that need to reach distant markets, a combination of cold storage and controlled atmosphere is utilized. The apparent ripening synchronization of 'Hass' avocados under cold storage and the mechanism involved have not been studied in details; however, increased enzyme activity is observed after cold storage, which explains in part why stored fruit ripen faster than non-stored fruit [74].

6.2 Controlled atmosphere (CA) and modified atmosphere packaging (MAP)

In general, conditions of 2−5 kPa O_2 and 3−10 kPa CO_2 are employed to transport avocados over long distances with the main objective of reducing respiration and ethylene production and delaying ripening. In addition, the high carbon dioxide concentrations are used to reduce chilling damage and further retard respiration. However, concentrations of CO_2 higher than 10 kPa induce skin decoloration and off-flavors if the concentration of oxygen is below 1 kPa [71]. Cold storage in combination with CA is used to transport avocados overseas. Regarding ripening, differences have been reported between the classical static controlled atmosphere (SCA) in which the oxygen concentration is kept constant and dynamic controlled atmosphere (DCA) in which the conditions are modified based on the behavior of the fruit during storage [75]. DCA-stored avocado fruit (dry matter > 30% from 4 different orchards) ripened faster than SCA-stored fruit and on average at the same time as air-stored fruit [75]. In another experiment, air-stored 'Hass' avocado fruit at 5 °C compared to SCA-stored 'Hass' avocado batches (4 kPa O_2, 6 kPa CO_2) with different ripeness stages (23 and 26% DM) presented in the first case approximately the same ripening spread or heterogeneity, but higher for middle-season fruit. These results were presented in a graphical way and no statistical analysis of variances was carried out [74]. The use of cold storage at 1 °C combined with modified humidity packaging (MHP) for 28 days was reported as appropriate for 'Hass' avocado storage, with reduced water loss and skin spotting compared to air-stored fruit. The MHP treatment resulted in a slight increase in days to ripen but regarding the efficacy of this treatment on reducing ripening heterogeneity, no results were reported [70].

6.3 Ethylene application

Ethylene treatments are generally used at destination markets to ripen the fruit and to deliver a high-quality and consistent product for the "triggered" fruit and "ready-to-eat" markets. Ethylene has been reported to significantly reduce the average ripening time of a batch [71], but regarding the ripening heterogeneity the results are contradictory. Application of ethylene at concentrations of 10−100 ppm at 17−20 °C for 24−72 h (early-season fruit), 24−48 h (middle-season fruit) and 12−24 h (late-season fruit) are recommended [71]. However, for fruit stored for 3−4 weeks the benefit of adding an ethylene treatment can be low [71]. For the South African 'Hass' avocado industry, ethylene treatments have not been successful in controlling the ripening pattern or heterogeneity, with some fruit displaying asynchronous ripening or a total lack of ripening, possibly due to impairment of the ethylene receptors, inhibition of the biosynthesis of the ripening enzymes or functioning of these enzymes [76].

6.4 1-MCP application

1-MCP treatments have been reported to delay the onset of ripening in 'Hass' avocado [71]. 1-MCP concentrations of 50−100 ppb at 6 °C for 18−24 h are recommended for 'Hass' avocado fruit previously stored for more than 4 weeks [71]. No major impact on the ripening heterogeneity of 'Hass' avocados treated with 1-MCP were reported by Woolf *et al.* [71] in comparison with non-treated fruit. However, [73] described

a more pronounced ripening heterogeneity in batches of early- and middle-season 'Hass' avocado fruits treated with 1-MCP for 12 h at 5 °C (concentration of 1-MCP not provided) in comparison with SCA-stored and fruit air-stored for 30 days.

6.5 Heat treatments

Phytosanitary disinfestation is required by certain avocado-importing countries. These quarantine treatments could be either cold or heat treatments. 'Hass' avocado exposed to different temperature and time combinations (36, 38 or 40 °C for 5, 15 or 30 min, respectively) before cold storage had a reduced spread or heterogeneity of ripening in early-, middle- and late-season fruits [76], but the physiological reasons remain unknown. Heat treatments have been associated with the synthesis of heat shock proteins, and according to Blakey and Bower [76] this situation would have been protected the fruit, and allowed normal ripening after cold storage removal. Another theory of how a heat shock treatment synchronizes ripening is that following the stress there is synthesis of the cell wall disassembly enzymes and/or induction of abscisic acid [76]. Further work is needed to understand the mechanisms involved in this ripening synchronization when a heat treatment is applied.

7 Non-destructive and semi-destructive phenotyping opportunities

Dry matter content is the current harvest index for avocados. Dry matter correlates very well with oil content and it is used to determine the minimum content of 9% oil needed to guarantee good eating quality. There are several investigations of the use of near-infrared spectroscopy (NIR) to classify fruit based on dry matter [12,77] and NIR systems are being implemented online in packing houses to sort fruit before shipping and potentially reduce the postharvest ripening heterogeneity. The use of NIR to reduce postharvest ripening heterogeneity has recently been challenged by Pedreschi *et al.* [13] since dry matter was found not to be highly correlated with time to reach edible ripeness in individual avocado fruits. However, segregation of fruit using NIR is a promising technology to guarantee good eating quality for consumers.

In order to implement a non-destructive technique to segregate fruit at the gate, it is necessary first to identify suitable markers for early prediction of this postharvest ripening heterogeneity. In order to implement postharvest treatments to synchronize the ripening process of individual fruits within a consignment, it is necessary to understand the metabolic processes involved in the postharvest ripening synchronization process.

8 Post-genomic approaches to understand avocado postharvest ripening heterogeneity

Understanding the physiology (*e.g.*, at the biochemical level and at the different levels of cellular control) involved

in a particular 'quality trait' is key to improving and optimizing current storage technology. Avocado physiology is very complex. After more than 60 years of research on avocado there are still unanswered questions, including postharvest performance, and particularly postharvest ripening heterogeneity. Post-genomic platforms (*e.g.*, transcriptomics, proteomics and metabolomics) can be very useful tools not only to understand the mechanisms but to find "markers" to implement in practice.

Despite the economic importance of avocado, its genome is not publicly available and only limited sequence data exists (16,620 ESTs and 1,093 protein sequences are available in the NCBI database). Recently, Reeksting *et al.* [78] reported the massive sequencing of the root transcriptome of avocado exposed to *Phytophthora cinnamomi* and flooding using new generation sequencing platforms. The sequencing data generated is available at the NCBI database. Additionally, the transcriptome of *Persea americana* var. drymifolia for six different organs and three ripening stages has recently been published [79]. A total of 67,000 unigenes were annotated, allowing the identification of 34,128 proteins [79]. The data generated suggested that oil accumulation and fatty acid composition ceased as the fruit initiates ripening. Another high-throughput transcriptome analysis related to the oil biosynthesis in the avocado mesocarp has been released [80] and also constitutes a valuable tool for understanding the fatty acid metabolism of avocado fruit that seems to be involved in variable ripening [13].

To our knowledge, the only study on avocado postharvest ripening heterogeneity and on understanding the mechanisms involved is the one carried out by [13] but currently with more genome and transcriptome resources available for *Persea americana*, gaining more understanding of this avocado fruit's variable ripening seems feasible. Fruit biopsy sampling has previously been used on individual fruits to control the variability [3,81], even though previous sampling approaches did not seem to be optimal [13]. Fruit biopsy combined with functional post-genomic approaches (*e.g.*, transcriptomics, proteomics, metabolomics) are powerful platforms to understand the metabolic events involved in the postharvest ripening heterogeneity of 'Hass' avocados.

9 Conclusions and perspectives

The observed variable ripening or postharvest ripening heterogeneity in 'Hass' avocado is the result of its complex fruit physiology, and preharvest and postharvest factors. Fruits of very different ages hang on the tree, since the fruit cannot ripen on the tree. At harvest, fruit quality measurements of color, firmness and dry matter cannot predict the postharvest variable ripening. Previous work carried out on the topic has challenged the role of C_7 sugars as ripening inhibitors and as a potential trigger of ripening in avocado. However, new information is available in relation to the potential role of fatty acid, amino acid and cell wall metabolism being involved in this trait.

Postharvest treatments such as heat, cold and modification of the atmosphere seem to contribute to the synchronization of avocado ripening. Understanding the biochemical and molecular mechanisms involved in such synchronization would be

useful for practical implementations. Using NIR for determining dry matter/oil combined with looking at genes involved in calcium transport and/or action (*i.e.* calmodulin, Ca-ATPase) might be one direction to follow.

With the current available genomic resources recently released for *Persea americana* and non-destructive techniques to measure certain quality attributes, there are opportunities to understand the mechanisms involved in this observed variable ripening and the implementation of practical procedures to induce ripening synchronization after a proper classification of fruit based on their ripening capacity.

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