Ripening of Nectarine Fruit

Changes in the Cell Wall, Vacuole, and Membranes Detected Using Electrical Impedance Measurements

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Electrical impedance measurements were used to characterize changes in intracellular and extracellular resistance as well as changes in the condition of membranes during ripening of nectarines (Prunus persica [L.] Batsch cv Fantasia). These measurements were related to changes in fruit texture assessed by flesh firmness and apparent juice content. An electrical model indicated that, during ripening (d 1-5) of freshly harvested fruit, the resistance of the cell wall and vacuole declined by 60 and 26%, respectively, and the capacitance of the membranes decreased by 9%. Accurate modeling of the impedance data required an additional resistance component. This resistance, which declined by 63% during ripening, was thought to be associated with either the cytoplasmic or membrane resistance. Changes in tissue resistance measured using low frequencies of alternating current were closely related to flesh firmness. After storage at 0°C for 8 weeks, the nectarines developed a woolly (dry) texture during ripening at 20°C. The main difference between these chilling-injured nectarines and fruit ripened immediately after harvest was the resistance of the cell wall, which was higher in woolly tissue (4435 Ω after 5 d at 20°C) than in nonwoolly tissue (2911 Ω after 5 d at 20°C). The results are discussed in relation to physiological changes that occur during the ripening and development of chilling injury in nectarine fruit.

Fruit ripening involves a complex series of changes including cell wall degradation, alteration of membrane condition and function, changes in compartmentation of solutes, and metabolic changes associated with the climacteric (Brady, 1987). In stonefruit, these changes result in the softening of the mesocarp tissue and development of a juicy texture. When stonefruit such as peaches and nectarines are stored at low temperatures for more than 3 weeks, they tend to develop chilling injury and ripen abnormally (Lill et al., 1989). As a result of this abnormal ripening, the cell wall fails to degrade according to the usual pattern, and although the mesocarp softens, the texture of the tissue becomes dry (Ben-Arie and Lavee, 1971; Dawson et al., 1992). Fruit with this dry texture are often described as being woolly or mealy.

Cell wall changes during nectarine ripening have been studied by Dawson and co-workers (1992). They found that during normal ripening the pectic polymers were solubilized, had their galactan side chains removed, and were depolymerized to lower molecular weights. In comparison, pectins from woolly nectarines were not depolymerized, nor were the side chains removed to the same extent as in normally ripened fruit. These results suggest that altered pectic polymer breakdown is associated with the development of woolliness. In peaches, chilling injury has been related to an imbalance between pectinesterase and polygalacturonase, which cause an accumulation of esterified pectin (Ben-Arie and Sonego, 1980; Ben-Arie et al., 1989). These pectins are thought to form a gel-like structure in the cell wall and interfere with the release of juice into the mouth during chewing (Ben-Arie and Lavee, 1971), even though the water content of the tissue is not excessively altered (Ben-Arie et al., 1989). Harker and Sutherland (1993) examined fracture surfaces following application of tensile tests to plugs of nectarine tissue and found that the surface of cells from ripe tissue was covered in juice, but the surface of cells from woolly tissue was dry.

Changes in the condition of the tissue can be inferred from studies of electrolyte leakage. Electrolyte leakage was greater in ripe than unripe peach tissue and was lower in ripe woolly than in ripe nonwoolly tissue (Furmanski and Buescher, 1979). These results suggest that the permeability/leakiness of the plasma membrane and tonoplast might have changed during ripening and during development of mealiness. However, the cell wall can also provide a barrier to leakage of electrolytes from fruit cells, and Furmanski and Buescher (1979) interpreted the reduction in electrolyte leakage from mealy tissue as being related to increased binding of electrolytes into the cell wall. Dawson et al. (1993) found that changes in cation-binding capacity of the cell wall in mealy nectarines could modify calcium uptake into and efflux from cells. Thus, whereas increases in electrolyte leakage during normal ripening may reflect increases in membrane permeability, the reductions in leakage that occur during development of chilling injury may be due to cell wall changes.

Electrical impedance may provide a method of simultaneously examining changes occurring in fruit tissue during ripening, since it can be used to detect changes in the resistance of intracellular and extracellular compartments (Stout, 1988). In plants, electrical impedance has been used mainly

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Abbreviation: AJC, apparent juice content.
to examine chilling injury and cold acclimation (Stout, 1988; Zhang and Willison, 1992). At low frequencies, electrical current is unable to cross the plant plasma membrane and is confined to an extracellular pathway, whereas at high frequencies the current will travel via the symplast (Stout, 1988). Evidence for this was elucidated during early studies using cell cultures (Cole, 1972, and refs. therein). More recently, models based on circuit diagrams have been developed that allow complex impedance relationships to be resolved into resistances of the cell wall, cytoplasm, and vacuole, as well as the capacitances of the plasma membrane and tonoplast (Zhang and Willison, 1991). Although based on cell structure, such models are adapted empirically by adding or deleting components until the mathematical function gives the best fit to the impedance data. Thus, the only evidence that specific resistance or capacitance terms are associated with cell structures derived from early studies (Cole, 1972, and refs. therein) that demonstrated that intracellular and extracellular zones are separate and that intact membranes are required for capacitance measurements.

Previous studies have investigated the conductivity (inverse of resistance) of whole peaches at low frequencies of alternating current (Furmanski and Buescher, 1979; von Molendorff et al., 1992). In both studies conductivity increased during ripening but was lower in ripe woolly than in ripe nonwoolly peaches. However, these studies did not differentiate between conductivity of the fruit flesh and conductivity associated with electrochemical interactions occurring between the metal electrodes and the fruit tissue. The resistances associated with electrochemical interactions occurring at the electrode are often greater than the resistance of the fruit itself (Harker and Dunlop, 1994).

In the present study, we have used a wide range of frequencies to characterize the impedance of blocks of nectarine tissue, taking care to differentiate between electrode and tissue effects. This has allowed a more detailed characterization to be made of the changes in impedance that occur during fruit ripening. Changes in cell wall, cytoplasmic and vacuolar resistance, and membrane resistance and capacitance have been modeled using the data from the impedance study.

**MATERIALS AND METHODS**

**Plant Material**

Mature nectarines (*Prunus persica* [L.] Batsch cv Fantasia) weighing approximately 200 g were harvested from a commercial orchard in Hawkes Bay. Fruit were assessed after ripening at 20°C for 1, 3, 5, and 7 d or placed in cool storage at 0°C within 1 d of harvest. Samples of fruit were removed from cool storage after 1, 2, 3, 4, 6, and 8 weeks and assessed after 1, 3, and 5 d at 20°C. At each sampling date 10 fruit were assessed for flesh firmness, AJC, and tissue impedance. Firmness (skin removed) was assessed by a single measurement at the equator of each nectarine, using a hand-held Effigi-type penetrometer with a 7.5-mm-diameter probe. Single plugs of mesocarp tissue were removed from each fruit and assessed for AJC using the method of Lill and van der Mespel (1988). To measure impedance, a tangential block of mesocarp tissue 10 × 10 × 50 mm was removed along the equator of the fruit from the opposite side of the fruit to the firmness measurement. The tissue block was impaled onto a linear array of five silver electrodes (0.6 mm diameter), such that the electrodes were oriented in a radial position with respect to the original fruit. At each sampling time, impedance measurements were made in blocks of tissue from five fruit using the full range of AC frequencies. Results from these fruit were used for impedance modeling. Blocks of tissue from the remaining five fruit were assessed at frequencies of 50 Hz and 300 kHz.

**Impedance Measurements**

Impedance was measured using methods described in detail previously (Zhang and Willison, 1991; Harker and Dunlop, 1994) using a function generator (Thurby Thandar model TG230, Huntingdon, UK), an oscilloscope (Iwatsu model SS-7610, Tokyo, Japan), and an array of five electrodes. Alternating current at frequencies between 50 Hz and 1 MHz were passed along the length of the tissue block, and impedance was measured at interelectrode distances of 10, 20, and 30 mm. All measurements were made inside a Faraday cage. Complex impedance was separated into its resistive and reactive components (reactance being related to the capacitance of the tissue) using formulas described by previous workers (Zhang and Willison, 1991). The impedance characteristics of the tissue were separated from electrochemical interactions that occurred at the electrode by plotting resistance and reactance against interelectrode distance. The resulting slope relates to tissue characteristics and the intercept on the y axis to the electrochemical interaction between the metal electrode and the fruit tissue (Zhang and Willison, 1991). Only tissue resistance and reactance were considered further. In the figures, a single ± value based on a pooled estimate of the SD is presented whenever the variance is sufficiently homogenous to make this acceptable.

**Modeling of Impedance in Fruit Tissue**

The values for tissue resistance and reactance were fitted to the mathematical model described by the circuit diagram shown in Figure 1A. This model was developed during research on parenchymatous plant tissues (Zhang et al., 1990; Zhang and Willison, 1991) and is used to separate tissue impedance into the resistive and capacitive components associated with cell structures, including the cell wall, plasma membrane, cytoplasm, tonoplast, and vacuole. Fitting of the nectarine data to the circuit diagram was achieved using a function (nlmin) in S-PLUS (Statistical Sciences Inc., 1991). The function (nlmin) requires the following parameters: (a) the name of an S-PLUS function that for each set of input parameters gives the value of the criterion to be minimized (total of the sum of squares of residuals for resistance and reactance), (b) starting values, and (c) information concerning how to scale parameters so that they are comparable. The S-PLUS function that calculated the sum of the squares of residuals criterion used complex number arithmetic to implement the formulas displayed in Figure 2. Alternatively, one may use the more complicated formulas given by Zhang and Willison (1991), which use real arithmetic. Values for $C_τ$ (tonoplast capacitance) and $C_p$ (plasma membrane capacitance) were set equal. Justification for this is: (a) the area of plasma membrane and tonoplast will be similar given the
blocks of tissue from 10 fruit, and the mean resistance was calculated. Changes in the resistance of the low-frequency (50 Hz, extracellular) pathway and the high-frequency (300 kHz, intracellular) pathway through the tissue in response to storage and ripening are presented in Figure 3. The resistance at 300 kHz is relatively low (approximately 200 Ω) and does not change during storage or ripening (Fig. 3B). The resistance at 50 Hz declined from approximately 7000 to 3500 Ω in response to ripening (Fig. 3A). After fruit had been cool stored for 4 or more weeks, the resistance (50 Hz) did not decline to the same extent during ripening at 20°C as fruit cool stored for shorter periods. The low-frequency (50 Hz) resistance was closely related to the flesh firmness of the fruit (Fig. 4A). Flesh firmness was measured on one side of the fruit, and resistance was measured on the other side. The different sides may have been at different stages of ripeness, which would contribute to scatter (Fig. 4A). Low-frequency resistance was also closely related to the AJC of the nectarine flesh (Fig. 4B).

Compartment Analysis

Analysis of impedance in cell compartments, using the circuit diagram (Fig. 1A), was accomplished using blocks of

vacuolated nature of fruit cells, (b) the values for specific capacitance are relatively consistent across a diverse range of animal and plants (1 μF/cm²; Cole, 1975), and (c) calculations that allowed distinct values gave estimates for C₃ and C₄ that were nearly identical. Other studies have also found that C₃ and C₄ are similar (Zhang and Willson, 1991).

In addition, two alternative models (Fig. 1, B and C) proposed by Hayden et al. (1969) and Zhang et al. (1990) were used to analyze the impedance data from an unripe and ripe nectarine. The results of these alternative analyses were compared with those obtained using the circuit diagram shown in Figure 1A.

RESULTS

Resistance at High and Low Frequencies

At each sampling time, resistances measurements were made at alternating frequencies of 50 Hz and 300 kHz on

Set

\[ Z_1 = \frac{1}{R_2 + j(2\pi fC_3)^{-1}} \]

Then

\[ R_t - jX_t = \frac{1}{R_t + jZ_1 - j(2\pi fC_3)^{-1}} \]

where

- \( R_t \) = resistance
- \( X_t \) = reactance.
- \( j \) is the complex square root of \(-1\), \( W_t \) is the frequency of the applied voltage, and we assume \( C_3 = C_5 \).

Figure 2. Formulas used to model circuit diagram (Fig. 1A) using S-PLUS. Components are as in Figure 1.

Figure 3. Changes in tissue resistance at 50 Hz (A) or 300 kHz (B) of nectarines cool stored at 0°C for 0 to 8 weeks before ripening at 20°C for 5 to 7 d. Each series of successive points represent assessments at d 1, 3, 5, and 7, and each point represents the mean value for 10 fruit. The SE is calculated from a pooled estimate of the SD and is presented in the upper right corner of each graph. The number of weeks the fruit was stored before ripening at 20°C is indicated by the number above each curve.
tissue from nectarines ripened at 20°C after cool storage for 0 and 8 weeks at 0°C. Impedance measurements were made using 14 different frequencies of alternating current. Cole-cole plots (reactance plotted against resistance for each frequency used) produced semicircular patterns that contracted as the fruit ripened (Fig. 5). When blocks of tissue were freeze-thawed, all points on the semicircle were superimposed at a single position close to the origin (Fig. 5).

The raw data (resistance and reactance at different frequencies) were modeled using the circuit diagram (Fig. 1A). Figure 6 is an example of the fit of the model to the raw data. During ripening (d 1–5) of freshly harvested nectarines, cell wall resistance \( R_1 \) declined by 60%, cytoplasm resistance \( R_2 \) by 63%, vacuole resistance \( R_3 \) by 26%, and membrane capacitance \( C_3 \) and \( C_4 \) by 9% (see Fig. 7 for precision of measurements). The decrease in capacitance was 0.10 nF/d \( (s_e = 0.04, P = 0.028) \). Compared with nectarines stored for 0 weeks, fruit stored for 8 weeks showed (a) a slower decline in \( R_1 \) (33 versus 60%, \( P < 0.005 \)) and (b) after a substantial decline in \( R_2 \) during cool storage (42%, \( P < 0.01 \)) little further change so that \( R_2 \) on d 5 was similar to that for unstored fruit (Fig. 7).

In addition to the primary model proposed by Zhang and Willison (1991; Fig. 1A), we examined both a simpler version of the model (as proposed by Hayden and co-workers, 1969; Fig. 1B) and a more elaborate version (as proposed by Zhang et al., 1990; Fig. 1C), which includes membrane resistances.

**Figure 5.** Cole-cole plots showing the relationship between reactance and resistance in individual tissue blocks excised from unripe (●) or ripe (□) nectarines and in a tissue block that had been frozen and then thawed (▲). Arrows indicate the frequencies used to give values at particular points.

**Figure 4.** Relationship between tissue resistance at 50 Hz and flesh firmness (A) or AIC (B) of nectarines at different stages of ripening after 0 to 3 weeks of cool storage at 0°C. In A points represent flesh firmness (N) and resistance (Ω) measured on opposite sides of each fruit; \( y = 2833 \pm 115 + 70.68 \pm 3.93\times \) (correlation between intercept and slope \( r = 0.681 \)). In B points represent AIC (%) and resistance (Ω) measured on different parts of each fruit; for AIC \( ≤ 35\% \) the curve is close to linear, with equation \( y = 824.8 \pm 139 \) (correlation between intercept and slope \( r = -0.898 \)). The curve was obtained using the S-PLUS lowess smoothing function.

**Figure 6.** An example of the fit of the model (circuit diagram, Fig. 1A) to the data collected during impedance measurements using a block of tissue excised from an unripe nectarine. Points represent experimental measurements and curves are fitted using the model.
in parallel to membrane capacitances. The values for \( R_1 \) and \( R_4 \) and \( C_1 \) and \( C_3 \) were relatively consistent over all models, as were the changes during ripening (Table I). Because we set \( C = C_1 = C_3 \), both the Hayden (Fig. 1B) and the primary Zhang and Willison (Fig. 1A) models have the same number of parameters. The Hayden model, which includes a membrane resistance (\( R_3 \)) but not a cytoplasmic resistance (\( R_2 \)) (whereas the primary Zhang and Willison model has \( R_2 \) but not \( R_3 \)), did not fit well. We found it impossible to get a good fit to the data with any model that had less than four parameters. The Hayden and the primary Zhang and Willison models predict reductions in membrane or cytoplasm resistance, respectively, during ripening (Table I). The Hayden model underestimated resistances at frequencies between 50 and 300 Hz, overestimated resistances between 300 and 1000 kHz, and overestimated reactance between 3 and 10 kHz. Moreover, the final values were unstable, depending on the starting value used in the S-PLUS program. In the elaborate version of the Zhang and Willison model (Zhang et al., 1990; Fig. 1C), membrane resistances (\( R_3 \)) were exceedingly high, unstable for ripe fruit, and had little influence on estimates of \( R_1, R_2, R_4, C_1, \) and \( C_3 \). Thus, there was no reason to use it. The primary Zhang and Willison model (Fig. 1A) was used in subsequent analysis of impedance data.

**Fruit Texture**

Nectaries stored for 0 to 3 weeks at 0°C ripened normally, developing a juicy melting texture, as is shown by the increase in \( A_{JC} \) during the ripening period (Fig. 8). Fruit stored for 4 to 8 weeks developed a dry texture when allowed to ripen, as is indicated by the low \( A_{JC} \) after 5 d of ripening (Fig. 8). However, the dryness of the flesh was associated with a slightly tougher texture than usually found in chill-injured stonefruit.

**DISCUSSION**

**Identification of Compartments**

The exclusion of low-frequency, alternating current from symplastic pathways has been demonstrated using single cells and complex tissues from animals and plants (Cole, 1972). In plant tissues, the resistance of an extracellular pathway should be high because of the small cross-sectional area of

Table 1. Comparison of the values for resistances and capacitances of specific cell structures as were predicted by different electrical models for an individual unripe and ripe nectarine

<table>
<thead>
<tr>
<th>Components</th>
<th>Models</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Zhang and Willison</td>
</tr>
<tr>
<td></td>
<td>Hayden</td>
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<tr>
<td></td>
<td>Elaborate version of</td>
</tr>
<tr>
<td></td>
<td>Zhang and Willison</td>
</tr>
<tr>
<td>Unripe nectarine</td>
<td></td>
</tr>
<tr>
<td>Cell wall resistance (( R_1 ))</td>
<td>7347</td>
</tr>
<tr>
<td>Vacuole resistance (( R_4 ))</td>
<td>245</td>
</tr>
<tr>
<td>Membrane capacitance (( C ))</td>
<td>4.39</td>
</tr>
<tr>
<td>Membrane resistance (( R_3 ))</td>
<td>71 ( \times 10^1 )</td>
</tr>
<tr>
<td>Cytoplasm resistance (( R_2 ))</td>
<td>4206</td>
</tr>
<tr>
<td>SS of residuals</td>
<td>717</td>
</tr>
<tr>
<td>Ripe nectarine</td>
<td></td>
</tr>
<tr>
<td>Cell wall resistance (( R_1 ))</td>
<td>2884</td>
</tr>
<tr>
<td>Vacuole resistance (( R_4 ))</td>
<td>218</td>
</tr>
<tr>
<td>Membrane capacitance (( C ))</td>
<td>4.52</td>
</tr>
<tr>
<td>Membrane resistance (( R_3 ))</td>
<td>14 ( \times 10^4 )</td>
</tr>
<tr>
<td>Cytoplasm resistance (( R_2 ))</td>
<td>1561</td>
</tr>
<tr>
<td>SS of residuals</td>
<td>296</td>
</tr>
</tbody>
</table>

2884

218

8051

247

4.61

75 \( \times 10^3 \)

4276

681

2884

218

4.52

33 \( \times 10^6 \)

1561

296
the wall and the low concentration of mobile ions. When cell membranes are damaged by freeze-thawing or boiling, compartmentation is broken down and low-frequency current is able to pass through the entire cross-section of the tissue, resulting in a reduction in resistance (Fig. 5; Hayden et al., 1969). The low-frequency resistance of freeze-thawed tissue is similar to the high-frequency resistance of undamaged tissue, confirming that the high-frequency resistance of tissue was associated with the intracellular concentration of mobile ions. In nectarine tissue, the resistances measured at high frequencies were associated mainly with vacuole resistance, as is indicated by similar values for resistances at 300 kHz (Fig. 3B) and vacuole resistance (Fig. 7). This would be expected since the vacuole fills most of the intracellular volume of fruit cells and contains high concentrations of ions.

A number of models (circuit diagrams) have been used to describe the flow of current through plant tissues. Zhang and Willison (1991) fitted these models to data collected using blocks of tissue excised from carrot root and potato tuber, and they found that the model presented in Figure 1A most closely fit their data. Inherent in this model is the transmembrane resistance, which is generally assumed to be so high that it can be excluded from the analysis (Zhang et al., 1990). However, in nectarine fruit tissue this assumption may not be correct since membranes are known to become leaky during ripening of stonefruit (Furmanski and Buescher, 1979; Dawson et al., 1993).

Justification for the identification of \( R_t \) and \( R_v \) as the cell wall and vacuole resistances is well established, as discussed earlier. A further term, \( R_s \) (Fig. 1A), is required to obtain a good fit of the model to the data. Zhang and Willison (1991) identified \( R_s \) as the cytoplasmic resistance, although without experimental justification. One alternative is that \( R_s \) may be associated with membrane resistance. In another model proposed by Hayden et al. (1969), a term for membrane resistance occurs in a position that will have a similar influence on impedance to \( R_t \) in the Zhang and Willison model (Fig. 1A and B). Preliminary analysis of the impedance changes during nectarine ripening using the Hayden model (Fig. 1B) indicated that the influence of membrane resistance during fitting of the data is similar to the influence of \( R_t \) in the Zhang and Willison model (Fig. 1A; Table I). Establishment of the identification of \( R_s \) as either cytoplasmic or membrane resistance is important since \( R_t \) declined during nectarine ripening (Fig. 7).

The changes in \( R_t \) during fruit ripening may reflect a decrease in the membrane resistance for the following reasons. First, an increase in membrane permeability during ripening of stonefruit has been demonstrated in ion leakage studies (Furmanski and Buescher, 1979; Dawson et al., 1993), whereas there is no information available concerning changes in the cytoplasm. Second, the contraction of impedance arcs during ripening (Fig. 5) follows a pattern similar to those observed in Laminaria (Cole, 1972) and frog skin (Smith, 1971) due to changes in membrane resistance. The position of \( R_t \) in the model (Fig. 1A) is, however, not consistent with a membrane resistance. We suggest that identification of components cannot be made in the precise manner claimed in previous studies (Zhang and Willison, 1991) because there are electrical interconnections that are not allowed for in the arguments used to develop the models. Specifically, the analysis of tissues (complex of cells) as serially connected parallel circuits may be too simplistic.

Capacitance of the plasma membrane and tonoplast is related to the area and specific capacitance of each membrane. The measurement of a capacitance indicates that the membranes are structurally intact, and capacitive reactance is lost when membranes become damaged, as occurs in freeze-thawed tissue (Fig. 5). There was a slight (9%) decrease in capacitance during ripening of freshly harvested fruit. This seems too small to be of much physiological significance.

### Cell Changes during Ripening

During normal fruit ripening, flesh firmness declines and the melting texture characteristic of nectarine fruit develops because of changes in cell wall composition and cell wall hydration. With impedance measurements, we were able to follow these changes during nectarine ripening. Cell wall resistance declined from 7181 to 3342 \( \Omega \) (Figs. 3A and 7) as freshly harvested fruit ripened, and this decline was closely related to changes in fruit texture (Fig. 4). A decrease in cell wall resistance may be related to increased concentration of mobile ions in the cell wall and/or an increase in cross-section of the cell wall accessible to low-frequency current. Both alternatives have been demonstrated with ultrastructural studies, which indicate dissolution of the cell wall (King et al., 1989), and studies that indicate leakage of ions from intracellular compartments during ripening (Furmanski and Buescher, 1979). Increases in ion concentrations in the cell wall were not due to breakdown of the structural integrity of plasma membrane or tonoplast since membrane capacitance could be measured at all sampling times (Fig. 7).

The resistance term \( R_t \) declined from 4817 to 1861 \( \Omega \) as freshly harvested fruit ripened (Fig. 7). This indicates considerable changes in either the cytoplasm or membrane resistance during ripening, as discussed earlier. During storage at
0°C, $R_s$ decreased (Fig. 7). However, when the nectarines were subsequently removed from cool storage and ripened, there was little further reduction in $R_s$. The end result was that $R_s$ was similar in nonwoolly fruit (ripened after 0 weeks in storage) and in woolly fruit (ripened after 8 weeks in storage; Fig. 7).

Changes in the resistance of the vacuole were relatively small (Fig. 7). This was expected since the vacuole takes up greater than 90% of the cell volume (the cytoplasm is barely visible as a thin layer adjacent to the cell wall; King et al., 1989) and contains the highest concentrations of ions. It was expected that redistribution of mobile ions from the vacuole to the cytoplasm and cell wall during ripening would have a minimal effect on the absolute concentrations in the vacuole.

Impedance measurements indicate a number of interesting similarities and differences between woolly and nonwoolly nectarines. Woolly nectarines could not be discriminated from nonwoolly fruit, according to taste or AJC, until the fruit had ripened for 3 to 5 d (Fig. 8). At this stage, the concentration and mobility of ions in intracellular compartments were probably similar in both woolly and nonwoolly tissues according to high-frequency resistance measurements (Fig. 3B) and according to electrical models ($R_v$; Fig. 7, d 5). This suggests that the quality of the cell contents (juice) was no different in woolly and nonwoolly fruit. The structural integrity and area of membranes were also expected to be the same in woolly and nonwoolly nectarines since membrane capacitances were similar ($C_1$ and $C_2$; Fig. 7, d 5). The main difference between woolly and nonwoolly nectarines was in the cell wall resistance, which was higher in woolly than in nonwoolly tissue ($R_v$; Fig. 7, d 5). The high resistance of the cell wall in woolly nectarines could have occurred as a result of inhibition of cell wall breakdown and/or as a result of formation of pectin gels in the wall, which reduce the mobility of ions in the cell wall. Thus, the results from this study support earlier conclusions (reviewed by Ben-Arie et al., 1989) that the development of woolliness is primarily related to dysfunction of cell wall degradative processes.

In conclusion, measurements of low-frequency resistance indicate that the extracellular environment changes considerably during ripening of nectarine fruit and that chilling injury inhibits some of these changes, eventually resulting in the development of a dry, woolly texture. However, measurements of high-frequency resistance were relatively consistent in tissue at different stages of ripening as well as in woolly tissue. This indicated that there was little change in the mobility of electrolytes in intracellular compartments of the nectarine tissue. None of the electrical models was able to predict all of the changes expected to occur during ripening. The models have improved our understanding of nectarine ripening in that they indicate that (a) membrane capacitance changes are relatively small and (b) either membrane or cytoplasm resistance decreased during ripening. This suggests that the cell membranes remained structurally intact during the period of ripening, although membrane permeability and function may have changed.

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LITERATURE CITED