Anatomical and Physiological Responses of Melting- and Nonmelting-flesh Peaches to Postharvest Chilling

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ABSTRACT. A study to compare the response to postharvest chilling (4 °C) for up to 3 weeks of melting-flesh (MF)—FL 90-20, FL 90-21W, and FL 91-16—and nonmelting-flesh (NMF)—‘Oro A’, FL 90-35C, and FL 90-47C—peach (*Prunus persica* L.) genotypes revealed that MF fruit were notably more susceptible to the development of mealiness than NMF types. Cell separation in mealy fruit was demonstrated by the release of mesocarp cells to an aqueous medium, allowing determination of mealiness severity. At a histological level, chilling brought about an impressive expansion of the intercellular spaces in MF mesocarp tissue but did not affect NMF fruit. A decrease in flesh electrical resistance after 1 week of chilling was observed only in MF fruit. However, electrical resistance increased in MF and NMF fruit following 2 and 3 weeks at 4 °C. Electrical resistance also decreased with ripening of MF fruit but did not change when NMF fruit were ripened. Unlike NMF fruit, the MF genotypes FL 90-21W and FL 91-16 showed an increase in respiration rate due to chilling. The rate of ethylene production decreased after 1 week at 4 °C in MF and NMF genotypes. However, two MF and two NMF genotypes exhibited rising ethylene levels after the second week of storage at 4 °C, while ethylene production in one MF and one NMF genotype continued to decline.

While lower temperatures contribute to prolonging peach storage life (Hardenburg et al., 1986), it has also been shown that temperatures in the range of 2.2 to 7.7 °C lead to the development of the physiological disorder known as chilling injury or internal breakdown (Anderson and Penney, 1975; Ben-Arie and Lavee, 1971; Crisosto et al., 1996). This disorder becomes evident when chilled fruit is transferred to higher temperatures that allow ripening to proceed (von Mollendorff and de Villiers, 1988).

Although variable among peach varieties, classic symptoms of chilling injury include flesh browning; a dry, coarse texture resembling corn meal (mealiness), wool (wooliness), or leather (leatheriness); failure to ripen and/or to develop normal flesh color; lack of characteristic aroma; translucency of the flesh; and, indirectly, a decreased resistance to the invasion of pathogens (Mitchell and Kader, 1989).

The leakage of solutes due to chilling injury was measured as an increase in electrolyte leakage as well as in flesh electrical conductivity. Increases in both parameters, which are thought to result from an alteration in membrane permeability, were also observed in fruit that had been ripened with no prior chilling exposure (Furmanski and Buescher, 1979). While the measurement of electrolyte leakage and electrical conductivity produced similar results, these authors noted that electrical conductivity was more sensitive than electrolyte leakage in the detection of chilling injury in peaches.

Rates of respiration and ethylene production following low

temperature exposure have provided indirect evidence of chilling injury in peaches. It has been reported that the respiration rate of ‘Peregrine’ peaches decreased sharply at the onset of wooliness, which occurred when the fruit were transferred from 2 to 10 °C. While the rate of ethylene production increased upon transfer of the fruit to 10 °C, the magnitude of the increase was lower for fruits that would ultimately develop wooliness than for those that did not (von Mollendorff and de Villiers, 1988).

Anatomically, chilled fruit with visual symptoms of mealiness are characterized by a separation of mesocarp parenchyma cells leading to increased intercellular spaces and accumulation of pectic substances in the intercellular matrix. Minimal structural changes were apparent in the cellulosic component of the cell wall of mealy fruit (Luza et al., 1992). A similar study on nectarines also related mealiness to an increase in the size of the intercellular spaces (von Mollendorff et al., 1992). In fruit that developed leatheriness rather than mealiness, intercellular spaces also increased, but the mesocarp cell walls appeared to have thickened and adopted a very irregular contour (Luza et al., 1992).

Fresh-market peach fruit is usually of MF type. Recent breeding efforts aimed to produce a firmer fresh-market fruit with a higher tolerance to mechanical damage have resulted in fresh-market NMF genotypes (Sherman et al., 1990). The main physiological distinction between MF and NMF fruit lies in their different enzymatic capacity for pectin degradation (Lester et al., 1996). A relationship between the development of mealiness and the metabolism of pectic substances has been established, with results differing among researchers (Ben-Arie and Lavee, 1971; Buescher and Frumanski, 1978; Cantor et al., 1992). Based on the different capacity for pectin degradation observed between MF and NMF peaches, experiments were conducted to determine possible differences in the anatomical and physiological responses to postharvest chilling between the two types of fruit.

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Materials and Methods

PLANT MATERIAL 1995. Plant material for 1995 as well for 1996 was obtained from the Univ. of Florida Peach Breeding Program. With the exception of 'Oro A', which is of Brazilian origin, all other NMF genotypes are the product of the hybridization of MF Florida selections with Mexican-origin clingstone genotypes. The study started in Spring 1995 with two genotypes: the MF genotype FL 91-16 and the NMF genotype FL 90-47C. Unripe fruit from each genotype were randomly obtained from trees planted at the Teaching Orchard, Horticultural Sciences Dept., Univ. of Florida, Gainesville. Both genotypes were harvested when they had reached a comparable maturity stage based on their ground color. Immediately after harvest, the fruit were separated into five lots of 20 fruit each. One lot was selected for the "unripe" evaluation. Another lot was stored at 20 °C for 3 d and was designated ripe fruit with no chilling exposure. The other three lots were stored at 4 °C and sequentially removed after 1, 2, and 3 weeks of storage, then transferred to 20 °C for 3 d, thus representing ripe fruit with 1, 2, and 3 weeks of storage, respectively. Fruit in each lot were visually rated for mealiness development. Subsequently, the same fruit were used for the measurement of electrical resistance, and samples of pericarp tissue from fruit proceeding from the unripe, ripe with no chilling exposure, and ripe with 3 weeks of storage treatments were fixed as described below for a histological study.

VISUAL RATING FOR MEALINESS DEVELOPMENT. Fruit were cut in half and evaluated for the development of symptoms of mealiness, including a coarse texture and dry, stringy appearance of the area of contact between the mesocarp and the endocarp. Fruit were classified as either mealy or not mealy. Results were expressed as percentage of mealy fruit.

ELECTRICAL RESISTANCE MEASUREMENT. The electrical resistance of the flesh was measured using a Shigometer (model OZ-86) electrical resistance detector (Osmose Wood Preserving, Buffalo, N. Y.). Measurements were conducted on intact fruit, with a small section of the peel being removed and the probes inserted 1 cm into the flesh.

MICROTECHNIQUE. For the histological study, blocks of 3 × 3 × 5 mm were sectioned from the midpoint of the fruit's mesocarp (at the equator and halfway between endocarp and exocarp). Specimens were preserved in a fixative composed of 4% glutaraldehyde, 0.2 M dipotassium phosphate, 0.1 M citric acid monohydrate, and 4% glucose at pH 7 (Luza et al., 1992). The choice of this fixative is critical, since mature peach fruit cells fixed with FAA (formalin-acetic acid-alcohol), are especially susceptible to plasmolysis with regularly recommended light microscopy fixatives. In order to speed fixation, infiltration of the fixative was promoted by placing the samples under a slight vacuum for 30 min. Before embedding, the specimens were washed in 128 mmol·L⁻¹ NaCl, 10 mmol·L⁻¹ phosphate buffer at pH 7.2, and transferred every 30 min through a series of alcohol dilutions according to the following schedule: 1) 10% ethanol, 2) 25% ethanol, 3) 50% ethanol, 4) 75% ethanol, 5) 50% LRWhite resin/47.5% alcohol/2.5% distilled water, and 6) 75% LRWhite resin/23.5% alcohol/1.5% distilled water. Four percent sucrose was added to each of the alcohol dilutions in order to approximate the osmolality of the tissue (Luza et al., 1992). One resin change was carried out before the final embedding in LRWhite resin. Blocks were trimmed, and 2-μm sections were cut using glass knives on a LKB 3-8800 ultramicrotome (LKB, Bronna, Sweden). For pectin localization, sections were stained in a 0.5% aqueous solution of ruthenium red (Gahan, 1984). Slides were observed using a Labophot-2 light microscope (Nikon, Tokyo, Japan) at 25× and 100× magnification. Photographs were taken

using a Microflex UFX-DX photomicrographic attachment (Nikon, Tokyo, Japan).

PLANT MATERIAL 1996. In Spring 1996, three MF genotypes—FL 90-20, FL 90-21W, and FL 91-16—and three NMF genotypes—'Oro A', FL 90-35C, and FL 90-47C—were studied. The source of the fruit was the same as in 1995 and pairs of MF and NMF genotypes at a comparable maturity were harvested on the same date. Following harvest, all fruit were stored at 4 °C. After 1, 2, and 3 weeks of storage, lots of 15 fruit were removed from storage and transferred to 20 °C for 3 d for ripening and/or symptom development.

ETHYLENE PRODUCTION AND RESPIRATION RATE DETERMINATION. One hour before the removal of the fruit from 4 °C, and 24 h after the transfer to the 20 °C, respiratory and ethylene production rates were measured using a static system. Ethylene production and respiration rate were measured on three replicates of three fruit each, which were sealed for 1 h in 1.75-L glass jars. For headspace sampling, syringes were inserted through rubber septa affixed on the lid. Samples for the determination of ethylene were analyzed using a gas chromatograph equipped with an activated alumina-packed column and a photoionization detector. Samples for the determination of CO₂ were analyzed using a gas chromatograph equipped with a Columnpack-packed column and a thermal conductivity detector.

VISUAL RATING FOR MEALINESS DEVELOPMENT. After removal from 20 °C, each lot of 15 were visually evaluated for mealiness as

Fig. 1. Flesh electrical resistance of unripe and ripe fruit and of fruit stored for 1, 2, and 3 weeks at 4 °C and subsequently ripened at 20 °C. Treatments: 0 W + R = no storage at 4 °C and 3-d ripening at 20 °C; 1 W + R = 1-week storage at 4 °C and 3-d ripening at 20 °C; 2 W + R = 2-week storage at 4 °C and 3-d ripening at 20 °C; 3 W + R = 3 week-storage at 4 °C and 3-d ripening at 20 °C. MF = melting flesh, NMF = nonmelting flesh. Results are means of 20 measurements. Bars represent standard error.

Fig. 2. Light micrographs of mesocarp cells of unripe FL 91-16 (MF) and FL 90-47C (NMF) fruit. MF fruit at 25 $\times$ (A) and 100 $\times$ (B) and NMF fruit at 25 $\times$ (C) and 100 $\times$ (D). MF = melting flesh, NMF = nonmelting flesh.

described for the 1995 study. The rating was based on a four-point scale with the following categories: not mealy, slightly mealy, moderately mealy, and severely mealy. Results were expressed as percentage of fruit in each category.

CELL SEPARATION PROCEDURE. A subplot of the 15 fruit used for the visual evaluation were subjected to a cell separation procedure, which was developed by Ahrens (1989) to assess variations in mealiness among tomato genotypes. For this procedure, 40 mesocarp disks 5 mm in diameter and 3 mm in thickness were cut from five fruit using a cork borer and a razor blade to slice the individual disks. The disks were placed in 30 mL of isotonic (7.48%) sorbitol, as deduced from the work of Luza et al. (1992). Flasks (three per genotype) were sealed with parafilm and shaken at 100 rpm at room temperature using a gyratory shaker. After 1 h, 3-mL aliquots of the bathing solution were drawn from each flask and pipetted into cuvettes for spectrophotometric analysis of the optical density at 600 nm using a Spectronic 20 (Bausch and Lomb, Rochester, N.Y.) to quantify the number of cells released to the solution.

Results and Discussion

1995 STUDY. The visual rating for mealiness development revealed that the NMF genotype, FL 90-47C, did not show symptoms of this disorder at any point during the 3-week storage period. On the other hand, 62% and 58% of fruit of the MF genotype FL 91-16 showed evidence of mealiness after the second week and the

third week of storage, respectively. This difference in behavior between the two types of fruit as a result of a chilling exposure was also observed when measuring the flesh electrical resistance. In ripe MF fruit, electrical resistance (Fig. 1) followed an upward trend with increased chilling exposure, similar to that observed by Furmanski and Buescher (1979) in the genotypes 'Dixired', 'Loring,' and 'Redhaven'. Ripening of MF fruit in the absence of chilling brought about a decrease in the flesh electrical resistance, which could be attributable to an increase of electrolyte leakage associated with the ripening process. The flesh electrical resistance was also depressed after 1 week at 4 °C plus 3 d at 20 °C compared with the levels of unripe fruit. This decrease may have been caused by the increased levels of electrolyte leakage that result from the disruption of membranes due to chilling injury, or possibly ripening, since 1 week at 4 °C was not enough to produce visible symptoms of chilling injury. The increase in electrical resistance observed in the MF genotype after 2 or 3 weeks at 4 °C plus 3 d at 20 °C might be due to the binding of ions to the low methoxyl pectic substances that become available after a chilling exposure (Ben-Arie and Lavee, 1971). Dawson et al. (1993) concluded that the high calcium uptake and cation exchange capacity of mealy fruit as opposed to normal fruit were due to the increase in high-molecular weight, partially esterified pectins, which are rich in binding sites and occur in association with mealiness.

While an increase in electrical resistance was also observed in NMF fruit following 2 and 3 weeks of chilling exposure, there was no decrease in flesh electrical resistance associated with either ripening or 1 week of chilling exposure (Fig. 1). Apparently, membrane permeability was not severely compromised during the ripening of the NMF fruit. Similarly, chilling did not translate into

a significant efflux of ions that could be detected by changes in electrical resistance.

Histological analysis of unripe MF and NMF fruit revealed a fair resemblance between the two types of fruit (Fig. 2). Although the contour of the mesocarp cells in NMF fruit tended to be more angular, in both MF and NMF fruit there was a wide range of cell dimensions, and cells appeared turgid, well-structured, and with sharply defined intercellular spaces. The intensity of the ruthenium red stain (shown in the Figures as dark-gray to black tone) between cells of MF and NMF fruit reflected the integrity of the middle lamella.

In fruit that were ripened without a chilling episode, a distinction could be made between the two types of fruit (Fig. 3). In MF fruit, cells had undergone separation (dissolution of the middle lamella as evidenced by a lack of stain between the cells) and, frequently, intercellular spaces adopted the form of crevices among cells. Despite cell separation in MF tissue, cell integrity remained uncompromised. In NMF fruit, cells retained good contact, the red stain followed the contour of the cells, and intercellular spaces were more prevalent in the areas where more than two cells faced one another.

Likewise, a clear distinction between MF and NMF fruit could be made in fruit that were ripened after 3 weeks of storage at 4 °C (Fig. 4). In MF fruit, which had developed the classical symptoms of mealiness, the most obvious characteristics were a complete lack of staining for pectin and an impressive enlargement of the intercellular spaces to create pockets in certain regions of the tissue. In addition, some of the cells had adopted an irregular contour. In NMF fruit, although cells had become somewhat more contorted, the general anatomy of the tissue did not differ substan-

tially from that of ripe fruit that had not undergone a chilling episode.

The histological observations validate the different behaviors observed between MF and NMF fruit with regard to their propensity to develop mealiness. While the mesocarp cells of MF fruit underwent a massive separation following chilling, the cellular organization of NMF fruit remained almost unaltered from its unripe stage. Similarly, in a comparative study between an early-season (chilling-resistant) and a late-season (chilling-susceptible) nectarine cultivar, King et al. (1989) noted that chilling injury in the susceptible cultivar was evidenced as an incomplete process of cell wall degradation, which compromised the middle lamella, but not the remainder of the cell wall.

An increase in the size of the intercellular spaces of mesocarp cells with chilling injury was also reported by Luza et al. (1992) and von Mollendorff et al. (1992). Based on our staining procedure, no pectin was detected in those spaces. On the other hand, physical estimations of the internal air space in mealy nectarine tissue provide support to our findings. Higher volumes of air space were found in the mesocarp of nectarines that ripened after cold storage as opposed to those ripened with no prior chilling exposure (Harker and Sutherland, 1993; Dawson et al., 1993). Furthermore, nuclear magnetic resonance imaging and X-ray computed tomography of chill-injured nectarines, revealed the appearance of small and numerous gas inclusions in the mesocarp tissue of mealy nectarine fruit (Sonogo et al., 1995).

Fig. 3. Light micrographs of mesocarp cells of ripe, nonchilled FL 91-16 (MF) and FL 90-47C (NMF) fruit. MF fruit at 25× (A) and 100× (B) and NMF fruit at 25× (C) and 100× (D). MF = melting flesh, NMF = nonmelting flesh.

Fig. 4. Light micrographs of mesocarp cells of chilled and further ripened FL 91-16 (MF) and FL 90-47C (NMF) fruit. MF fruit at 25 $\times$ (A) and 100 $\times$ (B) and NMF fruit at 25 $\times$ (C) and 100 $\times$ (D). MF = melting flesh, NMF = nonmelting flesh.

1996 STUDY. While none of the three NMF genotypes harvested in 1996 developed visual symptoms of mealiness, the MF genotypes did. Two of the MF genotypes (FL 90-20 and FL 91-16) developed mealiness after 1 week of storage at 4 °C and the third MF genotype (FL 90-21W) developed mealiness after 2 weeks of storage (data not shown).

The cell separation procedure used to assess mealiness in the fruit harvested in 1996 proved to be an effective approach for the objective determination of tissue mealiness (Table 1). In all NMF genotypes, the absorbance of the bathing solution remained fairly stable after 1, 2, and 3 weeks of storage. This would indicate that the number of cells released to the medium was not substantially altered by the length of the chilling exposure of the fruit. On the other hand, in the MF genotypes FL 90-20 and FL 91-16, where mealiness developed after the first week of storage, the increase observed in the absorbance of the bathing solution is an indication of the increase in the number of cells released into the medium. In the MF genotype FL 90-21W, however, in which mealiness was in fact observed after 2 weeks of chilling exposure, no increase in absorbance could be detected. Due to the fact that this was the only white-fleshed genotype, it is likely that the wavelength at which absorbance was being measured (600 nm) was ineffective in the quantification of the apigmented cells.

An experiment was conducted to determine if the pattern of cell separation of MF fruit was the same for ripe fruit that underwent chilling and those that did not (Fig. 5). Microscopic observation of aliquots of the bathing solution of disks of chilled and nonchilled

fruit revealed that mesocarp cells of nonchilled, ripe fruit were generally released individually, while mesocarp cells of chilled fruit were released in clumps. These dissimilar patterns of separation are in agreement with the histological work conducted in 1995. While many cells appeared to have reached a high degree of separation in nonchilled ripe fruit, cell separation was not as extensive in chilled ripe fruit and it occurred mostly in the form of large air pockets among groups or clumps of cells.

The respiration rate of peaches at 4 °C and 24 h after transfer from 4 to 20 °C is shown in Fig. 6. While the respiration rate of both MF and NMF genotypes tended to increase slightly with storage time at 4 °C, more pronounced rises were observed in the MF genotypes FL 90-21W and FL 91-16 when the fruit were transferred to 20 °C after 1, 2, and 3 weeks of storage at 4 °C. Conversely, in the NMF

Table 1. Absorbance (600 nm) of bathing solution of tissue disks after 1 hour of incubation.

Genotype	Storage time (weeks)		
	1	2	3
MF ^(y)			
FL 90-20	0.09 $\pm$ 0.002 ^z	0.13 $\pm$ 0.007	0.19 $\pm$ 0.002
FL 90-21W	0.06 $\pm$ 0.001	0.05 $\pm$ 0.002	0.05 $\pm$ 0.001
FL 91-16	0.07 $\pm$ 0.000	0.12 $\pm$ 0.003	0.21 $\pm$ 0.008
NMF			
Oro A	0.05 $\pm$ 0.000	0.05 $\pm$ 0.000	0.07 $\pm$ 0.001
FL 90-35C	0.08 $\pm$ 0.001	0.08 $\pm$ 0.001	0.07 $\pm$ 0.000
FL 90-47C	0.07 $\pm$ 0.001	0.06 $\pm$ 0.000	0.07 $\pm$ 0.000

^zAverages of three replications $\pm$ standard errors.

^yMF = melting flesh, NMF = nonmelting flesh.

Fig. 5. Pattern of cell separation in ripe nonmealy (A) and mealy (B) melting flesh fruit.

genotypes 'Oro A' and FL 90-47C, transfer of the fruit from 4 to 20 °C resulted in decreases of the respiration rate over storage time. Although the experimental setup was different, these results are in contrast to those of von Mollendorff and de Villiers (1988), who noted that mealiness was associated with a decrease in the respiration rate.

The rate of ethylene production as affected by the chilling exposure is shown in Fig. 7. Except in the NMF genotype FL 90-35C, a substantial drop in ethylene production upon removal of the fruit after 2 weeks of storage at 4 °C was observed compared to the levels seen after 1 week at 4 °C. This decrease can be interpreted as an inhibition in the production of ripening-related ethylene as a result of chilling. It was noted by von Mollendorff and de Villiers (1988) that chill-injured peaches had a reduced capability for ethylene production. After the third week, however, four of the genotypes (FL 90-20, 'Oro A', FL 90-21W, and FL 90-35C) showed an increase in the production of ethylene. Presumably, the mechanism of synthesis was restored and the release of the gas was resumed. The increased ethylene production after 3 weeks at 4 °C in those genotypes may be stress-associated. As pointed out by Mitchell and Kader (1989), later season peach cultivars tend to increase in susceptibility to chilling injury and this might explain why the later season genotypes, FL 91-16 and FL 90-47C, did not recover their ethylene production capability in the latter part of the storage period.

It is unclear whether the lower susceptibility to mealiness development observed in the NMF genotypes can be traced to a

lower sensitivity of these genotypes to chilling injury or to a block in the mechanisms leading to symptom development. Some physiological determinations did not correspond closely to the visual evaluation of mealiness. It should be noted that although ethylene production and respiration did not reveal a consistent difference between MF and NMF fruit, electrical conductivity, a determination that provides a key indication of chilling injury, did not decrease in NMF fruit as a result of the chilling exposure.

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Fig. 6. Respiration rate following 1, 2, and 3 weeks at 4 °C and transfer to 20 °C for 24 h. (A) FL 90-20 (MF) and Oro A (NMF). (B) FL 90-21W (MF) and 90-35C (NMF). (C) FL 91-16 (MF) and FL 90-47C (NMF). MF = melting flesh, NMF = nonmelting flesh.

Fig. 7. Ethylene production following 1, 2, and 3 weeks at 4 °C and transfer to 20 °C for 24 h. (A) FL 90-20 (MF) and Oro A (NMF). (B) FL 90-21W (MF) and FL 90-35C (NMF). (C) FL 91-16 (MF) and FL 90-47C (NMF). MF = melting flesh, NMF = nonmelting flesh.

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