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ORIGINAL ARTICLE

Post-harvest banana peel splitting as a function of relative humidity storage conditions

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Abstract Peel splitting is a major physiological disorder affecting post-harvest banana quality. This phenomenon occurs only 3–6 days after ripening induction in specific cultivars such as cv. 925 when stored in saturating humidity conditions. In these conditions, Cavendish cultivars (Grande Naine, cv. GN) are not susceptible to splitting. Cvs. 925 and GN were thus investigated to detect possible determinants associated with splitting. Splitting intensity was tentatively found to be associated with an inverse water flux at high relative humidity (RH) through an osmotic peel to pulp water flux resulting from the higher sugar content in the pulp than in the peel. Rheological properties were measured, and although the peel resistance and elasticity in cv. 925 were surprisingly higher than in cv. GN, saturating humidity conditions (100 % RH) substantially reduced the peel resistance. However, the peel epicuticular wax in cv. 925 was clearly thinner than that in cv. GN, thus leading to limitation of peel hydration in cv. GN. Peel splitting in cv. 925 was also associated with a boost in respiration, an increase in oxidative stress markers (H_2O_2), resulting in an increase in cellular damage markers (MDA, PEL). Overall, our results suggest that peel splitting at high RH in cv. 925 is related to fast decrease peel water content and the induction of high oxidative stress damage.

Keywords Banana · Peel · Humidity · Splitting · Wax · ROS

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Introduction

Fruit cracking is a serious physiological disorder that has a negative effect on the fruit appearance, decreases its shelf-life, and is considered as preferential entry site for fungal pathogens (Gibert et al. 2009), thus rendering the fruit unmarketable. Fruit cracking is a physical failure of the fruit skin that presents as shallow or deeper fractures in the peel or cuticle of certain fruits. This disorder is also called fruit splitting, since it is an extreme form of cracking that penetrates deep into the pulp (Opara et al. 2000).

Several studies have associated a number of physiological, biochemical, environmental, cultural, anatomical, and genetic factors with the high incidence of fruit cracking (Khadivi-Khub 2015). However, the causes of fruit cracking are difficult to study because of a lack of experimental methods to induce and control the range of cracking.

Skin characteristics have been studied in relation to crack resistance, as these outer surface layers of fruit—including the cuticle, as well as epidermal and subepidermal tissues—confer mechanical strength to fruit (Lara et al. 2014). Cuticle mechanical properties and thickness have been shown to play a prominent role in this disorder (Matas

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et al. 2004). Geometrical aspects of the cell structure, such as shape, size, and intercellular spaces, are crucial for understanding the mechanical properties (Sekse 1995) and have been reported to differ between cracking-susceptible and cracking-resistant cultivars of various fruit species (Huang et al. 2000; Marshall et al. 2009). Analysis of wax and cutin layers in fruit cultivated under different climatic conditions and genetic differences revealed that these layers are involved in fruit cracking (Bargel et al. 2006; Martin and Rose 2014; Peschel et al. 2007).

The relative contribution of cuticular components and thickness to cuticle permeability and, therefore, to transpiration has received considerable attention. Indeed, the unbalanced water flux into and out of the fruit (Opara et al. 1997) could result in an increase in internal pressure acting on the fruit skin that would constitute a driving force in the fruit cracking process, as suggested by Sekse (1995). Peet (1992) and Peet and Willits (1995) studied tomato cracking in the greenhouse and in the field and proposed that cracking most likely occurs when the movement of water and solutes into the fruit is rapid and protracted. In addition to the cell size and arrangement and cell wall structure, turgor pressure is thought to have a major influence on tissue strength and macroscopic fruit firmness. Other peel characteristics impacting water loss were evaluated under different humidity storage conditions, such as the stomatal density and their opening/closure ratio (Burdon et al. 1993). Burdon et al. (1994) observed that banana stored at low RH exhibited large increase in peel ethylene production compare to banana stored at high RH. Banks (1984a) suggested that stomata are a major route for gas exchange.

The relationship between peel cracking and stress-generated reactive oxygen species (ROS) was studied recently in stored blueberry fruit (Zhou et al. 2014). Although the production of $^{\cdot}OH$ by H_2O_2 and $O_2^{\cdot-}$ during ripening and senescence is largely recognized and associated with oxidative damage of plasma membrane lipids, Dumville and Fry (2003) suggested that $^{\cdot}OH$ could also cause polysaccharide scission, leading to loss of tissue mechanical properties. Hence, cell weakening would be due to the action of ascorbate-generated hydroxyl radicals through the Fenton reaction (Schweikert et al. 2000), which in turn can cause non-enzymic scission of polysaccharides.

The aim of this study was, therefore, to evaluate the key aspects of this disorder from anatomical, physiological, and biochemical viewpoints. The Grande Naine variety (Cavendish subgroup; AAA) and the CIRAD925 hybrid (*Musa acuminata*, AAA group), which was recently created in the framework of the CIRAD banana breeding program, were chosen as models due to their contrasted behaviors towards splitting. Post-harvest relative humidity conditions were managed to induce and control this disorder in fruit of the susceptible cultivar, i.e., the CIRAD925 hybrid. Microscopy analyses were carried out to describe the banana peel fracture, and measure the cell size and peel characteristics. Then, carbon and water balances were assessed on the basis of the fruit respiration, transpiration, and dry matter contents of the various compartments. Finally, changes in the oxidative status, membrane damage, and the enzymatic and non-enzymatic antioxidant defense system were studied.

Materials and methods

Experimental conditions, treatments, and fruit sampling

Two banana cultivars were used, i.e., Grande Naine (Cavendish AAA subgroup, hereafter called GN) and one hybrid produced by CIRAD's plant breeding program, CIRAD925 (*Musa acuminata*, AAA group, hereafter called 925), as they presented contrasted susceptibility to peel splitting. Bananas were grown at the Experimental Station of CIRAD (Neufchateau, Guadeloupe, French West Indies; latitude 16°08 N, longitude 61°60 W, elevation 250 m) on continental alluvial soil. During the bunch growth period, the mean daily temperature was 26.0 ± 0.5 °C without any drip irrigation. Similar agronomic and cropping practices (suckering, bunch management) were used. The flowering-to-harvest time (Chillet 2008) and temperature sums of bunches indicated the fruit age. Temperature sums represented the mean daily temperature sum (calculated in degree days, °C days) accumulated by the fruit during its growth from flowering to harvest using a baseline temperature of 14.0 °C (Ganry and Meyer 1975) and 14.7 °C (pers. comm.), for GN and 925, respectively. Fruit were harvested at 900 and 800 °C day, for GN and 925 (physiological reference set at 14 °C), respectively. At each harvest day, three bunches, corresponding to three replicates, were harvested for both cvs. Each hand (from 2 to 5) from the three different bunches was cut in two equal parts and distributed to the following post-harvest treatments: high relative humidity (RH) storage (i.e., storage in plastic bags with 0.01 dm^2/m^2 perforations, corresponding to RH close to 100 % during fruit ripening) and low RH storage (i.e., storage without a plastic bag, corresponding to RH of about 50 % during fruit ripening). During the first 4 days after harvest, all sampled hands were stored at 20 °C, in plastic bags with 0.01 dm^2/m^2 perforations, corresponding to an RH of close to 100 %. Then, bananas underwent ethylene treatment (1 ml/L for 16 h) to trigger the ripening process. Fruit ripening was monitored at 20 °C for 8 days for the four treatments, i.e., 925-high RH storage, 925-low RH storage, GN-high RH storage, and GN-low RH storage.

Measurement of fruit transpiration, respiration, and rheology

Each day after ethylene induction, the length, grade, and fresh mass of fruit were measured on a set of 10 nonsplit fingers for both treatments, sampled from hand 2 of the 3 bunches. Each day after ethylene induction, 1 nonsplit finger was sampled from hand 2 of each of the 3 bunches. Fruit length, grade and fresh mass, and the peel and pulp masses were immediately measured. A sample of peel and pulp was used for dry matter content assessment by comparing its fresh mass and dry mass measured after drying at 70 °C for 48 h.

Fruit respiration was monitored daily after ethylene induction, for both treatments, on one nonsplit finger, sampled from hand 3 of each of the 3 bunches. Fruit respiration was evaluated by measuring exhausted CO_2 of each fruit after 2 h in 2-L jars using a carboxymeter instrument (Pekly/Hermann-Moritz, Thiron-Gardais, France). RH was kept constant at 50 and 100 % using salt NaCl and water added in the bottom of the jar, respectively.

Fruit surface conductance (g cm/h) was calculated via nondestructive monitoring of daily fruit fresh mass changes according to Léchaudel et al. (2013).

The impact of stomata aperture and epicuticular wax on fruit water loss was evaluated on the harvest day on 18 fruits of similar size from each cultivar, 6 fingers sampled on hand 4 of each of the 3 bunches. A first batch of 6 fruits per cultivar was dipped in 200-mL flasks (3/4 of the fruit submerged) containing water. The epicuticular wax of the six fruits of the second batch was removed by pouring 100 mL chloroform at 25 °C consecutively six times over the fruit. Fruits were then dipped in 200-mL flasks (3/4 of the fruit submerged) containing water. A third batch of six fruits per cultivar was dipped in 200-mL flasks (3/4 of the fruit submerged) containing abscisic acid (20 µM). For all fruits, the top of the pedicel of each fruit was recut while maintaining the fruit submerged in the dipping solution to avoid embolism that could limit fruit transpiration. Flasks were sealed with transparent film to avoid water evaporation. Fruits within the flasks were stored at 20 °C, at 50 % RH, and were weighed every day for 8 days.

Each day after ethylene induction, for both treatments, one nonsplit finger was sampled from hand 3 of each of the 3 bunches. A 2-cm peel ring at the central zone of each fruit was sampled for textural analysis. A TA-XT Plus Texture Analyzer (Swantech, Surey, UK) was used and the force to induce ring rupture was measured. A specific probe was designated to mimic the peel volume extension to avoid any distortion. This probe consisted of two independent half-cylinders (2 cm total diameter) that moved (2 mm/s) until the peel ring broke. The maximum force applied (expressed in N) and the time to break the peel were recorded. The slope of the force/time curve (expressed in N/s) stands for the fruit elasticity, as proposed by Bugaud et al. (2006).

Measurement of oxidative stress and antioxidant response

Oxidative stress and its damage (H_2O_2, MDA, peel electrolyte leakage), antioxidant compounds (ascorbate), and antioxidant enzymes (SOD, CAT) were determined daily after ethylene induction, in three split fingers of the 925-high RH storage treatment from the day when the disorder appeared and in three nonsplit fingers of the three other treatments, as follows.

Peel electrolyte leakage (PEL) was determined according to Bugaud et al. (2014) and immediately after sampling for PEL measurement, each fruit was peeled, cut, and the peel was blended in a Waring blendor (Waring, US). The resulting puree was stored on ice until biochemical analyses, which were performed the same day. All absorbances were read with a thermostabilized TECAN microplate reader (TECAN Infinite M200 PRO, Grödig, Austria).

Cold banana peel puree (5 g) was mixed using an Ultra-Turax in an ice bath with 20 mL 0.1 % (w:v) TCA. The homogenate was centrifuged at 12,000×*g* for 15 min at 4 °C. Hydrogen peroxide contents were determined as described by Velikova et al. (2000) using a part of the supernatant. Another part of the supernatant was used for the thiobarbituric acid (TBA) test, which determines the content in malonyldialdehyde (MDA) as an end product of lipid peroxidation (Velikova et al. 2000).

Total ascorbate (AsA plus DHA) and AsA contents were measured according to Kampfenkel et al. (1995), but scaled down for microplates. The extract was prepared from a 2-g sample of peel puree mixed using an Ultra-Turax in 10 mL of cold 6 % (w:v) trichloroacetic acid (TCA).

Protein extraction and determination was performed according to Korbel et al. (2013) using the bicinchoninic acid determination method.

For enzyme activity measurements, peel puree (5 g) was mixed in 20 ml of 50 mM MES/KOH buffer (pH 6.0), containing 40 mM KCl, 2 mM $CaCl_2$, and 1 mM AsA. Extracts were centrifuged at 4 °C for 15 min at 16,000×*g*, and the supernatants were immediately analyzed for SOD and CAT activity measurement. SOD activity was optimized from that of Dhindsa et al. (1981). SOD activity was assayed in a 1.0 mL reaction mixture containing 50 mM potassium phosphate (pH 7.8) buffer, 13 mM methionine, 75 µM nitro blue tetrazolium (NBT), 0.1 mM EDTA, 10 µL of sample supernatant, and 2 µM riboflavin. Tubes were briefly vortexed and triplicate 200 µL aliquots were taken from each tube and placed in plastic 96-well plates. The plates were then placed under white light provided by a commercial

overhead transparency projector (Horizon, Model Apollo, Lincolnshire, IL, USA) for 5 min. After the light treatment, absorbance readings were taken at 560 nm with a plate reader. SOD in the extract inhibited photochemical reduction of NBT to blue formazan. Activity was expressed in units of SOD from the standard curve of activity units versus absorbance. CAT activity was measured using a method adapted from that of Aebi (1984) in a reaction mixture containing 50 mM phosphate buffer (pH 7.0).

Measurement of peel characteristics

On the harvest day, for each cultivar, one fruit was sampled from hands 2–5 in each of the three bunches (total of 12 fruits per cultivar) to assess the epicuticular wax content. The protocol of Burdon et al. (1993) was applied. The fruit epicuticular wax was removed by pouring 100 mL chloroform at 25 °C over the fruit six times (extractions from a total of 12 fruits per cultivar). The chloroform extracts were cleaned by filtration through glass wool, and the total amount of wax was determined gravimetrically using a rotavapor after chloroform removal. The total peel area of the 12 fruits was determined from the peel fresh mass of all fruits and by weighing a 12.5 cm^2 peel disk, corresponding to a 4-cm diameter disk sampled in the central zone of each fruit.

The optimized method developed by Banks (1984b) using photonic microscopy was implemented to estimate the average cell size, stomatal density, and the number of stomata opened on each fruit surface. Each day after ethylene induction, one split finger from the 925-high RH storage treatment, if not non-split finger, and one non-split finger from each of the other treatments, i.e., 925-low RH storage, GN-high, and low RH storage, were sampled from hand 5 of each of the 3 bunches. The day after fruit harvest, imprints of the central zone surface of 3 fingers per treatment were obtained by applying a thin clear undiluted nail varnish to the peel surface. Dried imprints were removed using transparent adhesive tape and mounted on glass slides. This protocol was performed at low and high humidities in plastic chambers to avoid stomatal opening distortion results. Glass plates were observed using a Nikon photonic microscope (Eclipse Elite, Tokyo, Japan) with a 100× to 400× zoom observation (100×, stomates; 400× cell size). Cell size, stomatal density, and aperture were measured using ImageJ free software (NSA, 1.48, US) on a 4 mm^2 square on the concave (CC) and convex (CX) sides of each fruit.

Electronic microscopy for characterization of banana peel splitting

Six days after ethylene induction, a sample of banana peel (1 cm^2) from one split finger was taken from the concave side of the fruit at the splitting zone. These samples were fixed in a 3 % sodium phosphate buffered glutaraldehyde solution (0.1 M, pH 7.2) for 4 h and then rinsed three times in sodium phosphate buffer (0.1 M, pH 7.2) for 10 min. Samples were washed seven times in distilled water for 10 min. Then, they were dehydrated in successive acetone baths of increasing concentration (30, 50 % for 30 min, then 70, 85, 95, 100 % for 1 h and finally 100 % overnight at 4 °C). Acetone was substituted by liquid CO_2, and thereafter, the samples were dehydrated until the critical point was reached at 32 °C and 74 bar (Biorad, Polaron Critical Point Drier). Prior to analysis under a scanning electron microscope (Hitachi S-2500 at 20 kV accelerating tension), samples were fixed to aluminum support stubs and gold sputter coated (BioRad SC500 Sputter Coater) to make them conductive.

Results

Macroscopic and anatomic characteristics of banana peel splitting

The observed peel splitting changes according to cultivar and post-harvest treatments revealed peel splitting only in fruit from cv. 925 maintained under 100 % RH storage conditions, with about 40 % of fruits from this treatment presenting this disorder: the difference in behavior between the 2 cvs. irrespective of the post-harvest treatment. Ripening induction was critical from 3 to 5 days after the ethylene treatment as it represented a critical period corresponding to peel splitting onset in cv. 925 fruit under 100 % RH storage conditions.

Figure 1a shows the whole split cv. 925 with the targeted banana peel surface zone used for specific SEM observations. This section observed by SEM upstream of the banana peel tear zone shows collapsed epidermal cells without apparent lesions (Fig. 1b). The more enlarged view (Fig. 1c) shows that the epidermal cells are intact and quite compact without intercellular spaces, even around the tear zone. Figure 2a shows a cross section of a cv. 925 banana revealing flat peel segments attached to corner sections. These junctions appear to be weakness zones, since that is where splitting always occurred. Indeed, no peel splits were ever observed into in the flat sections. On the left side of the slice, no splitting was noted, and this corner region was amplified by SEM (Fig. 2b). At the bottom of the slice (Fig. 2c), the corner region shows internal development of a cracking zone. The corner region was closely studied, since cracking always occurred in these weakness regions. These findings clearly showed that peel cracking was invisible to the naked eye and that the phenomena developed from the inner to the outer epidermal zone.

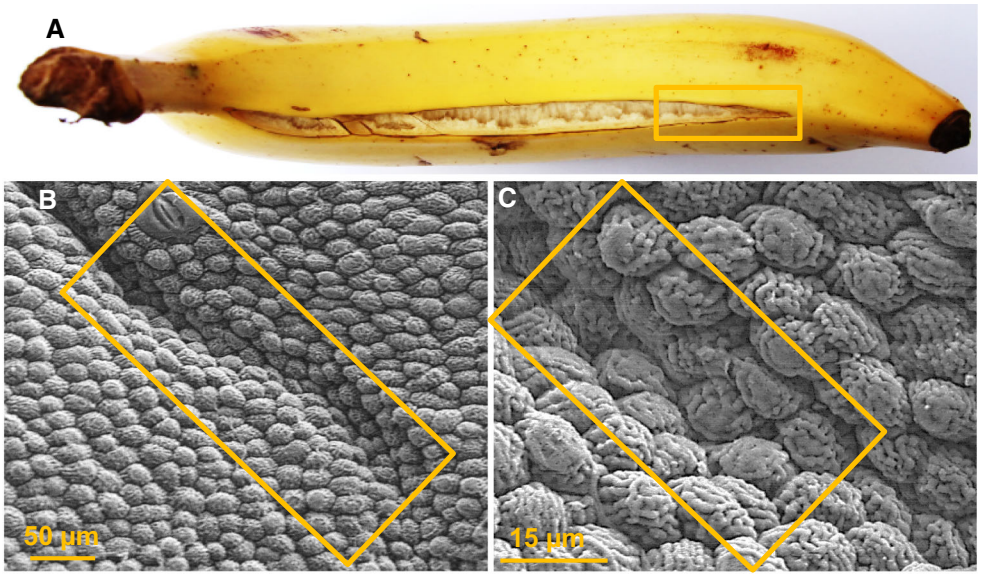

Fig. 1 Whole split cv. 925 banana with the banana peel surface zone targeted for specific SEM observations at two zoom levels (**b**, **c**). The split zone on the cv. 925 banana peel is highlighted as being due to cellular collapse

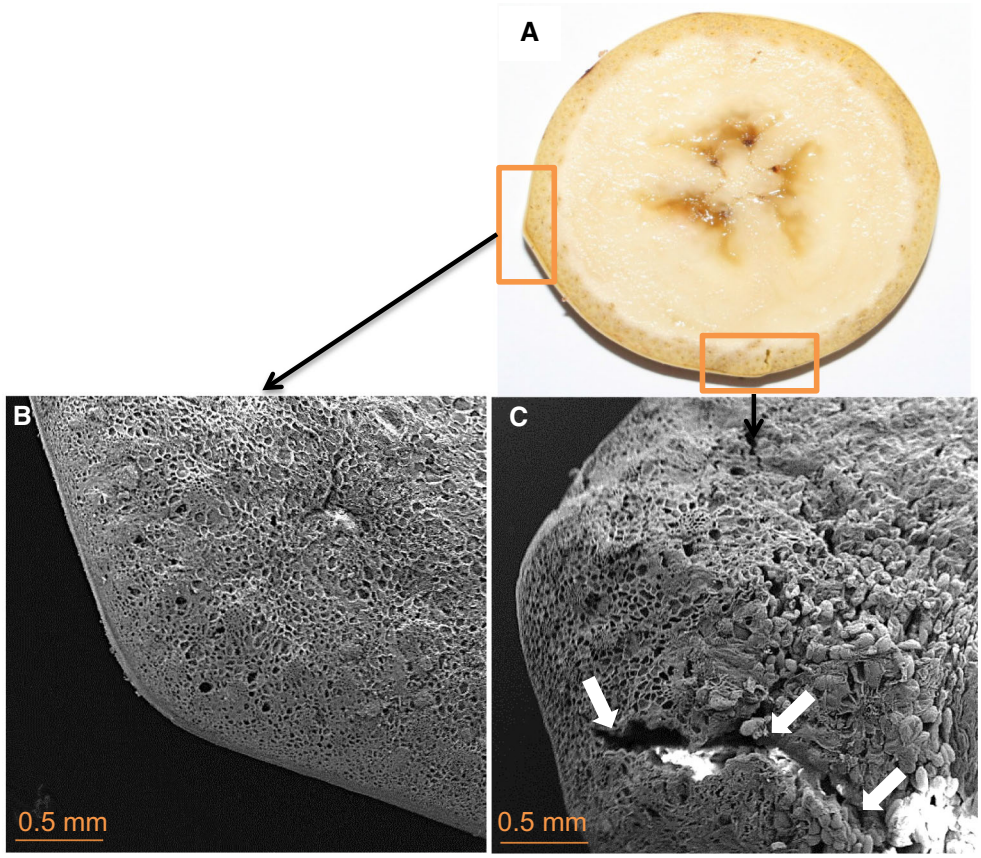

Fig. 2 SEM images of a cross section of the corner zone without splitting (**b**) and with a peel split zone (**c**). *White narrows* show the break zone inside the epidermis

Carbon and water balances within fruit peel and pulp

Figure 3a shows the relative variations in fruit mass loss according to RH conditions and cultivars. Although a marked and clear difference in transpiration between wet and dry post-harvest conditions could be logically attributed to the differences in water vapor pressure (~12 % weight loss after 8 days at 50 % RH), no significance difference was observed between the two cultivars. The variations in fruit diameter (Fig. 3b) under different humidity conditions did not show any fruit diameter change during ripening at 100 % RH, while a 6 % decrease (34.5–32.5 mm) was noted in cv. 925 bananas stored for 8 days at 50 % RH. The difference in behavior between these two cvs. regarding peel splitting, i.e., ~30–40 % peel splitting for cv. 925 at 100 % RH mainly occurring from days 3–6, could, therefore, not be directly related to the weight and diameter variation patterns throughout ripening.

The water and dry matter (DM) balances during ripening in different RH conditions was also studied according to variations in dry matter content and peel and pulp fresh mass (Fig. 3c, d, respectively). The peel DM of cv. 925 was about 20 % higher than in cv. GN whatever the RH condition. Interestingly, the peel DM content (Fig. 3c) was constant from days 3 to 6 at 100 % RH, while it increased under low RH conditions whatever the cultivar. Pulp dry matter content patterns (Fig. 3d) presented an opposite trend from days 3 to 6, since it continuously decreased for both cultivars, but cv. GN dry matter content was much higher than for cv. 925. No impact of storage humidity

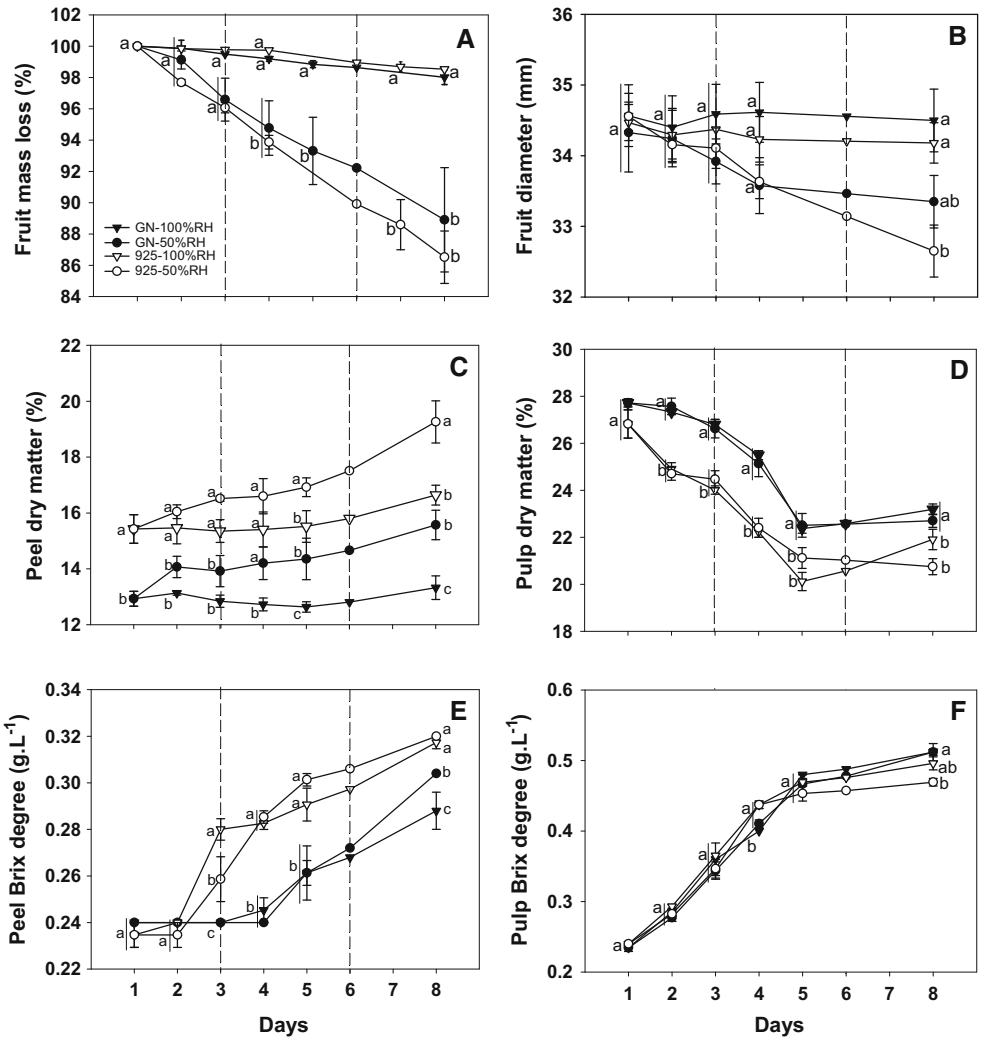

Fig. 3 Impact of the cv. and RH conditions on the variations in banana fruit mass (**a**), diameter (**b**), peel and pulp dry matter (**c**, **d**, respectively) and peel and pulp Brix degree (**e**, **f**, respectively) during ripening. The values are means (±standard error) for three fruits per variety and for each treatment at each ripening stage. *Lower case letters* indicate the significance between the treatments at $P < 0.05$ (according to the LSD Fischer's test)

Table 1 Impact of the cv., RH conditions and dewaxing (ECW) on the transpiration rate and conductance of banana peel (with or without wax) after 5 days of ripening

	Total wax (μg/cm)	Transpiration (mg/h/cm^2)	Transpiration without wax (mg/h/cm)	Conductance (cm/h)	Conductance without wax (cm/h)
925					
100 % RH	92	0.042 ± 4E−06 e	0.100 ± 7E−06 e	2.40 ± 0.19 b	6.81 ± 0.40 a
50 % RH	–	0.500 ± 4E−06 c	1.500 ± 1E−04 a	0.58 ± 0.01 e	1.71 ± 0.15 cd
GN					
100 % RH	146	0.031 ± 5E−06 e	0.036 ± 1E−06 e	1.76 ± 0.29 c	2.02 ± 0.07 c
50 % RH	–	0.400 ± 1E−05 d	1.100 ± 7E−05 b	0.41 ± 0.01 e	1.26 ± 0.08 d

Values are means (±standard error) of three fruits per variety and treatment at each ripening stage. Lower case letters indicate the significance (for transpiration and conductance separately) between treatments and cvs. at $P < 0.05$ (according to the LSD Fischer's test)

conditions on the pulp DM content was noted. Moreover, for both cultivars, the pulp sugar contents were higher than in the peel (+56 and +66 % for cvs. GN and 925, respectively, Fig. 3e). Note that the peel fresh mass was lower for the cv. 925 than for cv. GN, whatever the post-harvest treatment (data not shown). The effect of storage conditions on changes in peel fresh mass during ripening changed depending on the cv., i.e., the fresh mass of cv. 925 peel decreased continuously and to the same extent at low and high RH. For cv. GN, the peel fresh mass tended to increase during the first days of ripening and then to decrease very slowly and sharply under high and low RH conditions, respectively.

Transpiration depending on the saturating vapor pressure at the fruit surface was partially or totally related to the water flux through the cuticle. The 3-to-5-day ripening period was critical for cv. 925 in terms of peel splitting. After 5 days of ripening, the fruit surface conductance of the 100 % RH treatment was fourfold higher than that of the 50 % RH treatment for both varieties (Table 1). At 100 % RH, cv. 925 had a significantly higher conductance than GN, whereas at 50 % RH, no difference between the two varieties was noted. Conductance was logically increased by dewaxing the peel, regardless of the treatment. The highest increase was observed for cv. 925, which reached 6.81 cm/h after 5 days at 100 % RH.

Influence of the stoma aperture on water loss was estimated using abscisic acid (i.e., aiming at closing stomata), and dewaxing (i.e., using chloroform). No significant water loss was measured after stomata were closed stomata with abscisic acid. Only a dewaxing of the cuticle clearly increased to 50 % the fruit surface conductance after 8 days of ripening.

For both cvs., changes in the fruit respiration rate and in the intensity of the climacteric peak were highly dependent on the RH conditions and the cultivar (Fig. 4). Indeed, the maximum respiration rate of cv. GN reached 0.04 and 0.06 g CO_2/h/g after 3 days of ripening at 100 and 50 % RH, respectively. Conversely, the maximum of respiration rate of cv. 925 was significantly higher, i.e., 0.08 g CO_2/h/g after about 5–6 and 7 days at 100 and 50 % RH, respectively.

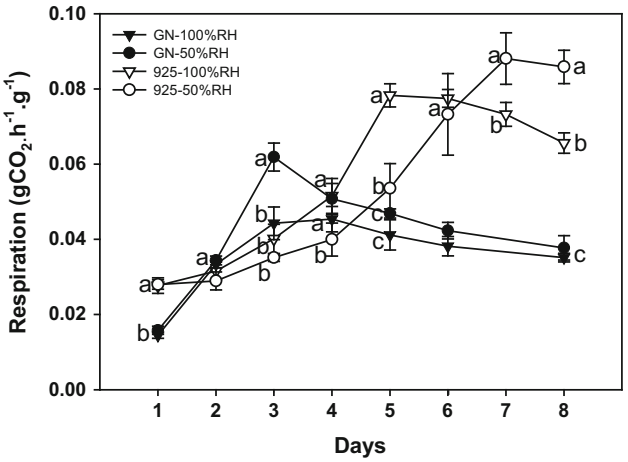

Fig. 4 Impact of the cv. and RH conditions on the banana peel respiration rate during ripening. The values are means (±standard error) of three fruits per variety and per treatment at each ripening stage. *Lower case letters* indicate the significance between treatments at $P < 0.05$ (according to the LSD Fischer's test)

Peel characteristics

As the water flux could be critical with respect to the peel cracking intensity, the stomatal density (Fig. 5a) and opening of the concave and convex surfaces (Fig. 5b, c, respectively) were studied during ripening for both cvs. at 50 and 100 % RH. Whatever the surface, cv. GN presented a higher stomatal density than that of cv. 925, with 4 and 2.5 stomata/mm^2 on the concave surface of cvs. GN and 925, respectively. Stomatal opening during ripening matched the respiration behavior of both cvs. under the two different RH conditions. Indeed, the stomatal opening ratio of the concave surface of 925 and GN cvs. at 100 % RH

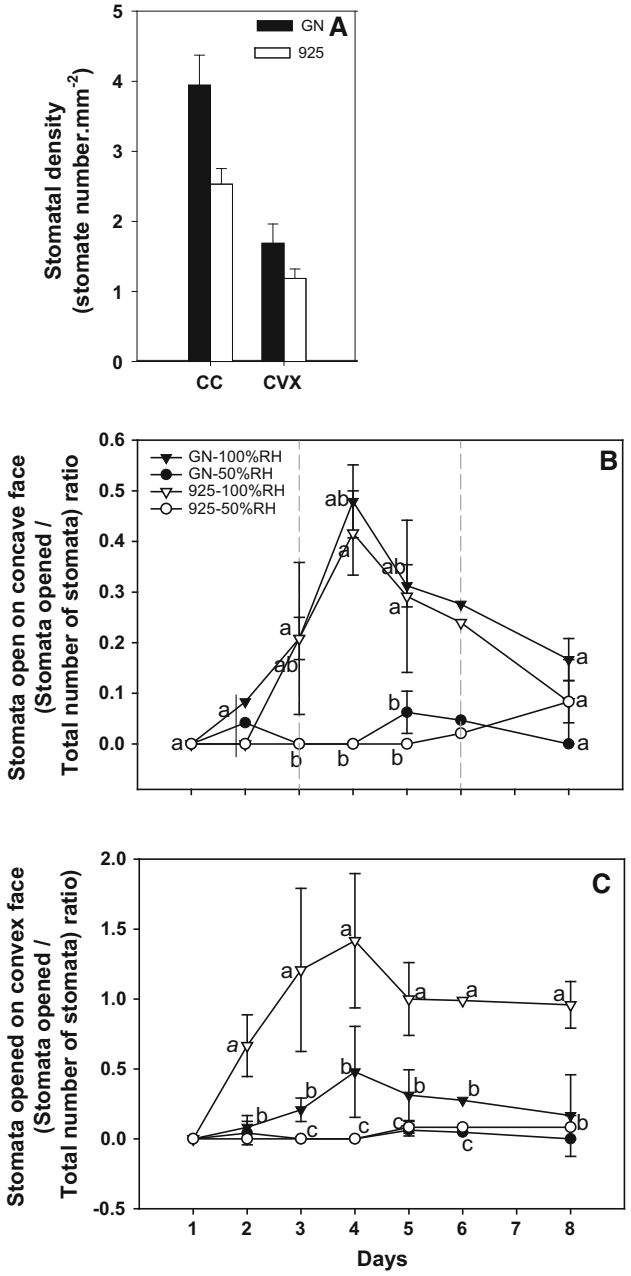

Fig. 5 Impact of the cv. and RH conditions and fruit surface (concave surface, CC; convex surface, CVX) on the stomatal density (**a**), the opening ratio of CC and CVX stomata (**b**, **c**, respectively)

reached a peak after 4 days of ripening, with 50 and 20 %, respectively (Fig. 5b). At 100 % RH, the stomatal opening ratio of the convex surface (Fig. 5c) of both cvs. reached about 25 %, while all stomata were closed after 4 days of ripening at 50 % RH.

The cuticle thickness and stomata aperture were tentatively correlated with the fruit transpiration rate (Table 1). The water flux evaporation through stomata was clearly negligible, and closing stomata with abscisic acid did not have a significant effect on the transpiration rate (Fig. 6).

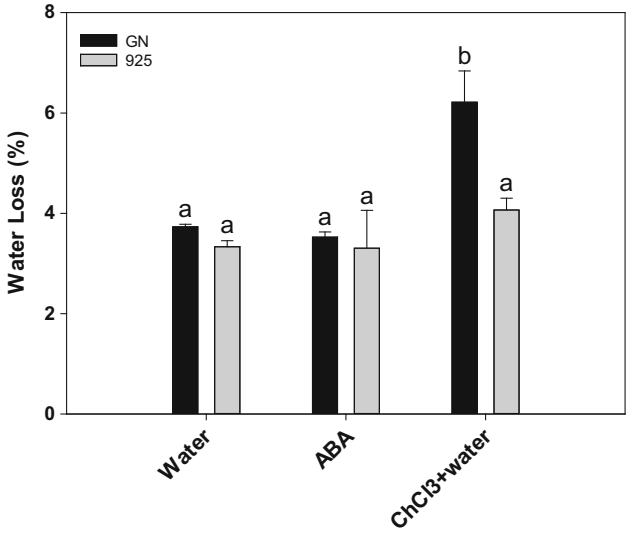

Fig. 6 Impact of abscisic acid and peel dewaxing on water loss (d). The values are means (±standard error) of three fruits per variety and per treatment at each ripening stage. *Lower case letters* indicate the significance between treatments at $P < 0.05$ (according to the LSD Fischer's test)

On the contrary, for both varieties, the transpiration rate of dewaxed peel after 5 days at 100 % RH stayed the same for both cultivars with or without epicuticular wax. At 50 % RH, the transpiration rate was threefold higher for both cvs. without epicuticular wax. The conductance with or without epicuticular wax did not vary between cultivars at 50 % RH. At 100 % RH, however, although no difference between conductance with or without epicuticular wax was observed for cv. GN, the conductance of the cv. 925 without epicuticular wax was twofold higher than with it.

The epicuticular wax average content (Table 1) of cv. 925 was 37 % lower than that of cv. GN (92 and 146 μg/cm^2, respectively). The average epidermal cell area (Table 2) was studied during ripening while considering the RH and cv. differences. Independently to the ripening days, the cell area of cv. GN increased from 50 to 100 % RH under post-harvest conditions: after only 1 day of storage, the average external cell area of this cv. increased from 174.7 ± 2.2 to 213.1 ± 16.4 μm^2, while no difference was noted for cv. 925 Surprisingly, no difference was observed on the convex surface, with the cv. 925 cell area being constant at low or high RH.

Peel rheology

As peel cracking was linked to the tensile strength in the rupture zone, the mechanical properties (force to break the peel and elasticity) were measured during ripening. Overall and as expected, the peel strength markedly decreased during ripening irrespective of the storage conditions. The

Table 2 Impact of the cv., RH conditions and fruit surface (concave, CC; convex, CX) on the banana peel cell area during ripening

	100 % RH		50 % RH	
	925	GN	925	GN
Cell surface CC (μm^2)	107.4 ± 1.4 a	112.4 ± 8.8 a	98.6 ± 3.8 b	102.2 ± 2.2 b
Cell surface CX (μm^2)	152.7 ± 2.3 c	213.1 ± 16.4 a	152.1 ± 7.8 c	174.7 ± 2.2 b

The values are means (±standard error) of three fruits per variety and per treatment at each ripening stage. Lower case letters indicate the significance between treatments and cvs. at $P < 0.05$ (according to the LSD Fischer's test) for the concave and convex cell surface values

force to break the peel was significantly higher in cv. 925 than in cv. GN (Fig. 7a). At 50 % RH and after 3 days of ripening, the peel strength of cv. 925 was more than threefold higher than that of cv. GN. The effect of vapor pressure during fruit ripening was again noted for cv. 925 and but not for cv. GN, i.e., the peel strength of cv. 925 at 50 and 100 % RH decreased from 100 and 60 N after 3 days, respectively.

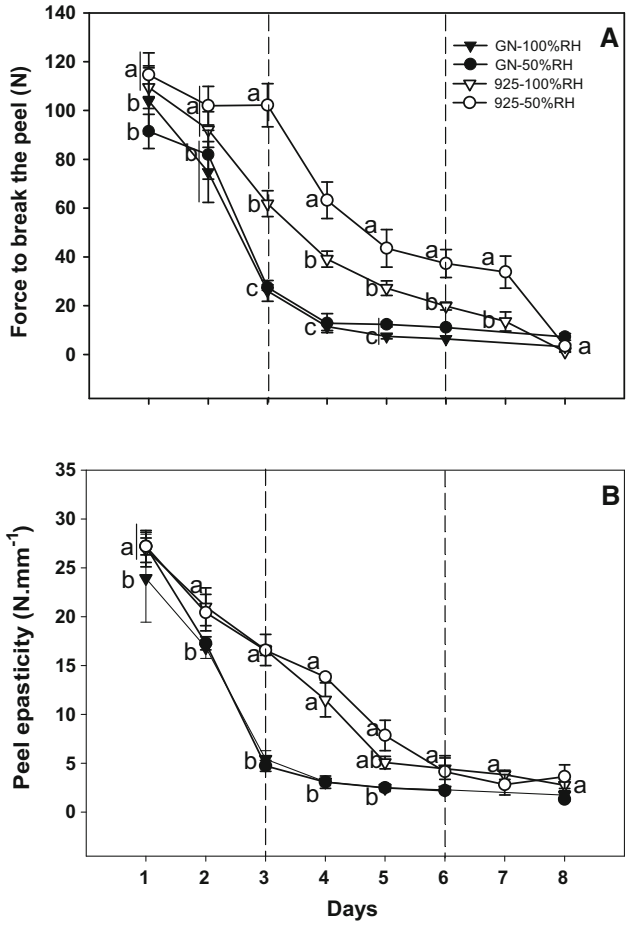

Fig. 7 Impact of the cv. and RH conditions on the evolution of the banana peel force to break (**a**) and the elasticity (**b**) patterns during ripening. The values are means (±standard error) of three fruits per variety and per treatment at each ripening stage. *Lower case letters* indicate the significance between treatments at $P < 0.05$ (according to the LSD Fischer's test)

Although the peel elastic properties (Fig. 7b) followed the same pattern as the strength, i.e., a marked decrease in peel elasticity during ripening, no effect of storage conditions was observed. The peel elasticity (Fig. 7b) was threefold higher between days 3 and 5 for cv. 925 than for cv. GN. Note also that a difference in skin strain before cracking was observed between treatments and varieties (data not shown). The peel of cv. GN indeed had greater strain than cv. 925 for lower strength. Peel stored at 50 % RH seemed to be more susceptible to deformation than peel stored at 100 % RH.

Oxidative stress and enzymatic and non-enzymatic antioxidant response

For both cvs., banana fruit ripening under low and high RH post-harvest conditions was accompanied by changes in reactive oxygen species (ROS) as well as in the antioxidant defense system. Lipid peroxidation, hydrogen peroxide, and linked detoxification enzymes were induced during ripening regardless of the cv. and RH treatment. Figure 8a shows the steady global superoxide dismutase (SOD) activity during ripening, whatever the cv. and RH conditions. Catalase, a hydrogen peroxide detoxifying enzyme, presented a marked difference in behavior between the cvs. The CAT activity of cv. 925 (Fig. 8b) was twofold to threefold lower than that of cv. GN during the "splitting period." However, no significant difference could was noted for this cultivar between the HR conditions.

Produced hydrogen peroxide (Fig. 8c), as an oxidative stress marker, presented a significantly higher level in cv. 925 peel than in cv. GN peel. Indeed, 1 µmol/g DM of H_2O_2 was still quantified at day 6 for cv. 925, while only trace amounts of H_2O_2 were detected for cv. GN at this ripening stage.

The ratio between reduced and oxidized forms of ascorbate (AsA/DHA ratio, Fig. 8d), i.e., a marker of an imbalance in ascorbate peroxidase activity and to stress oxidizing conditions, followed the same trend. During the ripening period, and especially during the period prone to peel splitting, i.e., days 3–6, the AsA to DHA ratio increased in cv. GN peel, and

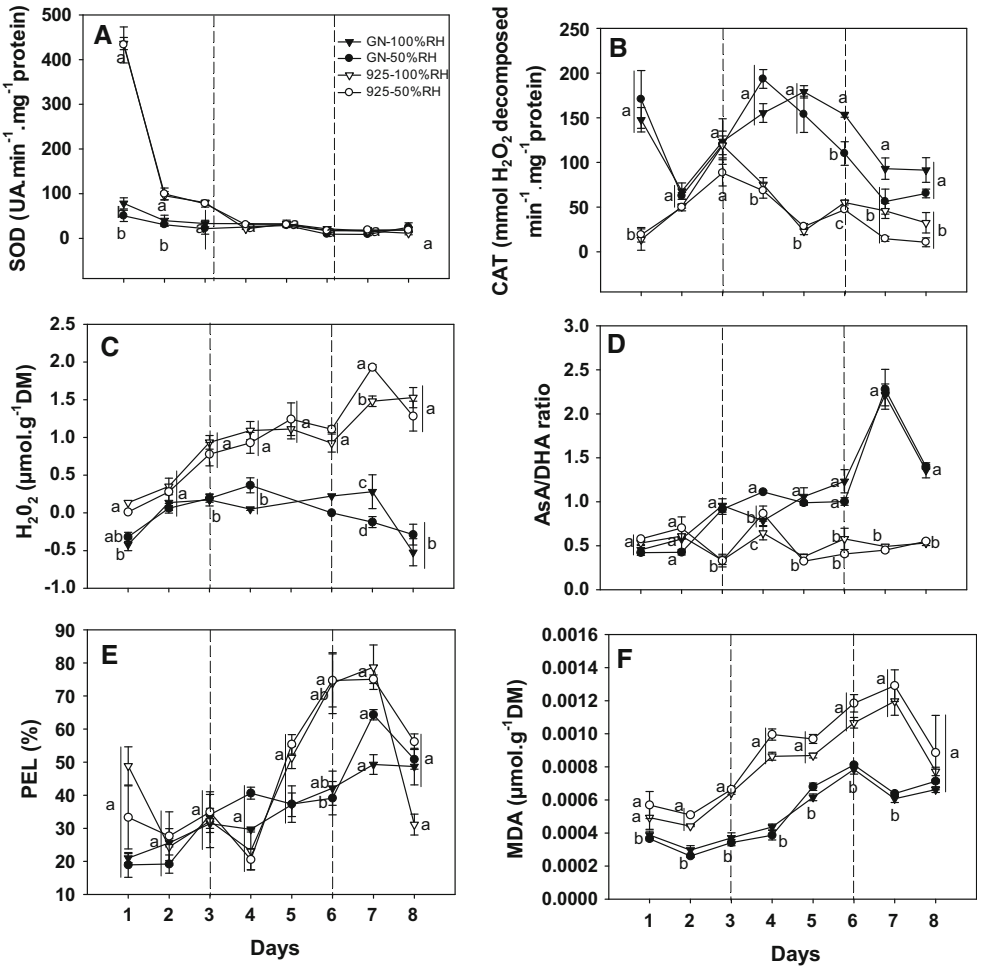

Fig. 8 Impact of the cv. and RH conditions on patterns regarding SOD activity (**a**), CAT activity (**b**), H_2O_2 (**c**), AsA/DHA ratio (**d**), PEL (**e**), and the MDA quantity (**f**) of the banana peel during ripening. The values are means (±standard error) for three fruits per variety and each treatment at each ripening stage. *Lower case letters* indicate the significance between treatments at $P < 0.05$ (according to the LSD)

approximately half of the ascorbate was in oxidized form at day 6 for cv. 925, whereas the oxidized form was twofold higher for cv. GN at the same ripening stage. For this ratio, no effect of HR storage conditions was noted.

Greater lipid peroxidation, as measured by the malondialdehyde (MDA, Fig. 8f) content, was observed in cv. 925 than in cv. GN. Between ripening days 3–6, levels of peroxide lipids of both cvs. increased almost twofold, while the MDA level was significantly higher for cv. 925 (1.2 nmol/g dm, 100 % RH) than for cv. GN. The peel electrolyte leakage pattern (PEL, Fig. 8e) closely matched the changes in MDA content. At 6 days of ripening, the PEL reached 70 % for the cv. 925 while not exceeding 40 % for cv. GN. A substantial increase in PEL during the climacteric crisis was noted for cv. 925 (30–70 %), especially during the peel splitting period for this cultivar at high RH. Conversely, cv. GN did not present any PEL burst during the critical period.

Discussion

Water flux and dry matter balances: what impact on peel splitting?

Contrary to the well-known cultivar GN, which is not prone to peel splitting, cv. 925 was found to be susceptible to peel splitting from 3 to 6 days after ripening onset, when stored at saturating humidity (100 % RH). Macroscopic and SEM observations in cv. 925 confirmed that peel junctions between two flat segments in that genotype were weakness zones where splitting was initiated and internal development of this disorder was found to be related to epidermal cell collapse without apparent lesions.

When studying tomato peel cracking, Peet (1992) put forward several hypotheses to explain this phenomenon by associating the impact of high humidity, i.e., low vapor pressure deficits and thus low transpiration, to possible water accumulation in the peel, leading to cuticle

weakening. Knoche and Peschel (2006) developed the same hypothesis to explain peel cracking in sweet cherry. They demonstrated that high humidity conditions increased the onset of micro-cracks in sweet cherry cuticle which could lead to higher susceptibility to peel splitting. The impact of high relative humidity on peel splitting was already observed on banana by Ullah et al. (2006), and these authors attributed splitting during growth to excessive water intake in fruit.

An internal water flux leading to a change in turgor pressure because of membrane degradation and to a decrease in cellular cohesion (Jiang et al. 2004; Wade et al. 1992) may be hypothesized to explain the differences in behavior between cvs. 925 and GN under high RH storage conditions. To assess water fluxes, differences in vapor pressure between the fruit and the outer storage environment were experimentally maintained by controlling the RH storage conditions. Variations in fruit fresh mass and diameter, and in the dry matter content of both peel and pulp at high RH, did not confirm the hypothesis of excess water influx since no significant water gain in the peel was observed during ripening (Fig. 3).

Consequently, the resulting evaporation gradient was strong enough at low RH (50 %) to lead to high fruit fresh mass loss during ripening without inducing fruit splitting, whatever the cultivar. At high RH, the vapor pressure difference was very low, which limited cuticular and/or stomatal transpiration through the peel. In these conditions, the fruit surface conductance of the 100 % RH treatment was fourfold higher than that of the 50 % RH treatment for both varieties. The stomatal density observed for cv. 925 was in the same range as that of dessert banana, which was about 2.5 stomata/mm^2 (Banks 1984b; Johnson and Brun 1966), although we understand that his could differ depending on the cultivar (Vandenhout et al. 1995). The stomatal opening may thus have influenced the water flux into the peel and then fruit splitting (Burdon et al. 1993). Note, however, that the banana stomatal density was very low compared to that of the leaves (Kallarackal et al. 1990), suggesting that stomata have a negligible impact on fruit transpiration, with most of the water being lost throughout the cuticle. Moreover, since bananas are stored in darkness, which causes stomata closing, it has been proposed that water transpiration occurs mostly through the banana peel cuticle (Banks 1984b). In our hands, this negligible water flux evaporation through stomata was also confirmed since stomata closure via abscisic acid did not significantly decrease the transpiration rate. Overall, the low stomatal density in the peel compared to that of the leaves (Kallarackal et al. 1990), their varying degrees of opening (Johnson and Brun 1966), and the constant rate of fruit mass loss during storage under controlled conditions, suggests that stomata have a negligible impact, and that most of the water is lost through the cuticle.

Happi Emaga et al. (2007) showed that the pulp dry matter decreased with ripening. For these authors, the increase in pulp water content could partially be explained by osmotic transfer from the peel to the pulp, since the percentage sugar content in the pulp was higher than in the peel (56 and 66 % for cvs. GN and 925, respectively) (Fernandes et al. 1979; Loesecke 1950). We thus speculate that this is what happened to our genotypes at low RH, since the total soluble solid contents were found to be higher in the pulp than in the peel. Similarly, Paull (1996) hypothesized that osmotic and subsequent turgor changes related to neutral sugar production during ripening led to water movement from the skin and possibly receptacle to the flesh. As a final consequence, the increase in receptacle diameter increased the stress on the flesh and skin, leading to fruit splitting.

Cv. 925 was prone to peel splitting at high RH and presented a clearly thinner cuticular wax layer compared to cv. GN. This layer difference directly impacts fruit transpiration (Léchaudel et al. 2013), and as revealed by Lara et al. (2014) and Knoche and Peschel (2006) in sweet cherry fruit, the conductance decreases as the cuticle thickens. Indeed, when assessing the role of epicuticular wax in banana transpiration, we showed that, at low RH, the transpiration rate and fruit surface conductance in dewaxed peel were significantly increased for both cvs (Table 1). However, at high RH without epicuticular wax, the water loss through cv. GN peel was very little affected, whereas the transpiration rate and surface conductance of the cv. 925 peel wax were more than twofold higher. Indeed, in sweet cherry fruit, Knoche et al. (2000) showed that dewaxed cuticle led to a higher conductance and transpiration rate than waxed cuticule.

How could the higher transpiration of cv. 925 at high RH and peel splitting be explained?

In tomato peel, the higher conductance at 100 % RH was attributed to micro-crack onset (Matas et al. 2004). The presence of micro-cracks as a function of post-harvest conditions was also demonstrated by Matas et al. (2004) in cherry tomatoes and by Konarska (2013) in a fruit of the Rosaceae family. Therefore, at high RH, micro-cracks may favor higher transpiration, leading to peel splitting.

Changes in peel water content were possibly linked to specific rheological properties, leading to peel splitting (Knoche and Peschel 2006). Therefore, the better elastic properties of cv. 925 peel clearly highlight the lack of connection between the elasticity properties and cracking intensity. Post-harvest peel cracking is, hence, a different

mechanism than maturity bronzing, as discussed by Williams et al. (1989), who associated internal cracking to maturity bronzing and an insufficient epidermis elasticity.

The difference in wax thickness and its impact on the rheological properties of enzymatically isolated cuticle was studied by Petracek and Bukovac (1995). These authors claimed that wax on the cuticle only acts as a protective layer and act as a plasticizing agent on the cuticle, responding as a viscoelastic polymer under stress–strain. In agreement with these observations and hypotheses, banana cuticular membrane (dewaxed or not) became more elastic and susceptible to fracture when hydrated. At high relative humidity, the cuticle layer is thus theoretically more hydrated than at low RH. The higher thickness of the cv. GN wax layer, therefore, possibly did not limit the peel hydration and in turn the susceptibility to split. Matas et al. (2004) and Bargel and Neinhuis (2005) compared the mechanical behavior of isolated tomato cuticle and peel and found similar patterns. They suggested that cell walls contribute to the mechanical behavior of the peel to a substantial extent (resistance of the entire peel more than twofold higher than in isolated cuticle). This would potentially explain why cv. GN had a lower peel resistance and stiffness than cv. 925, whereas a thicker epicuticular wax layer would preserve the cuticle. Bargel and Neinhuis (2005) suggested that, for high strain intensity, cell walls play a key role in mechanical resistance, while at physiologically levels (i.e., at low strain), the cuticle would play a primary role in the mechanical properties.

During the critical period when peel splitting may occur, the catalase activity of cv. 925 markedly decreased, while the H_2O_2 content matched this reduction in the activity of this detoxifying enzyme (Fig. 8B). Consequently, the malondialdehyde level continuously increased as peroxidation of the lipidic membrane occurred, as previously observed (Velikova et al. 2000), and this behavior was also noted with cv. GN but to a lesser extent. This higher intensity of oxidative stress for cv. 925 was also confirmed by the higher proportion of oxidized ascorbate (dehydroascorbate form). The effect of relative humidity storage conditions on ethylene and respiration production was already studied. Burdon et al. (1994) revealed that the ACC oxidase activity of the peel reflected the ethylene production with a large increase in the low humidity stored fruit and later, a smaller increase in the high humidity stored fruit. Surprisingly, respiration and H_2O_2 production associated with an oxidative burst was not significantly different at low and high RH for the 925 cv. prone to peel crack (Fig. 8).

The higher level of electrolytes cell released through the measurement of the peel electrolyte leakage (PEL) still confirmed this trend: the critical period in terms of peel splitting was associated with a higher metabolite flux from the vacuoles to the apoplast compartment, with this flux being particularly intense for cv. 925 and associated with lipidic membrane degradation. Jiang et al. (2004) already observed this phenomenon in plantain peel during ripening.

Overall, ROS and lipidic peroxidation markers revealed that cv. 925 was highly susceptible to oxidative stress, i.e., the consequence of a set of detoxifying activities lower than that of cv. GN. Cheng et al. (2008) studied the effects of oxygen species on cellular wall disassembly of banana fruit during ripening, and suggested that this cell wall cohesion loosening might be related to non-enzymatic scission of polysaccharides (Dumville and Fry 2003). ROS, including $O_2^{\cdot-}$, H_2O_2, and OH, accumulates during ripening (Vicente et al. 2006) and OH-induced breakdown of cellular wall polysaccharides was reported in in vitro tests (Fry et al. 2002). The higher proportion of H_2O_2 in cv. 925 could partially and hypothetically explain some of the different behaviors with regard to peel splitting.

In summary, the thin cuticle and low wax content and, consequently, the specific epicuticular wax/cutin thickness ratio could act as mechanical structure regulator and directly impact fruit transpiration. The marked rise in cv. 925 fruit respiration under saturating humid conditions linked to higher solute consumption during ripening could hypothetically induce a marked decrease in the osmotic potential in fruit pulp associated with ripening. Peel water loss under saturating RH conditions would, therefore, cause a reduction in turgor pressure associated with a cellular collapse, as observed through microscopic analysis. This crack-prone cultivar showed a lack of ROS detoxifying enzymes compared to the GN reference. This not well-regulated oxidative stress for this cultivar could be one of the factors associated with peel splitting susceptibility. The much higher increase in hydrogen peroxide production for cv. 925 was indeed associated with a boost of MDA production and peel electrolyte leakage markers of cellular damage.

Authors contribution statement Pierre Brat: experimental design, planning and conducting experiments, publication writing and work coordination, students' supervisor. Mathieu Lechaudel: physiology experiments, results analysis, participation in preparing manuscript. Léa Segret: biochemical and physiological experiments, results analysis, participation in preparing manuscript. Raphaël Morillon: physiological expertise and advices, water flux measurements, participation in preparing manuscript. Olivier Hubert: fruit harvesting at targeted physiological age; rheology, microscopy experiments. Olivier Gros: microscopy experiments. Frédéric Lambert: fruit harvesting at targeted physiological age, fruits ripening. Sophie Benoit: peel splitting experiments, post-harvest conditions management. Christophe Bugaud: physiological expertise and

advices, banana ripening, peel splitting results analysis, participation in preparing manuscript. Frédéric Salmon: fruits production, banana ripening, whole post-harvest conditions management, participation in preparing manuscript.

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