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RESEARCH ARTICLE

Variations in mango fruit quality in response to management factors on a pre- and post-harvest continuum

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Summary

Fruit quality is a key factor – beginning with the producer, continuing through the supply chain, and ending with the consumer. It is described by multiple indicators and varies during the growth and ripening of the fruit. This study focused on two main aspects of Cogshall mango (*Mangifera indica* L.) quality: (i) the physical properties of the fruit with fresh mass (FM), pulp dry matter content (DMC), and pulp coloration; and (ii) the chemical properties with pulp sugar content and pulp acidity. These indicators were monitored on on-tree fruit, from about 60 days after bloom until full maturity. The same indicators were also monitored on fruit stored in cold storage rooms during ripening. The effects of leaf-to-fruit ratio (manageable by pruning or fruit thinning), maturity stage of fruit at harvest (manageable by harvest date), and storage temperature on the kinetics of quality traits of on-tree and stored fruit were assessed. In addition, a change-point analysis was applied to the sweetness index kinetics (used as a proxy of fruit ripening) to study fruit ripening induction. The leaf-to-fruit ratio mainly influenced fruit growth in terms of FM and pulp DMC, whereas it had less impact on the evolution of fruit chemical properties. The maturity stage of the fruit at harvest was a key factor in determining the potential quality at the ripe stage. Ripening occurs naturally at the mature green stage for on-tree fruit, but ripening at an earlier stage can be induced by harvesting the fruit. During the ripening phase, a low leaf-to-fruit ratio and a cold storage temperature tended to slow down the daily rate of sweetness increase. The use of cold temperatures during storage slowed down starch degradation and sucrose accumulation, while almost stopping the variation in fruit coloration and acidity.

Keywords: Leaf-to-fruit ratio; Maturity stage; Ripening

Introduction

Mango (*Mangifera indica* L.) is the fifth leading fruit produced in the world and the tonnage exported has been steadily increasing for several decades (FAOSTAT, 2021). The importance of fruit quality has also increased, and improving fruit quality management has become a key issue.

The quality of any fruit can be estimated using a wide range of indicators, from physical properties (e.g., size, shape, color) to chemical properties (e.g., sugars, acids, polyphenols). The taste quality of a fresh fruit is strongly related to the sweetness of the fruit, which reflects the perceived sweet taste of the sugars contained in the fruit. In fruit that accumulates soluble sugars,

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notably fructose and sucrose, sweetness increases over time, especially during the ripening and climacteric syndrome (Beckles, 2012; Mashilo *et al.*, 2022). Brix analysis is a simple and common way to measure the total soluble solids content in the pulp (Magwaza and Opara, 2015), which correlates well with total sugar content, especially in ripe fruit. Brix is generally used to define standard requirements for fruit marketing and inter-professional agreements. However, perceived sweetness does not correlate very well with this Brix indicator (Aprea *et al.*, 2017). Indeed, the perceived sweetness does not only depend on total sugar content but also and especially on the internal balance and sweetness properties of the different soluble sugars. The sweetness index, calculated on the basis of the content of each soluble sugar weighted by a sugar-dependent sweetness coefficient, would therefore be a more accurate indicator of sweetness perception (Magwaza and Opara, 2015). Another factor involved in fruit taste quality is fruit acidity (Aprea *et al.*, 2017; Borsani *et al.*, 2009). Fruit acidity can be estimated using various approaches and indicators, from simple pH measurements to measurements of individual acid levels. Total titratable acidity (TTA) is a commonly used indicator of fruit acidity that gives more complete information than pH without requiring the measurement of all of the acids (Lobit *et al.*, 2002). The balance between acidity and soluble sugars is probably one of the most important aspects of fruit taste quality. The quality of a fruit is also assessed by various external and physical properties such as fruit shape, mass, and color. The fresh mass (FM) of the fruit is a crucial aspect of fruit quality and is of great importance for marketing since it is used to classify the fruit into size categories. The color of the skin and pulp are also important points to consider when assessing the visual quality of the fruit. Finally, the dry matter content (DMC) of the pulp, i.e., the ratio of dry mass to FM of the pulp, is used as an index of internal (Gamble *et al.*, 2010; McGlone *et al.*, 2003) and textural (Palmer *et al.*, 2010) quality.

The key factors of the final quality of the fruit, i.e., when they are ready for consumption, are their growing conditions in the field and, for those harvested before maturity and stored, their quality at harvest (Ceccarelli *et al.*, 2019; Léchaudel and Joas, 2006). In the field, fruit are exposed to constantly changing environmental conditions (e.g., water availability, temperature, light exposure, etc.). Environmental and agronomical factors each play an important role in plant physiology and the development of fruit quality (Bertin and Génard, 2018; Musacchi and Serra, 2018). Agricultural practices can either modify environmental conditions, for example, by providing water through irrigation, managing light penetration through tree pruning, or the preferential selection of shaded or light-exposed fruit during thinning, or they can modify physiological processes at the plant and fruit scale. Fruit thinning is a practice commonly used to improve fruit growth by increasing the availability of carbohydrates to the fruit by changing the source/sink relationships. It is used to increase fruit size and to ensure better overall quality of the harvested fruit (Léchaudel and Joas, 2006). The age of the fruit at harvest is a critical point in fruit quality control. Early harvest can reduce fruit size and quality, while late harvest can reduce shelf life (Léchaudel and Joas, 2006; Minas *et al.*, 2018). In addition, fruit harvesting deeply alters carbohydrate metabolism, ethylene emissions, and respiration of fruit, and induces changes in fruit texture and color. After harvest, fruit storage conditions (e.g., temperature, humidity, atmospheric composition) are more easily controllable than these factors on the tree and could be managed not only to increase storage time but also to control the fruit ripening process (Léchaudel and Joas, 2006; Lufu *et al.*, 2020). These conditions can either allow the quality of the harvested fruit to be fully expressed if they are well controlled or deteriorate the overall quality if they are not. While the effects of pre- and post-harvest factors have been widely studied, only a few studies have reported on the combined impact of pre-harvest agricultural practices and post-harvest storage conditions on the ripening process and the multi-faceted development of fruit quality along the pre- and post-harvest continuum (Khakpour *et al.*, 2022; Léchaudel and Joas, 2006).

The first objective of the study was to identify and quantify the effect of leaf-to-fruit ratio (used as a proxy of carbohydrate availability), maturity stage (or fruit age) at harvest, and storage temperature on the kinetics of a wide range of quality traits of on-tree and stored mango fruit. In order to assess the multiple facets of fruit quality, the following quality traits were monitored: fruit FM, pulp DMC, content of the four main carbohydrates (starch, sucrose, fructose, and glucose), TTA, and pulp color. The second objective of the study was to assess the effect of the previous management factors on the induction of fruit ripening and, more specifically, to provide information to support the hypothesis of harvest-induced forced fruit ripening.

Materials and Methods

Plant material and experimental treatments

Data were collected during two fruit production seasons, in 2017 and 2018, in two mango tree orchards (cultivar 'Cogshall' grafted onto 'Maison Rouge' rootstock) located on Reunion Island. The first orchard (orchard A) is an experimental orchard located at the CIRAD (French Agricultural Research Center for International Development) research station in Saint-Pierre. The second orchard (orchard B) is a commercial orchard located in Saint-Gilles-les-Bains. Both were well irrigated and managed according to standard commercial practices. Climatic conditions are described in Supplementary Materials (Fig. S1).

In orchard A, two leaf-to-fruit ratio (LF) treatments were applied at 58 ± 1 days after bloom (DAB) on girdled branches of about 10 mm in diameter and relatively well-exposed to light. It was assumed that cell division was complete and that the number of cells was fixed at that time, so that the growth of the fruit was solely due to cell expansion (Léchaudel *et al.*, 2005a). Girdling isolates the branch from the tree and ensures that the only source of carbohydrate for the fruit is provided by photosynthesis of the branch leaves. The two LF ratios were 100 leaves per fruit (LF100) to simulate a high (potentially nonrestrictive) fruit carbohydrate supply, and 25 leaves per fruit (LF25) to simulate a severely restricted supply. For pre-harvest monitoring, about 30 fruit of each LF ratio treatment were regularly sampled on the trees, starting from about 60 DAB up to fruit maturity at 137 ± 12 DAB. For post-harvest monitoring, two fruit samples were collected at two different stages of maturity (Stage). The first stage, referred to as green (G), corresponds to immature fruit harvested at 93 DAB. The second stage, referred to as mature green (MG), corresponds to fruit harvested at 110 DAB. MG fruit are physiologically mature but not yet ripe. These two stages are generally used when there is a need for transport and storage time for marketing the fruit. Since changes in chlorophyll activities begin to occur in the MG stage, the two stages – both with green skin – could be differentiated nondestructively using chlorophyll fluorescence (Léchaudel *et al.*, 2010). Chlorophyll fluorescence of the fruit peel varied between 800 and 950 for MG fruit and 1000–1200 for G fruit. Four batches of 30 fruit were harvested for each combination of the two stage × two LF ratio modalities. From each batch of fruit, three fruit were used for analysis at harvest, and the remaining fruit were randomly assigned to two storage temperature treatments (Temperature). The first, referred to as 20°C, corresponded to storage of the fruit at 20°C for 15 days, simulating the storage conditions of mangoes intended for the local market. The second, referred to as 12°C, corresponded to storage of the fruit at 12°C for 18 days, simulating the storage conditions during transport of mangoes intended for export. The relative humidity in the storage rooms was maintained between 74% and 96% for both temperature treatments. During storage, three fruit were regularly sampled at random for analysis. The experiment was conducted in orchard A during two production seasons (2017 and 2018) for the pre-harvest study (treatments: LF (25 and 100)), and only during one production season (2018) for the post-harvest study (treatments: LF (25 and 100) × Stage (G and MG) × Temperature (12°C and 20°C)).

In orchard B, the LF ratio treatment was not applied. Since the fruit-bearing branches were not isolated from the rest of the tree, it was assumed that the carbohydrate supply to the fruit was not (or only slightly) restrictive. Fruit were harvested at G and MG maturity stages (at 94 and 103 DAB, respectively), randomly assigned to the two storage treatments (12°C and 20°C), and regularly sampled for analysis, as described for orchard A (except that fruit were stored for only 12 ± 1 days at 20°C). The experiment was conducted in orchard B only during one production season (2017) and exclusively for the post-harvest study (treatments: Stage (G and MG) × Temperature (12°C and 20°C)).

Measurements of fruit quality

The fruit quality traits measured on fruit were fruit FM(g), pulp color described using hue angle (hue angle, °), pulp TTA (meq.100 gFM^{-1}), pulp soluble sugars and starch content (sucrose, glucose, fructose and starch, $g.gFM^{-1}$), and pulp DMC ($gDM.gFM^{-1}$). All fruit were destructively analyzed according to a unique protocol, starting with the random sampling of fruit in the orchard or the storage rooms. The fruit were first weighed to measure their FM. They were then peeled, the pulp removed, and the stone scraped with a knife to remove any remaining pulp. The peel and stone were weighed and the pulp mass was calculated as the difference between the fruit mass and the peel and seed masses. The pulp was sliced to expose a flat section on both sides of the fruit on which CIELAB coordinates (L*, a*, b*) were measured using a chromameter (Minolta CR-400). Hue angle was calculated from CIELAB coordinates (McLellan *et al.*, 1995). A fruit with a hue angle of about 90° is yellow, and its hue tends toward yellow-green as the value increases, and toward yellow-orange as it decreases. Lastly, pulp samples were placed in liquid nitrogen and ground into a fine powder that was stored at −80°C for future chemical analysis. The TTA was measured on 2 g of pulp powder mixed with l8 mL of water, using an automatic titrator (TitroLine@ 5000, SI Analytics) with a 0.05 mol L^{-1} NaOH solution. Another fraction of the powder was placed in an oven at 60°C for 72 hours to measure the DMC. Finally, the rest of the powder was freeze-dried and used for titration of soluble sugars and starch using micro-plate array (Gomez *et al.*, 2007). In this study, fruit that were destructively analyzed on the day of harvest were referred to as ‘on-tree’ fruit. All other fruit analyzed after a period of storage were referred to as ‘stored’ fruit.

Statistical analysis

Effect of management factors on the kinetics of quality traits of on-tree and stored fruit

The first analysis aimed to assess the effect of pre- and post-harvest management factors on the kinetics of fruit quality traits (i.e., the response variables). The following factors were tested: (i) LF ratio on on-tree fruit (pre-harvest study in orchard A in 2017 and 2018); (ii) maturity stage at harvest and storage temperature on stored fruit (post-harvest study in orchard B in 2017); and (iii) LF ratio, maturity stage at harvest and storage temperature on stored fruit (post-harvest study in orchard B in 2018). First, the maximum likelihood-like approach of Box and Cox (Box and Cox, 1964) was applied to each response variable in order to test and, when required, select a power transformation of the variable to conform with normality and homoscedasticity. The kinetic of fruit quality traits was then fitted using generalized additive models (GAMs), with the restricted maximum likelihood method (Wood, 2004). GAMs are generalized linear models in which the response variable is linearly dependent on non-parametric smooth functions of covariates plus, possibly, parametric terms. In this study, the fitted GAMs comprised smooth functions of time, representing the trend in the response for each combination of factor modalities, and parametric terms associated with the effect of each factor (including their main and interaction effects). Time was expressed in DAB for the pre-harvest study and in days after harvest (DAH) for the post-harvest study. Smooth functions were parameterized using thin-plate regression splines (Wood, 2003). Their degree of smoothness was determined automatically while leaving the possibility to be manually constrained to avoid excessive smoothness. Finally, Wald tests of the significance of each parametric and smooth term were performed, allowing for an assessment of the overall effect of management factors over time and the treatment-specific effect of time on the response variables.

Effect of management factors on the induction of fruit ripening

The second analysis aimed to assess the effect of management factors on the induction of fruit ripening and, more specifically, to test the hypothesis of harvest-induced forced ripening of stored fruit compared to the on-tree fruit. The sweetness index was considered a proxy of fruit ripening. Fruit sweetness (g eq. sucrose gFM^{-1}) was calculated based on the content of each soluble sugar weighted by the sweetness rating relative to sucrose of each sugar, as follows: $Sweetness = 1 \times Sucrose + 1.75 \times Fructose + 0.77 \times Glucose$ (Génard and Souty, 1996). The sweetness index was assumed to evolve into two distinct monotonic phases: (i) an almost stationary phase when carbohydrates were stored as starch; and (ii) an increasing phase when the climacteric syndrome and ripening began, resulting in starch degradation and the rapid accumulation of soluble sugars. Therefore, sweetness index kinetics were analyzed with a change-point regression model with two linear and joined segments, as follows:

$$Sweetness = \begin{cases} \alpha_1 + \beta_1(DAB - DAB_0), & \text{if } DAB < cp \\ \alpha_1 + \beta_1\left(cp - DAB_0\right) + \beta_2\left(DAB - cp\right), & \text{if } DAB \geq cp \end{cases} \tag{1}$$

where α_1 (g eq. sucrose gFM^{-1}) is the intercept of the first segment representing the initial value of sweetness at $DAB_0 = 59$ DAB, β_1 and β_2 (g eq. sucrose $gFM^{-1}.DAB^{-1}$) are the slopes of the first and second segments representing daily rates of sweetness increase, and cp (DAB) is the change-point date, i.e., the date when the sweetness kinetics switch from the first to second phase.

The regression model (Equation 1) was fitted on pre- and post-harvest data collected in orchard A during the 2018 production season, for each of the ten treatments defined by the combination of factor modalities (i.e., two LF modalities for on-tree fruit and eight LF × Stage × Temperature modality combinations for stored fruit). Parameter α was set at 0.028 (±0.0064) g eq. sucrose gFM^{-1}, which is the mean (±SD) value of sweetness measured at 59 DAB. For on-tree fruit, parameters β_1, β_2, and cp were first estimated for each of the two LF treatments. For stored fruit, parameters β_2 and cp were estimated for each of the eight LF × Stage × Temperature treatments, while β_1 was set at the value estimated on on-tree fruit subjected to the same LF treatment. This is because before being harvested, the stored fruit shares the same kinetics (and data) as the on-tree fruit. A Bayesian computational approach, which correctly quantifies the uncertainty around the change-points in contrast to non-computational methods (Lindeløv, 2020), was used for the change-point regressions, and 30 000 posterior samples were returned for all model parameters. The posterior samples allow parameter estimates (defined as the posterior means) to be calculated, and parameters to be compared between treatments using a distribution-free overlapping index η and a probability of superiority estimator A. η, which is normalized between 0 and 1, quantifies the similarity (η close to 1) or difference (η close to 0) between two samples by measuring the area intersected by their probability density functions (Pastore and Calcagnì, 2019). A is a non-parametric and robust statistic indicating the probability that a randomly sampled value from one distribution is higher than a randomly sampled value from a second distribution (Ruscio, 2008). Parameters cp and β_2 were compared (i) between stored and on-tree fruit (for each of the eight LF × Stage × Temperature treatments); (ii) between fruit stored at 20°C and 12°C (for each of the four LF × Stage treatments); and (iii) between LF100 and LF25 fruit (for on-tree fruit and for each of the four Stage × Temperature treatments of stored fruit).

All analyses and plots were generated using R software, v.4.0.4 (R Core Team, 2021). The Box-Cox tests were performed using the *powerTransform()* function of the *car* package (Fox and Weinsberg, 2019). GAMs were built using the *gam()* function of the *mgcv* package (Wood, 2017). The change-point analysis was performed using the *mcp()* function of the *mcp* package (Lindeløv, 2020). The overlapping indexes and the probabilities of superiority were estimated using the *overlapping* (Pastore *et al.*, 2022) and *RProbSup* (Ruscio, 2020) packages, respectively.

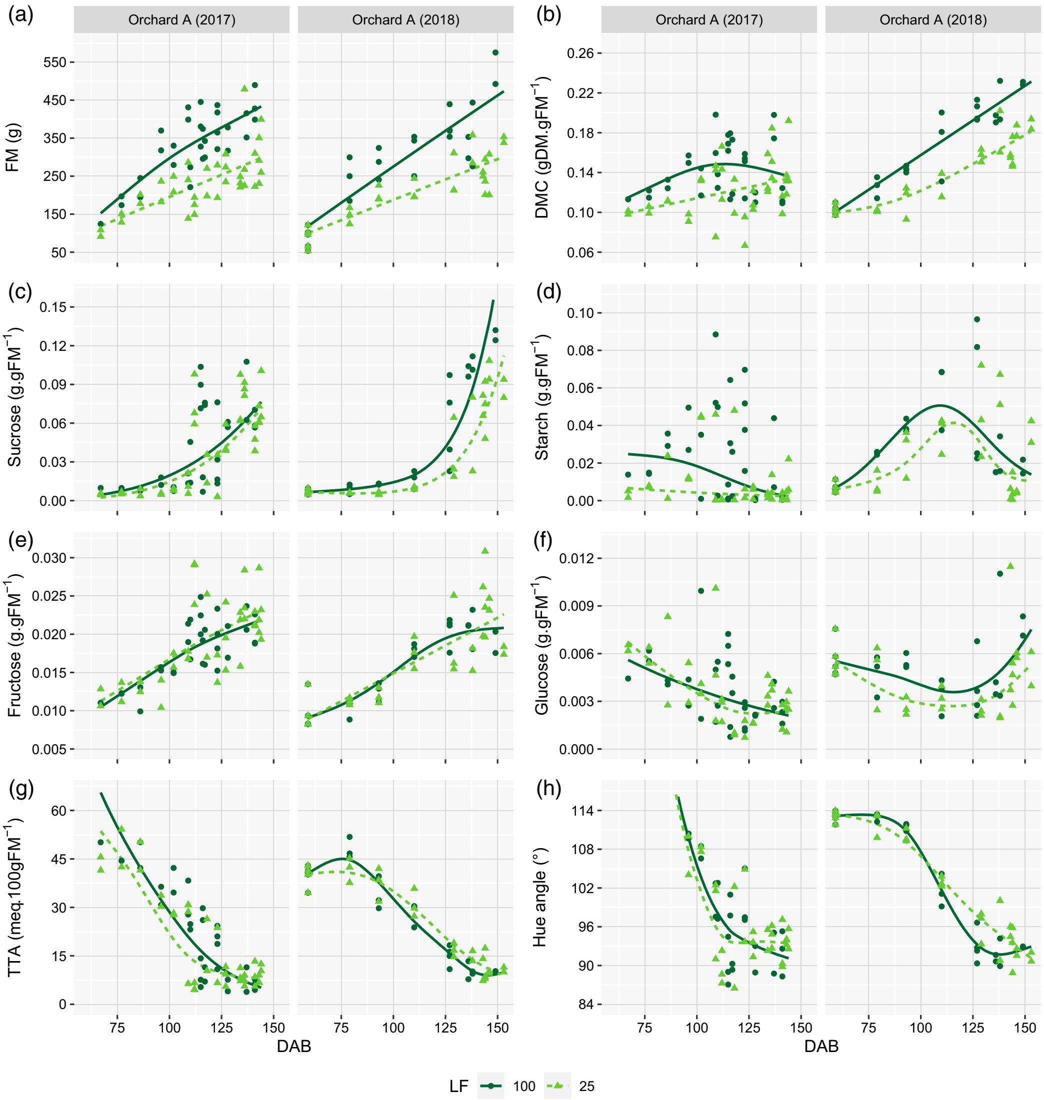

Figure 1. Kinetics of mango fruit fresh mass (a), pulp dry matter content (b), sucrose (c), starch (d), glucose (e) and fructose (f) contents in the pulp, total titratable acidity of the pulp (h), and pulp color characterized by hue angle (i) of on-tree fruit according to the leaf-to-fruit ratio (LF25, LF100), during the 2017 and 2018 production seasons in orchard A. Time is expressed in days after bloom (DAB). Points are measured values (one point represents one fruit) and curves are generalized additive model predictions.

Results

Effect of leaf-to-fruit ratio on the kinetics of quality traits of on-tree fruit

The kinetics of quality traits of on-tree fruit sampled in orchard A during the 2017 and 2018 production seasons are shown in Fig. 1. The effects of LF and time (expressed as DAB) on those quality traits are summarized in Table 1.

Fruit FM in both production seasons and pulp DMC in 2018 significantly increased with DAB, from about 100–120 g and 0.10 gDM.gFM^{-1} at 60 DAB to 300–470 g and 0.18–0.23 gDM.gFM^{-1}at full maturity (Fig. 1a, b). The increase was significantly greater for fruit with high LF ratios that reached up to 57% more FM and 27% more DMC than fruit with a low LF ratio. In 2017, the

Table 1. Wald test *p*-values indicating the statistical significance of the effect of time in days after bloom (DAB) and the effect of leaf-to-fruit ratio (LF) on quality traits of on-tree fruit sampled in orchard A during the 2017 and 2018 production seasons

	Orchard A (2017)		Orchard A (2018)	
Variable (unit)	**DAB**$^{\#}$	LF	**DAB**$^{\#}$	LF
FM (g)	<0.001	<0.001	<0.001	<0.001
DMC (gDM.gFM^{-1})	0.19; <0.05	<0.01	<0.001	<0.001
Sucrose (g.gFM^{-1})	<0.001	0.26	<0.001	<0.001
Starch (g.gFM^{-1})	0.06; 0.25	<0.05	<0.001; <0.01	0.07
Fructose (g.gFM^{-1})	<0.001	0.44	<0.001	0.95
Glucose (g.gFM^{-1})	<0.05; <0.01	0.64	0.11; <0.05	<0.05
TTA (meq.100 gFM^{-1})	<0.001	0.46	<0.001	0.26
Hue angle (°)	<0.001; <0.01	0.91	<0.001	0.10

[#] A *p*-value was generated for each of the two LF modalities. The two *p*-values, for LF100 and LF25, respectively, are reported when they are different. Otherwise, only the common *p*-value is reported.

increase in DMC with DAB was slower (LF25) or even not significant (LF 100). The kinetics of DMC observed in 2018 were consistent with those observed in a previous study (Léchaudel *et al.*, 2005b), suggesting that those observed in 2017, associated with high DMC variability, may be unusual.

Sucrose and fructose contents significantly increased with DAB during both production seasons (Fig. 1c, e). Starch content showed significant bell-shaped kinetics in 2018: it increased from 60 to 109 (LF100) and 116 (LF25) DAB, when it reached 0.05 (LF100) and 0.04 (LF25) g.gFM^{-1}, and then decreased (Fig. 1d). In 2017, starch showed high variability and the bell-shaped kinetics were not clearly observed. Glucose content significantly decreased with DAB in 2017, whereas in 2018, it decreased from 60 to 115 DAB and then increased (Fig. 1f). Fructose was not significantly affected by the LF ratio, while fruit with high LF ratios had significantly (or marginally) higher starch content in both production seasons, and significantly higher sucrose and glucose contents in 2018 than fruit with a low LF ratio. Sucrose was the main soluble sugar in the fruit. Its content reached about 0.07–0.15 g.gFM^{-1} at full maturity, whereas fructose and glucose contents were overall <0.025 g.gFM^{-1} and <0.008 g.gFM^{-1}, respectively.

During both production seasons, TTA and pulp color, characterized by hue angle, showed a similar pattern: they sharply decreased with DAB and were not significantly affected by the LF ratio (Fig. 1g, h). TTA decreased from >40 meq.100 gFM^{-1} at 60 DAB to 5–10 meq.100 gFM^{-1} at full maturity. The pulp color changed from light green (hue angle = 110–115°) at 60 DAB to a slightly yellow-orange color at full maturity (hue angle = 90–95°).

Effect of leaf-to-fruit ratio, maturity stage at harvest, and storage temperature on the kinetics of quality traits of stored fruit

The kinetics of quality traits of stored fruit sampled in orchard A during the 2018 production season and in orchard B during the 2017 production season are shown in Fig. 2. The effects of LF, maturity stage at harvest (Stage), storage temperature (Temperature), and time (expressed as DAH) on those quality traits are summarized in Table 2. The effect of the LF ratio was only tested in orchard A. No interaction terms were significant in orchard B (2017). In orchard A (2018), significant interactions were observed between Stage and LF for fructose content (*p*-value <0.05), between Stage and Temperature for TTA (*p*-value <0.05), and between all factors for glucose content. *P*-values of all the interaction terms are given in Supplementary Materials (Table S1).

In both orchards, fruit FM and pulp DMC remained broadly constant during storage, with values of around 170–360 g and 0.10–0.20 gDM gFM^{-1} (Fig. 2a, b). Although fruit lost an average

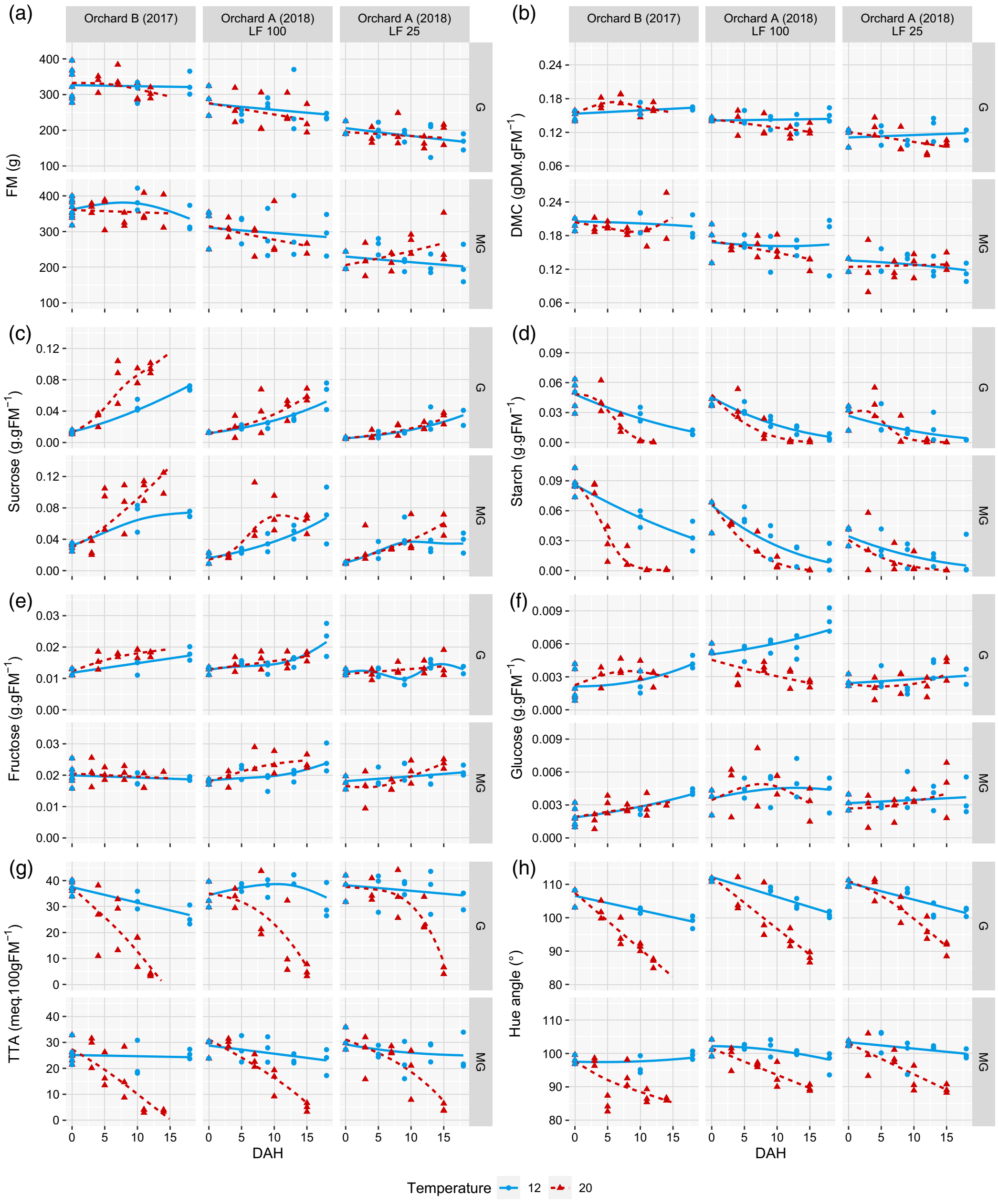

Figure 2. Kinetics of mango fruit fresh mass (a), pulp dry matter content (b), sucrose (c), starch (d), glucose (e) and fructose (f) contents in the pulp, total titratable acidity of the pulp (h), pulp color characterized by hue angle (i) of stored fruit according to the leaf-to-fruit ratio (LF25, LF100; in orchard A only), maturity stage at harvest (G: Green, MG: Mature Green) and storage temperature (12°C, 20°C) in orchard B during the 2017 production season and in orchard A during the 2018 production season. Time is expressed in days after harvest (DAH). Points are measured values (one point represents one fruit) and curves are generalized additive model predictions.

of 5.4% of their FM during storage, decreases in FM with DAH were not significant due to the large variability in initial FM between sampled fruit. Fruit harvested at the MG stage had significantly higher FM and DMC than those harvested at the G stage, and fruit with a high LF ratio (LF100) had significantly higher FM and DMC than those with a low LF ratio (LF25). In

Table 2. Wald test *p*-values indicating the statistical significance of the effect of time in days after harvest (DAH), and the main effect of leaf-to-fruit ratio (LF; in orchard A only), maturity stage at harvest (Stage), and storage temperature (Temp) on quality traits of stored fruit sampled in orchard B during the 2017 production season and in orchard A during the 2018 production season. *p*-values of all the interaction terms are given in Supplementary Materials (Table S1)

	Orchard B (2017)			Orchard A (2018)			
Variable (unit)	**DAH**[#]	Stage	Temp	**DAH**[#]	LF	Stage	Temp
FM (g)	ns	<0.01	0.83	ns[d]	<0.001	<0.05	0.48
DMC (gDM.gFM^{-1})	ns	<0.001	0.63	ns[e]	<0.001	<0.01	0.13
Sucrose (g.gFM^{-1})	< 0.001	<0.001	<0.01	<0.001	<0.001	<0.05	0.13
Starch (g.gFM^{-1})	<0.001	<0.001	<0.001	<0.01	0.08	0.10	<0.01
Fructose (g.gFM^{-1})	<0.01; ns[a]	<0.001	<0.05	<0.05; ns[f]	<0.001	<0.001	0.97
Glucose (g.gFM^{-1})	<0.05; ns[b]	0.87	0.49	ns[g]	<0.001	<0.01	<0.001
TTA (meq.100 gFM^{-1})	<0.01[c]	<0.001	<0.001	ns; <0.001[b]	0.93	<0.001	<0.001
Hue angle (°)	<0.01[c]	<0.01	<0.001	<0.001[h]	0.42	<0.001	<0.001

[#] A *p*-value was generated for each treatment, defined as the combination of the factor modalities. If *p*-values are different between some treatments, they are reported for each group of homogeneous treatments. Otherwise, only the *p*-value common to all (or almost all) treatments is reported.

[a]: G and MG treatments, respectively;

[b]: 12°C and 20°C treatments, respectively;

[c]: except for MG-12°C (ns);

[d]: except for LF25-MG-20°C (*p*-value < 0.05);

[e]: except for LF100-MG-20°C (*p*-value < 0.05);

[f]: LF100 and LF25 (except for LF25-MG-20°C; *p*-value < 0.01) treatments, respectively;

[g]: except for LF100-G-20°C (*p*-value <0.05);

[h]: except for LF100-MG-12°C and LF25-MG-12°C (ns). *p*-values of all the treatments are given in Supplementary Materials, Tables S2 and S3.

addition, fruit on non-girdled branches in orchard B had higher FM and DMC than those with a high LF ratio. Neither FM nor DMC was affected by storage temperature.

In both orchards, sucrose content significantly increased with DAH from about 0.005–0.03 g.gFM^{-1} at 0 DAH to 0.03–0.11 g.gFM^{-1} after storage (Fig. 2c), while starch content significantly decreased with DAH from about 0.03–0.09 to <0.01–0.03 g.gFM^{-1} (Fig. 2d). Sucrose was the main soluble sugar in the fruit since fructose and glucose contents were <0.025 g.gFM^{-1} and <0.007 g.gFM^{-1}, respectively (Fig. 2e, f). Depending on the treatment, fructose and glucose contents slightly increased with DAH or remained constant during storage. Fruit harvested at the MG stage had significantly higher sucrose and fructose contents and significantly (orchard B) or marginally (orchard A) higher starch content than those harvested at the G stage. Fruit with a high LF ratio had significantly higher sucrose, fructose, and glucose contents and marginally higher starch content than those with a low LF ratio, and slightly lower sucrose and starch contents than fruit on non-girdled branches. Fruit stored at 12°C had a significantly higher starch content than those stored at 20°C due to a slower decrease in starch content during storage. Conversely, fruit stored at 12°C had lower sucrose content (significant only in orchard B, although similar trends were observed in orchard A). The responses of fructose and glucose content to storage temperature and of glucose content to maturity stage did not show clear patterns, certainly due to their treatment-dependent temporal variations and interactions between factors.

TTA and pulp color, characterized by hue angle, showed a similar trend in both orchards. They strongly decreased with DAH for fruit stored at 20°C, while they only slightly decreased or remained constant during storage for fruit stored at 12°C (Fig. 2g, h). Consequently, the TTA and hue angle were significantly higher at 12°C than at 20°C. At 0 DAH, the TTA and hue angle were about 26–38 meq.100 gFM^{-1} and 98–112°, respectively. After storage, they decreased to 3–8 meq.100 gFM^{-1} and 86–91° for fruit stored at 20°C, but only to 23–34 meq.100 gFM^{-1} and 98–101° for fruit stored at 12°C. Pulp color of fruit after storage turned light orange for fruit stored at 20°C but remained light green for fruit stored at 12°C. TTA and hue angle were significantly affected by maturity stage at harvest in both orchards. At harvest, fruit harvested at the MG stage had lower TTA and hue angle values than fruit harvested at the G stage. After storage, these differences almost disappeared except for the TTA of fruit stored at 12°C. Neither TTA nor hue angle were significantly affected by the LF ratio.

Effect of leaf-to-fruit ratio, maturity stage at harvest, and storage temperature on the induction of fruit ripening

The kinetics of sweetness index and the values of the change-point dates (i.e., parameter cp in Equation 1) and daily rates of sweetness increase (i.e., parameters β_1 and β_2 in Equation 1) estimated on the ten treatments defined by the combination of factor modalities for on-tree and stored fruit are shown in Fig. 3.

For fruit harvested at the G stage, the low η (≤ 0.16) and high A (≥ 0.96) values for the change-point date clearly indicate that harvest induced earlier fruit ripening (Table 3). The ripening process started about 9–18 days earlier than for the fruit remaining on the tree. For fruit harvested at the MG stage, there was no harvest-induced ripening for LF100 fruit ($\eta \geq 0.64$ and $A \leq 0.61$) but an earlier ripening was assessed for LF25 fruit ($\eta \leq 0.41$ and $A \geq 0.82$), of 6 and 11 days when stored at 20°C and 12°C, respectively. However, the highest value was probably overestimated since the estimated cp value of 102.4 DAB for these fruit was well below the harvest date (i.e., at 110 DAB), which is supposed to induce ripening. After ripening induction, stored fruit had either lower or higher daily rates of sweetness increase than on-tree fruit, with no obvious pattern emerging. The largest variations were observed for fruit harvested at the G stage and stored at 12°C, with values 1.9 times higher for LF100 fruit ($\eta = 0.22$ and $A = 0.09$) and 3.2 times lower for LF25 fruit ($\eta = 0.11$ and $A = 0.97$).

Ripening induction of fruit stored at 12°C was clearly delayed by about 9 days, compared to those stored at 20°C ($\eta = 0.16$ and $A = 0.97$) for LF100 fruit harvested at the G stage (Supplementary Materials Table S4). However, this delay was not observed for the other treatments. The daily rate of sweetness increase of fruit stored at 20°C was 1.2 to 1.9 higher than those stored at 12°C ($\eta \leq 0.62$ and $A \leq 0.25$), except for LF100 fruit harvested at the G stage for which it was 2.1 times lower ($\eta = 0.26$ and $A = 0.93$).

Ripening induction did not show a clear pattern in response to LF ratio since it occurred for LF100 fruit either earlier ($A > 0.5$) or later ($A < 0.5$) than for LF25 fruit (Supplementary Materials Table S5). In contrast, the daily rate of sweetness increase was always higher, by 1.2 to 7.7 times, for LF100 fruit than for LF25 fruit ($\eta \leq 0.61$ and $A \leq 0.24$).

Discussion

Evolution of fruit quality on the pre- and post-harvest continuum

Fruit quality is characterized by several physical and chemical properties that change during fruit growth and ripening. Fruit FM of on-tree fruit increased during fruit growth and ripening due to water and dry matter accumulation. The proportion of dry matter that accumulates in the fruit, i.e., DMC, also increased over time, as already observed by Léchaudel *et al.* (2005b). Water and dry matter supplies cease after harvest, so the FM of stored fruit decreases slightly during storage due to water loss through fruit transpiration (Castellanos and Herrera, 2015) and dry matter used by respiration for fruit maintenance (Colombié *et al.*, 2015), whereas DMC remained almost constant.

Pulp acidity (TTA) and color (hue angle) showed monotonic and decreasing kinetics on on-tree fruit and stored fruit, especially when stored at 20°C. Decrease in pulp acidity on the tree or during storage has been previously observed in mango (Gill *et al.*, 2017; Joas *et al.*, 2009; Léchaudel *et al.*, 2005b). It is consistent with changes in citric acid, the main organic acid in mango (Léchaudel and Joas, 2006), involved in the ripening process (Etienne *et al.*, 2013). Activation of the GABA shunt that leads to citrate degradation occurs during pre- and post-harvest ripening of several fruits such as citrus or bananas. The change in pulp color from light green to light orange is

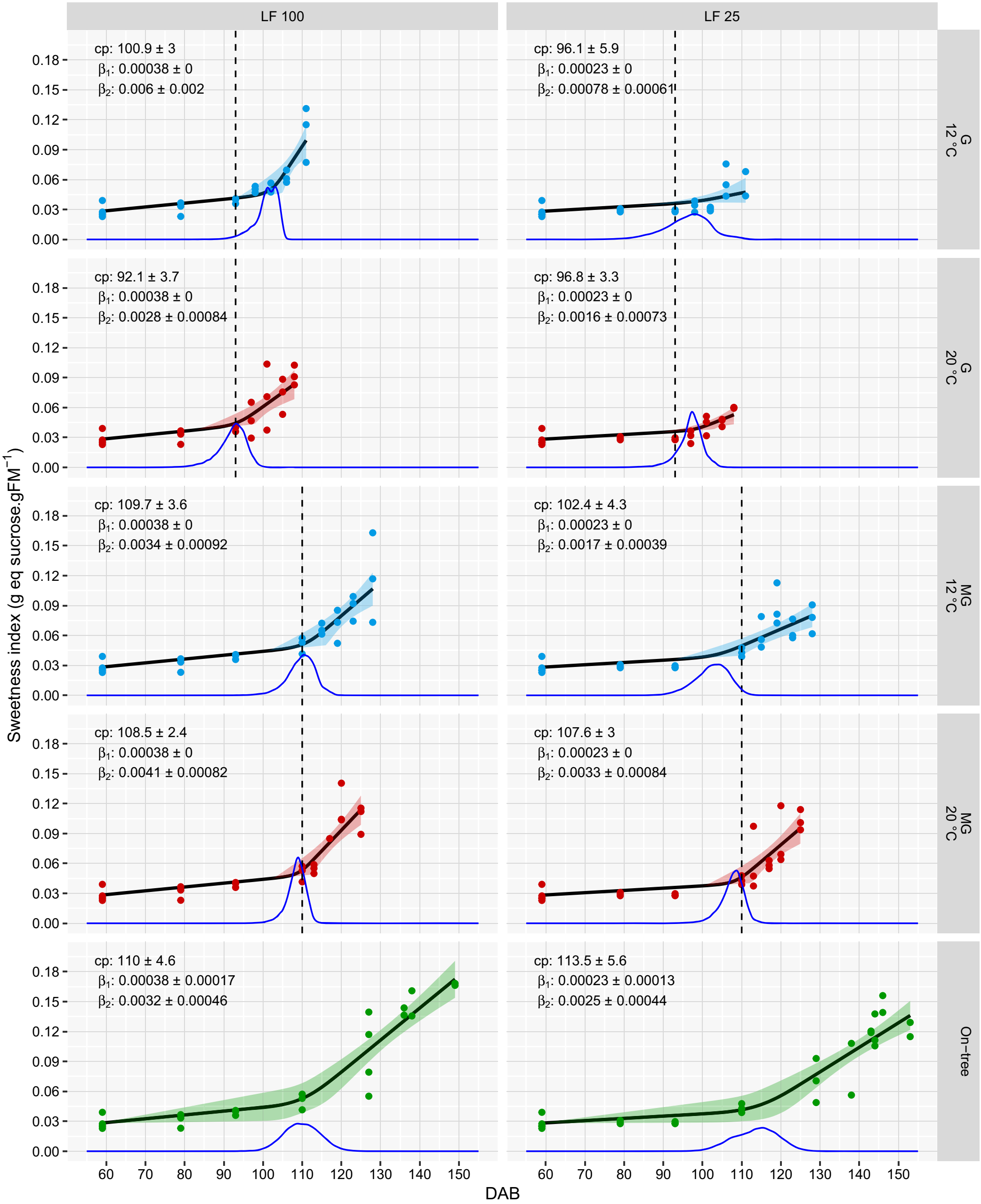

Figure 3. Kinetics of sweetness index on the pre- and post-harvest continuum according to the leaf-to-fruit ratio (LF25, LF100), maturity stage at harvest (G: Green, MG: Mature Green), and storage temperature (12°C, 20°C). Points are observed values measured in orchard A during the 2018 production season (one point represents one fruit). Vertical and dotted lines are the dates of harvest. Solid black lines and colored bands are predicted values and their 95% confidence intervals based on the model defined in Equation 1. Estimates (mean ± SD) of model parameters (*cp*: change-point date, in days after bloom (DAB); β_1, β_2: daily rates of sweetness increase before and after ripening initiation, in g eq. sucrose gFM^{-1}.DAB^{-1}) are indicated for each treatment. The solid blue lines are the change-point date (*cp*) posterior densities.

Table 3. Comparison of the change-point date and the daily rate of sweetness increase after ripening initiation (i.e., parameters *cp* and β_2 in Equation 1) between stored and on-tree fruit sampled in orchard A during the 2018 production season, based on the overlapping index (η) and the probability of superiority (*A*). Stored fruit were compared for each of the eight treatments defined by the combination of the leaf-to-fruit ratio (LF), maturity stage at harvest (Stage; G: Green, MG: Mature Green), and storage temperature (Temp) modalities, to on-tree fruit subjected to the same LF ratio. $A > 0.5$ indicates that the change-point date was later and that the daily rate of sweetness increase was higher for the on-tree fruit than the stored fruit

Treatment			Change-point date (*cp*)		Daily sweetness increase (β_2)	
LF	Stage	Temp	η	*A*	η	*A*
100	G	12	0.16	0.96	0.22	0.09
100	G	20	0.01	1	0.61	0.68
100	MG	12	0.83	0.51	0.69	0.46
100	MG	20	0.64	0.61	0.43	0.16
25	G	12	0.12	0.99	0.11	0.97
25	G	20	0.05	0.99	0.34	0.88
25	MG	12	0.26	0.94	0.34	0.91
25	MG	20	0.41	0.82	0.47	0.17

due to an accumulation of β-carotene (Rosalie *et al.*, 2019). The synthesis of β-carotene follows a complex metabolic pathway involving many enzymes (Liang *et al.*, 2020). It is known to suddenly increase during the maturation process (Nordey *et al.*, 2016).

In contrast to pigments and TTA, sucrose content showed monotonic and increasing kinetics for on-tree and stored fruit. The kinetics of starch content were different, with a bell-shaped pattern for fruit ripening on the tree, and a monotonous and decreasing pattern for stored fruit. As in other fruits, starch is first accumulated during fruit growth and then degraded to soluble sugars as the fruit ripens (Durán-Soria *et al.*, 2020). Sucrose is the main soluble sugar produced in mangoes (Datir and Regan, 2023; Li *et al.*, 2020). Fructose and glucose contents are low compared to sucrose and starch and show more variable kinetics, especially during storage. The balance between fructose and glucose varies between cultivars and depends on many factors, including fruit maturity at harvest (Joas *et al.*, 2009) and storage temperature (Hossain *et al.*, 2014).

Effect of the pre- and post-harvest management factors on the induction of fruit ripening

The change-point analysis revealed that harvest could force the ripening process of the fruit, leading to an earlier acceleration of the accumulation of sweetness (i.e., soluble sugars) in stored fruit than in on-tree fruit, especially when fruit were harvested at the early G stage. These results support previous findings from Nordey *et al.* (2016), who argue that harvest creates a stress that induces multiple metabolic changes in the fruit that lead to fruit ripening and climacteric syndrome. Moreover, the higher water imbalance between water inflow and outflow due to the cessation of water supply to the fruit induced by its detachment may trigger ripening of detached fruit. This assumption is supported by the study of Nakano *et al.* (2003) who reported that C_2H_4 synthesis in persimmon fruit tissue is modulated by water imbalance. At both the G and MG stages, the fruit has acquired the ability to ripen after harvest, indicating that it has reached physiological maturity. McAtee *et al.* (2013) suggested that the fruit acquires the ability to ripen once the seeds are mature, but have not yet begun the ripening process. When harvested at the MG stage, the onset of the ripening process occurred simultaneously in stored and on-tree fruit under no or low carbohydrate restrictions (LF100) and was only slightly delayed for fruit under higher carbohydrate restrictions (LF25). This suggests that the ripening process is naturally initiated at the MG stage, in contrast to the earlier G stage in which fruit only ripens after induction by harvest. Carbohydrate supply involves changes in sugar levels and, in particular, sucrose, which plays a major role in the regulation of fruit ripening through its interactions with hormones (Durán-Soria *et al*., 2020). Delayed ripening of carbohydrate-restricted fruit has been reported in mango (Nordey *et al*., 2016) and other fruits (Poiroux-Gonord *et al*., 2012; Souty *et al*., 1999; Wang *et al*., 2022). However, the date of ripening induction was not so different between on-tree fruit with a 25 and 100 LF ratio, with a delay of only 3.5 days. Finally, our results suggest that cold storage is more likely to slow down the increase in sweetness than to delay the onset of ripening.

Effect of the pre- and post-harvest management factors on fruit quality traits

The quality traits of mango fruit most impacted by LF ratio were fruit FM and pulp DMC. Fruit FM and pulp DMC increased with LF ratio, as for many other fruits (Bertin and Génard, 2018; Musacchi and Serra, 2018). Fruit on girdled branches are only supplied with carbohydrates by leaf photosynthesis and stored reserves from their own branch, whereas non-girdled branches can mobilize carbohydrates from the rest of the tree. The results suggested that 25 leaves per fruit were restrictive conditions of carbohydrate supply for mango fruit, even though leaf photosynthesis may have been stimulated by unbalanced source/sink relationships (Urban *et al*., 2004). They also suggest that 100 leaves per fruit could still be considered as a restrictive condition, compared to the most likely nonrestrictive condition of non-girdled branches that showed the highest fruit FM and pulp DMC. Fruit with a high LF ratio generally showed the highest sucrose and starch contents in on-tree fruit, while fructose and glucose contents, pulp color, and TTA were unaffected or only slightly affected. In other studies, however, peach (Wang *et al*., 2022), tomato (Bertin and Génard, 2018), mandarin (Poiroux-Gonord *et al*., 2012), and mango (Léchaudel *et al*., 2005b) fruits with a lower LF ratio had a lighter orange pulp color, higher glucose and fructose contents, and higher TTA. The effect of carbohydrate availability on these quality traits could depend on the fruit species and the level of carbohydrate restriction. Finally, the effect of LF ratio during the post-harvest stage was mainly related to the initial quality of the fruit when it entered storage, which is determined by pre-harvest conditions.

Fruit maturity stage at harvest, managed by harvest date, had a consistent and clear effect on fruit quality traits at the post-harvest stage. The earlier the fruit was harvested, the lower the indicator level was at harvest for quality traits that display a monotonically increasing kinetics (i.e., FM, DMC, sucrose, and fructose contents), and the highest the indicator was for those with decreasing kinetics (i.e., TTA and hue angle). Fruit harvested at the G stage are still accumulating starch (Joas *et al*., 2009) and are of a poor quality with limited sugar content and size at full maturity. The starch content in stored fruit decreased during ripening since starch is hydrolyzed into soluble sugars. At the MG stage (at around 110 DAB), the starch content of on-tree fruit was close to the maximum value, as previously observed in Léchaudel *et al.* (2005b). This suggests that the MG stage could ensure satisfactory fruit quality for storage, especially for quality traits related to primary compounds and starch accumulation. Harvesting fruit at a later stage did not increase fruit sweetness according to Joas *et al.* (2009).

After ripening processes were induced by fruit harvest, they were differently affected by storage temperatures. Cold storage at 12°C slightly slowed down starch hydrolysis and sucrose accumulation compared to fruit stored at 20°C but did not stop them. The same effect was observed on banana (der Agopian *et al*., 2011; Peroni-Okita *et al*., 2013), kiwi (Asiche *et al.* 2017), and melon (Wu *et al.* 2020) fruits. Pulp acidity and color were more strongly affected by storage temperature. Storage at low temperatures greatly reduced the changes in pulp color and TTA. Storage temperature has been reported to almost stop processes related to secondary metabolism and to slow down those related to primary metabolism (Pott *et al*., 2020; Rosalie *et al*., 2018). While fruit stored at 20°C were ripe after 15 days of storage, fruit stored at 12°C were still not ripe after 18 days. They require longer storage time or exposure to higher temperatures to fully ripen and complete changes in pulp color, TTA, and sugar content (Rosalie *et al*., 2018). Storage of mango fruit at cold temperatures could thus be used to extend the potential time a fruit can be stored, as is the case for many other fruits (der Agopian *et al.*, 2011; Jacobi *et al.*, 2002; Peroni-Okita *et al.*, 2013).

Conclusion

Pre-harvest conditions highly influence the quality of on-tree and stored fruit. The LF ratio, which modifies carbohydrate availability, had a strong effect on fruit FM and pulp DMC. This ratio could be managed by fruit thinning and pruning. From an applied point of view, this implies that it should be transposed in terms of fruit load recommendations for growers. Functional-structural models (e.g. V-Mango: Vaillant *et al.*, 2022) could help to extend the source-sink relationships established at the branch level to the tree level while considering the effect of branch-specific light environments and tree architecture. Although the current study did not identify an optimal LF ratio, it suggests that 100 leaves per fruit could still be considered a restrictive condition. The maturity stage at harvest is also a key factor for the final quality of fruit. The results suggested that the MG stage is optimal for harvesting the fruit, both for the export market with extended storage at cold temperatures and for the local market with a shorter storage time at ambient temperature. At the MG stage, the fruit have reached the end of the starch accumulation phase and, once harvested, cold storage could be used to control harvest-induced ripening by slowing down the increase in sugars and impacting acidity and color changes. This study described and quantified the effect of pre- and post-harvest management factors on the kinetics of a wide range of mango quality traits on the pre- and post-harvest continuum. Highlighting the mechanisms responsible for these kinetics and factor effects, which remain poorly studied, could open up avenues for improving mango quality management.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0014479723000182

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