BARD

FINAL REPORT

PROJECT NO. IS-2370-94

Woolliness in Peaches and Nectarines

S. Lurie, R. Ben-Arie, J. Labavitch, K. Shackel

2000

BARD Final Scientific Report
(Cover Page)

Date of Submission of the report: March 2000

BARD Project Number: IS-2370-94R

Project Title: Woolliness in Peaches and Nectarines

Address & e-mail of Investigators and Institutions:

Investigators	Institutions
Principal Investigator: Susan Lurie, zeslov@netvision.net.il	Dept. of Posharvest Science, ARO, P.O.B. 6, Bet Dagan, Israel
Cooperating Investigators:	
Ruth Ben Arie, fruitlab@netvision.net.il	ARO (saa)
John Labavitch, jmlabavitch@ucdavis.edu	Dept. of Pomology, UC Davis, Davis, CA, USA
Ken Shackel, kashackel@ucdavis.edu	UC Davis (saa)

Continuation of (Related to) Previous BARD Project:
☐Yes xNo Number:

Keywords *not* appearing in the title and in order of importance. Avoid abbreviations.
Cell walls, chilling injury, ethylene, ripening, pectin esterase, polygalacuronase, endo-glucanase

Budget: IS: $147,600 US: $131,400 Total: $ 279

l fume
Signature
Principal Investigator

Signature
Research Authority, Principal Institution

Publication Summary (numbers)

	Joint IS/US authorship	US Authors Only	Israeli Authors only	Total
Refereed (published, in press, accepted)			5	
Submitted, in review, in preparation	1			
Invited review papers				
Book chapters			1	
Books				
Master theses				
Ph.D. theses			1	
Abstracts			2	
Not refereed (proceedings, reports, etc.)				

Patent Summary (numbers)

	Israeli inventor only	US inventor only	Joint IS/US inventors	Total
Submitted				
Issued (allowed)				
Licensed				

Cooperation Summary (numbers)

	From US to Israel	From Israel to US	Together, elsewhere	Total
Visits/Meetings	1	1	1	3
Sabbaticals				
Postdoctorates				

- **Cooperation**, briefly explain whether synergistic, complementary or supportive. The collaboration was complementary, in that the US scientists worked on 2 objectives of the research, while the Israeli scientists worked on another 2. However, it was also supportive, in that we tried the same practical techniques on fruit from both countries.

Abstract

The overall goal of the research was to understand the processes involved in the development of woolliness in peaches and nectarines. Four specific hypotheses were proposed and in the course of the research evidence was gathered to support two of them and to not support two others. The hypotheses and a summary of the evidence are outlined below.

1. That woolliness arises from an imbalance between the activities of the cell wall pectin degrading enzymes. Using 'Flavortop' nectarines and 'Hermoza' peaches as model systems, storage regimes were manipulated to induce or prevent woolliness. The expression (mRNA abundance), protein content (Western blotting), and activity of polygalacturonase (PG) and pectin esterase (PE) were followed. Expression of the enyzmes was not different, but activity and the ratio between PG and PE activities were quite different in fruits developing woolliness or ripening normally. This was also examined by looking at the substrate, the pectin moiety of the cell wall, and in woolly fruit there were more high molecular weight pectins with regions of non-methylated galacturonic acid residues. Taking an *in vitro* approach it was found a) that PE activity was stable at 0°C while PG activity decreased; b) incubating the calcium pectate fraction of the cell wall with PE extracted from peaches caused the polymers to form a gel characteristic of the visual woolly symptoms in peaches.
2. That continued cell wall synthesis occurs during storage and contributes to structural changes in cell walls and improper dissolution and softening after storage. We tried to adapt our technique of adding 13C-glucose to fruit discs, which was used successfully to follow cell wall synthesis during tomato ripening. However, the difference in sugar content between the two fruits (4% in tomato and 12% in peach) meant that the 13C-glucose was much more diluted within the general metabolite pool. We were unable to see any cell wall synthesis which meant that either the dilution factor was too great, or that synthesis was not occurring.
3. That controlled atmosphere (CA) prevents woolliness by lowering all enzyme activities. CA was found to greatly reduce mRNA abundance of the cell wall enzymes compared to regular air storage. However, their synthesis and activity recovered during ripening after CA storage and did not after regular air storage. Therefore, CA prevented the inhibition of enzyme activation found in regular air storage.
4. That changes in cell wall turgor and membrane function are important events in the development of woolliness. Using a micro pressure probe, turgor was measured in cells of individual 'O'Henry' and 'CalRed' peaches which were woolly or healthy. The relationship between firmness and turgor was the same in both fruit conditions. These data indicate that the development and expression of woolliness are not associated with differences in membrane function, at least with regard to the factors that determine cell turgor pressure.

In addition, during the period of the grant additional areas were explored. Endo-glucanase, an enzyme metabolizing hemicellulose, was found to be highly expressed air stored, but not in unstored or CA stored fruit. Activity gels showed higher activity in air stored fruit as well. This is the first indication that other components of the cell wall may be involved in woolliness. The role of ethylene in woolliness development was also investigated at it was found a) that woolly fruits had decreased ability to produce ethylene, b) storing fruits in the presence of ethylene delayed the appearance

of woolliness. This latter finding has implication for an inexpensive strategy for storing peaches and nectarines.

Achievements

The achievements can best be divided into those at the basic research level, promoting a better understanding of the processes leading to woolliness, and at an applied research level, leading to techniques to delay or prevent woolliness development. Basic. The general conclusion of the data from the research indicates that woolliness arises from an impairment of the normal ripening process of cell wall degradation. 1. Ethylene present during 0°C storage does not cause softening during storage, but promotes normal ripening and softening after storage. 2. Delayed storage (DS), holding fruits 2 d at 20°C before 0°C storage does not cause softening during those two days, but allows softening to proceed slowly during storage, so that the fruit come out of storage softer than control fruit, and continue to ripen normally. In connection with this, nRNA and activity of PG are found during storage in DS fruits, but not in control fruits. 3. CA storage represses all enzyme activity, but also represses the inactivation that occurs during regular air storage. Therefore, during ripening after CA storage the cell wall enzyme message abundance and activity increases rapidly and normal ripening proceeds.

A major achievement at the basic level was the demonstration that peach PE enzyme could induce gel formation *in vitro* in a cell wall fraction of peach. This gel formation is like the visual appearance of woolliness in peaches. The presence of PG inhibited this process. Another achievement was showing that membrane function relating to cell turgor, regulation of solute and water movements, was similar in healthy and woolly fruit. Since woolliness is a form of chilling injury it was expected that membranes would be a site of damage and that loss of control over solute movement could enhance gel formation. This does not appear to be the case.

The recent finding that mRNA abundance and activity of endo-glucanase are elevated in woolly fruit opens new areas of investigation. Until now focus has been on the pectin component of cell walls, but this must be widened to include the hemicellulose component. How this relates to woolliness is yet to be determined, but research is continuing.

Applied. This research has led to a number of techniques to delay woolliness, although the only one mentioned in the objectives was CA. CA has been found to most effective for Israeli fruits at 10% CO_2, while US fruits may tolerate higher CO_2 levels. However, CA is not generally practical for stone fruits, and modified atmosphere conditions are being developed, based on the CA conditions found to be beneficial. Delayed storage (off the tree pre-ripening) works equally well with US and Israeli fruit, and is being developed in the US as a means of obtaining better after storage fruit quality. Ethylene during storage as a means of preventing the ripening inhibition is being adopted in Israel by storing the stone fruits together with apples, a reversal of our previous instructions to storage house operators.

Potential for application. As detailed above, the finding that ethylene in storage helps stone fruits sensitive to woolliness to ripen normally after storage has immediate application. Delayed storage is being developed as technique in the US, but needs to have parameters determined for each cultivar. Utilizing the data obtained on responses of the fruit to CA formulations to develop modified atmosphere storage bags is under development currently in Israel.

Details of cooperation. Cooperation was very close on this project. Two of the objectives (1 and 3) were investigated in Israel and two (2 and 4) in the US. Delayed storage was used in both countries as a means of delaying woolliness, while in the US a protocol was developed to encourage woolliness development. This was used in the cell turgor studies. A joint paper is in preparation combining data obtained in both countries. In addition, both countries began at the later stages of the project to investigate the role of ethylene in preventing woolliness, and this may be the basis of ongoing cooperation.

Background

The physiological disorder known as woolliness is found in cold stored peaches and nectarines after two weeks or more of storage below 8°C (Lill et al., 1989). This disorder is impossible to detect on removal from storage, and as the fruit ripens the outward appearance remains normal, but upon cutting the flesh has a fibrous, woolly texture. At this stage there is no flesh discoloration, but flavor and juice are lacking. In more advanced cases the flesh become light brown. Since it cannot be detected from without, these fruit are generally marketed and cause decrease in sales as customers finding the disorder cease buying the fruit for that season.

De Haan (1957) associated woolliness with metabolism of pectic substances and suggested that if the ratio of soluble to non-soluble pectin reached 2:1 woolly breakdown did not occur. Ben Arie and Lavee (1971) followed pectic changes in peach during storage and found that there was an increase in high molecular weight pectins with a low degree of methylation. The activity of PE increased during longer storage times and PG was almost undetectable in stored peaches (Ben Arie and Sonego, 1980). During subsequent ripening PG activity increased much less in stored than in non-stored peaches (Buescher and Furmanski, 1978; Ben Arie and Sonego, 1980). It is not known whether the increase in PE activity is due to activation of the enzyme at low temperature or increased enzyme presence. Conversely, it is not known whether PG is inhibited at the level of synthesis, activity, or both. In normally ripening peaches, Pressey et al. (1971) associated the appearance of PG activity with an increase in water soluble pectin and fruit softening. Pressey and Avants (1973) resolved the peach fruit PGs into an exo- and endo- form and Downs and Brady (1990) shoed that the activity is higher in ripe than mature fruit.

Detailed studies of cell wall components of nectarines during both normal ripening and the development of woolliness have shown a retention of high molecular-weight pectins in woolly fruit (Dawson, et al., 1992; Lurie et al., 1994). Normal ripening resulted first in solubilization of pectic polymers of high molecular weight and depolymerization at a later stage (Dawson et al., 1992). In woolly fruit there was

less solublization and more insoluble pectins remained in the cell wall (Dawson et al., 1992; Lurie et al., 1994).

A major indication of woolliness is a lack of extractable juice. Ben Arie and Lavee (1971) were the first to suggest that this was due to gel formation in the pectic cell wall fraction. They found that if woolly fruits were heated more juice could be extracted, which did not occur in normal fruit; an indication of trapped water being released. Von Mollendorff et al. (1989, 1992, 1993) found that some nectarine varieties passed through a stage of woolliness during ripening and then recovered and that extractable juice was lowest when woolliness was greatest. They concluded that woolliness developed when membrane permeability increased at a time when high molecular weight pectins were being solubilized and not metabolized further. In normal ripening membrane permeability increased also, but pectins were then metabolized and did not form a gel. Most chilling injury disorders are due to membrane dysfunction, and in stone fruits this may be masked by the changes in cell wall metabolism. However, it must be mentioned that actual gel formation has never been demonstrated, nor have changes in membrane functions in woolly fruit.

Methodologies and Materials

Mid- and late-season peaches and nectarines were harvested at commercial maturity and stored under conditions that either delay or accelerate the development of woolliness. Treatments to delay woolliness were:

1. Delayed storage - holding the fruit 2 d at 20°C before 0°C storage.
2. Controlled atmosphere storage at 10% CO_2 and 3% O_2.
3. Air storage containing 10 to 15 ppm ethylene at 0°C.

Treatments to accelerate woolliness were:

1. Immediate storage at 0°C for 5 weeks.
2. Immediate storage at 5°C for more than 2 weeks.

During ripening after storage woolliness was assessed visually as percent of fruits affected, and extractable juice determined (Lill and Ven der Mespel, 1988). Firmness was measured on pared sides of fruit using a penetrometer with an 11 mm tip. At various time points of the experiment tissue was frozen for enzyme and cell wall analysis (-20°C) and for RNA extraction (-80°C). Cell wall extraction, cell wall enzyme preparation and activity analysis, mRNA preparation and Northern

hybridization were all done as detailed in the papers published from the project (see publications).

PG and PE extracts from peach fruit ripened without storage were incubated at 20°C with pectin fractions extracted from peach cell walls. Five or 10% pectin solutions of 200 µl were mixed with 50 µl of the enzyme extracts in different proportions and observed daily for gel formation. In addition, commercial enzymes PG (Sigma, EC 3.2.1.15) and PE (Sigma, EC 3.3.3.11) were incubated with the pectin fraction.

Studies of cell wall synthesis in a tissue disc system were performed on discs of mature peach fruit using the 13C-glucose tracer technique (Greve and labavitch, 1991) and the disc system developed by Campbell et al., 1990). Turgor pressure was measured on peach fruit at various stages of softening or woolliness using a microprobe on tissue discs (Shackel et al., 1991).

Results

Woolliness, cell walls, and cell wall enzymes. An experiment comparing DS and CA stored fruit to immediately stored fruit found that both treatments alleviated or prevented woolliness in nectarine fruits stored for 4 or 6 weeks at 0°C (Fig. 1). The two storage processes appeared to prevent woolliness by different mechanisms. DS initiated ripening so that at removal from storage PG activity was higher and PE activity lower than in control fruits (Table 1). There was no difference in mRNA abundance of PE and PE between DS and control fruits (Fig. 2). CA repressed both mRNA levels and activity of PG during storage, but allowed recovery of activity during ripening. Endo-glucanase mRNA level was high in control fruits during ripening after storage, and almost undetectable in all treatments at all other times. The results support the hypothesis that the ratio between PG/PE either at removal (DS) or during ripening (CA) will determine whether woolliness develops or not.

Table 1. Changes of activities of exo-PG, endo-PG, PE, endo-glucanase and exo-PG to PE (endo-PG/PE), endo-PG to PE (endo-PG/PE) ratios

	4 weeks		6 weeks	
	Removal	+ 5d ripening	Removal	+ 5d ripening
exo-PG[1]				
Control	83 ± 5*	273 ± 26	123 ± 8	203 ± 16
DS	116 ± 16	400 ± 24	138 ± 8	222 ± 18
CA	31 ± 4	477 ± 14	73 ± 10	460 ± 13
endo-PG[2]				
Control	5 ± 0.6	19 ± 0.5	9 ± 1.3	13 ± 3.0
DS	13 ± 1.5	20 ± 0.3	12 ± 1.5	12.5 ± 1.7
CA	6 ± 0.6	18 ± 2.0	7 ± 0.2	14 ± 0.9
PE[3]				
Control	0.97 ± 0.021	0.65 ± 0.075	1.03 ± 0.088	0.66 ± 0.051
DS	0.85 ± 0.093	0.65 ± 0.030	0.90 ± 0.078	0.62 ± 0.070
CA	0.80 ± 0.026	0.56 ± 0.048	0.87 ± 0.105	0.53 ± 0.034
exo-PG/PE				
Control	86	420	119	308
DS	136	615	153	358
CA	39	852	84	868
endo-PG/PE				
Control	5.2	29.2	8.7	19.7
DS	15.3	30.8	13.3	20.2
CA	7.5	32.1	8.0	26.4
EGase[4]				
Control	2.0 ± 0.30	1.4 ± 0.12	1.3 ± 0.04	1.3 ± 0.02
DS	1.8 ± 0.30	1.0 ± 0.05	1.2 ± 0.02	1.0 ± 0.07
CA	1.9 ± 0.03	0.8 ± 0.07	1.4 ± 0.06	0.7 ± 0.13

1. One unit exo-PG defined as 1μg galacturonic acid released by per mg protein in one hour in reaction mixture. 2. One unit of endo-PG defined as 1 second change in viscosity by per mg protein in one hour in reaction mixture. 3. One unit of PE defined as 1mM NaOH consumed by per mg protein in one hour in reaction mixture. 4. One unit of EGase defined as 1 second change in viscosity by per mg protein in one hour in reaction mixture. * Standard deviation.

Cell wall fractions of water-, CDTA- and carbonate-soluble pectins were prepared from freshly harvested peaches and incubated with PE and PG from ripe peaches at different ratios. Only the CDTA-soluble fraction formed a gel with peach enzymes, and the rate of gelation increased with increasing amounts of PE relative to PG (Table 2). The PE extracted from peaches was stable when stored at 0°C for 9 days, while PG activity as stable for only 1 day (Fig. 3). We suggest that PE, acting on pectins in the cell wall *in vivo* may cause gel formation and that the CDTA-soluble polymers

have the capacity to bind apoplastic water and create the dry appearance observed in woolly fruit.

Table 2. Gelation of CDTA-soluble pectin extracted from Hermoza peaches, resuspended in water, and incubated with PG and PE extracts from ripe peach fruit. 200 µl of 10% CDTA-soluble pectins were mixed with 50 µl of enzyme extracts and incubated at 20°C.

	Final enzyme activities			
Gelation mixture:	Endo-PG* (units x 1000)	PE	Setting time (days)	pH:
CDTA + PG	15.104	0.509	6	6.5
+ PE	0	2.804	2	6.5
+ PE/PG (4:1, v/v)	3.021	2.345	2	6.5
+ PE/PG (3:2, v/v)	6.042	1.886	3	6.5
+ PE/PG (2:3, v/v)	9.062	1.427	4	6.5
+ PE/PG (1:4, v/v)	12.083	0.968	5	6.5

* PG activity was relative viscosity changes per 50 ul crude enzyme extract in 1 h, while PE activity was 1 mM NaOH consumed per 50 ul crude enzyme extract in 1 h.

Cell wall synthesis during ripening and storage. It has been shown that cell wall synthesis changes during ripening and differs amond cell types in tomato fruit (Greve and Labavitch, 1991; Huysamer et al., 1992). There have been no studies to indicate whether synthesis continues during storage, but it has been observed that the amount of cell wall material in peaches and nectarines increases during storage (Ben Arie and Lavee, 1971). This may play a role in the abnormal softening after storage and development of woolliness. Accordingly, using the 13C-glucose tracer technique and a fruit disc system attempts were made to see cell wall synthesis. However, because of the high sugar level in these fruits, no incorporation could be observed using this method.

Cell wall turgor, fruit firmness and woolliness. Only recently has it been shown that cellular turgor plays a role in fruit firmness. We have shown that the turgor of cells in

tomato pericarp tissue falls as ripening proceed (Shackel et al., 1991). It appears that fruit cell turgor is regulated by a membrane-controlled movement of solutes (primarily sugars, but also organic acids) between cellular and apoplastic compartments (Shackel et al., 1992). In peaches, also, a loss of fruit flesh firmness during ripening was associatied with a loss of fruit cell turgor (Fig. 4). When fruit which had been stored at 5°C before ripening and becoming woolly were compared to fruit ripened without storage, the relationship of firmness to turgor was essentially the same whether the fruit were developing woolliness or not (Fig. 5).

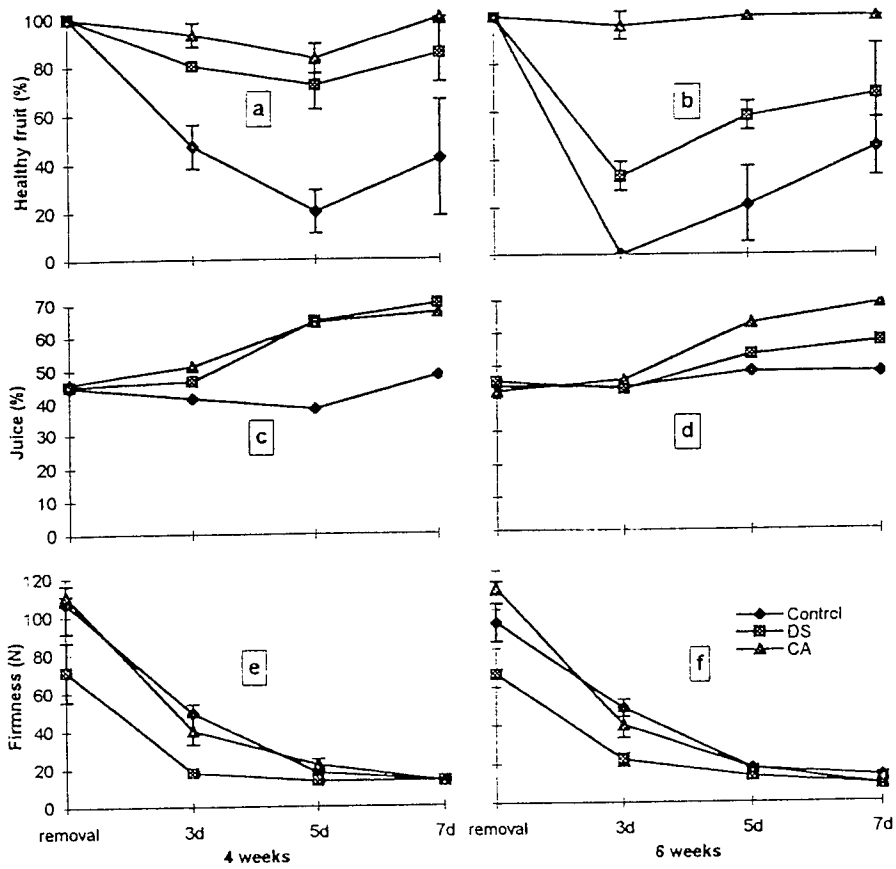

Fig. 1. 'Flavortop' nectarine fruit stored for 4 or 6 weeks and then ripened for 7 days at 20°C shelf life. Fruit with healthy flesh after 4 weeks (a) and 6 weeks (b); expressible juice from fruits after 4 weeks (c) and 6 weeks (d); firmness of fruits after 4 weeks (e) and 6 weeks (f).

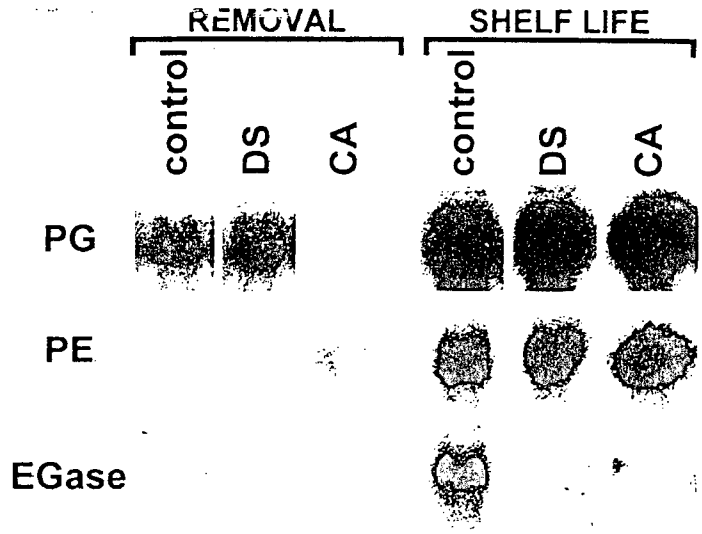

Figure 2. Changes in mRNA levels of polygalacturonase (PG), pectin esterase (PE) and endoglucanase (EGase) at removal from 4 weeks storage and after ripening for 5 days at 20C. Fruit were held in regula 0C storage (control), held for 48 h at 20C before storage (DS), or stored in controlled atmosphere (CA) storage.

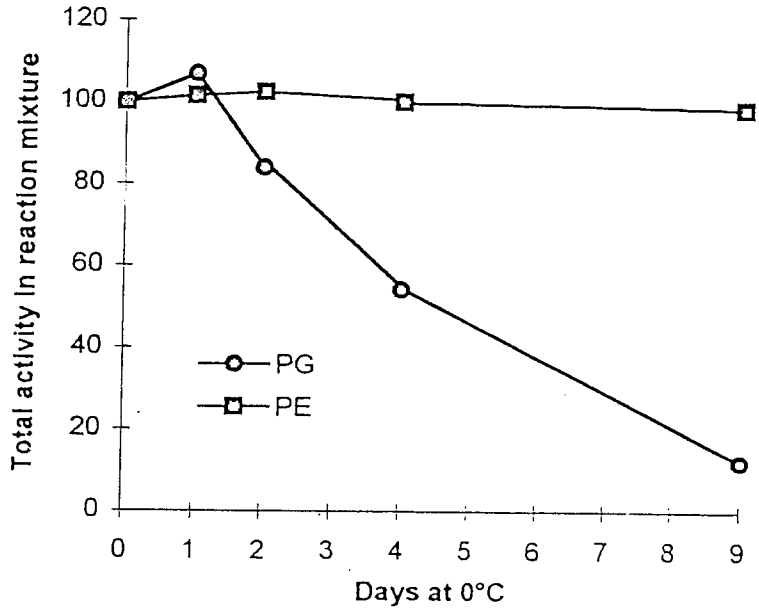

Fig. 3. *In vitro* PG and PE activities during storage of enzyme extracts at 0°C.

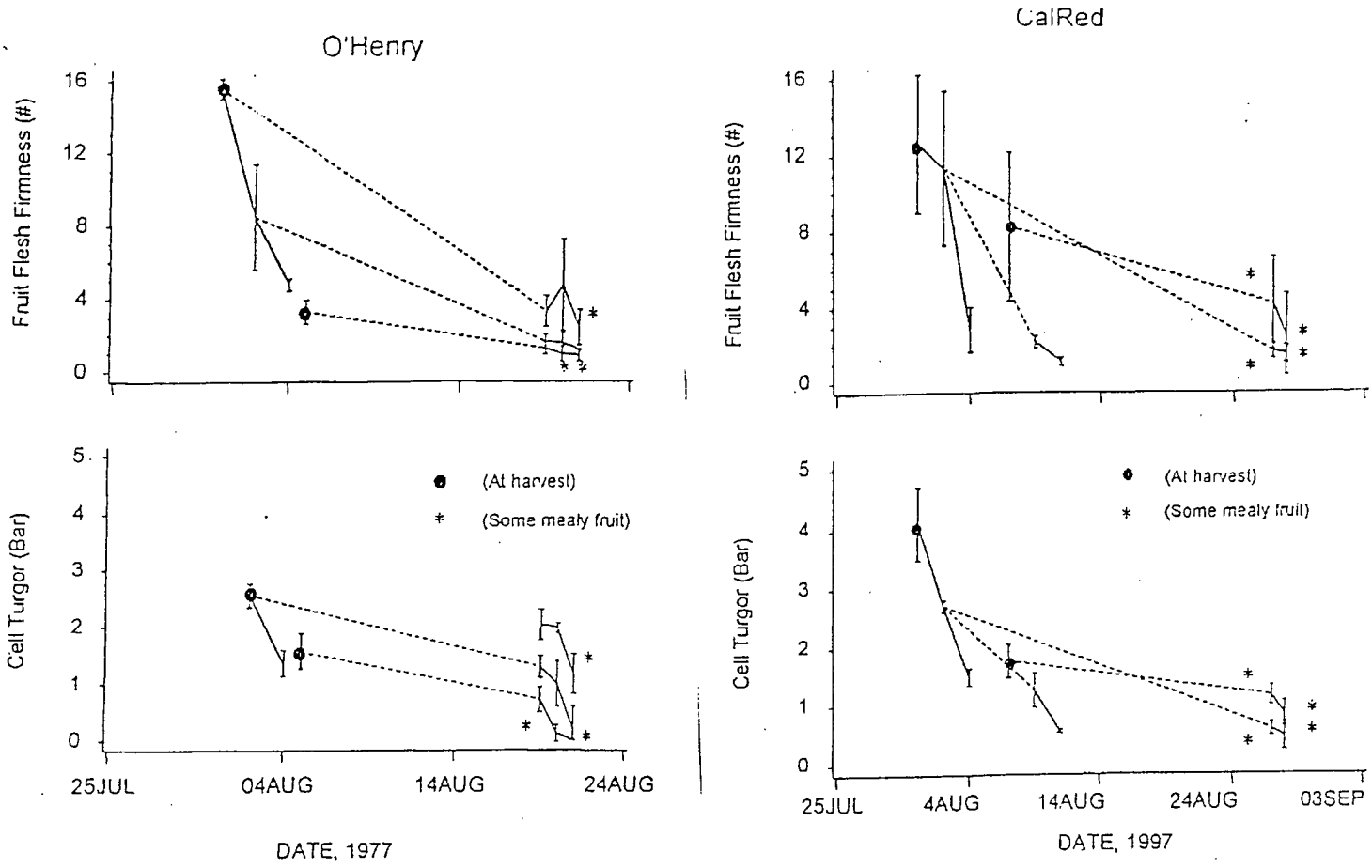

Figure 4. Loss of flesh firmness (top) and cell turgor pressure (bottom) for ripening CalRed and O'Henry peach fruit. Values at the time of harvest are shown as closed circles, with a solid line connecting the values for the same lot of fruit during ripening, and a dashed line indicating storage of the respective lot of fruit at 5C.

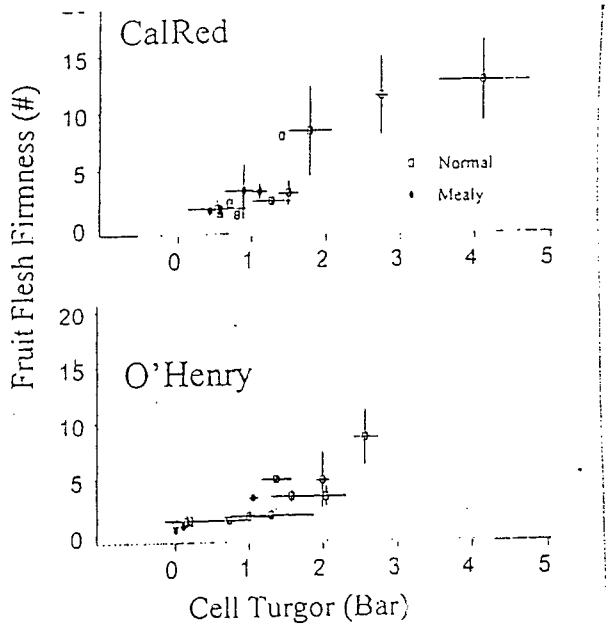

Figure 5. Relation of fruit flesh firmness to fruit cell turgor for both normal and woolly fruit from CalRed and O'Henry peaches. Means correspond to the respective mean turgor and firmness for each data and lot of fruit shown in Figure 4, except that separate means were calculated for woolly and non-woolly fruit.

Discussion and scientific implications

This work has shown for the first time that isolated peach cell walls can form a gel under the influence of peach cell wall enzymes. It was suggested 30 years ago that the dryness associated with woolliness was due to this binding of extracellular juice, but never demonstrated. It appears that the CDTA-soluble fraction, which is enriched in pectin polymers with few side chains, and also known as calcium-pectate, can be acted upon by PE until it forms a gel matrix. The presence of PG inhibits this process by decreasing the size of the polymers so that they to not interact to form a gel. We have calculated that even if only this fraction of the cell walls is involved in binding of juice, then it is in sufficient abundance in the cell wall to account for the loss of expressible juice, since the pectins of the CDTA-soluble fraction can bind 10 times their dry weight. From 5.5 g of fresh tissue about 0.022g of dry CDTA material is recovered. A woolly fruit wieghing 100 grams would have enough CDTA-soluble polymers to bind 40 ml of juice. This is enough to bind the extracellular juice and create a dry, woolly fruit.

The imbalance between PE and PG enzyme activity found in this study in control fruit would encourage woolliness, while DE and CA prevents this imbalance from developing during after storage ripening, albeit by different means. Both of these techniques show promise in extending storage life of peaches and nectarines. An interesting finding from this study was the elevation of the mRNA level of endo-glucanase in control, woolly fruit. Activity gels have also shown that these fruit have higher activity than healthy fruit (data not shown). It is unclear how endo-glucanase and woolliness are related, but further study is warranted.

Two innovative areas of investigation were to examine cell wall synthesis during storage, and to see if cell wall turgor was different in woolly fruit compared to healthy. The first area did not prove fruitful because of technical difficulties. However, the study of turgor changes as fruit softened and either ripened normally or became woolly showed that turgor was the same under both flesh conditions. Therefore, it does not seem that membrane function changes are involved in the development of woolliness, in contrast to other forms of chilling injury in stored commodities.

Potential impact on agriculture

The manipulations that were utilized in these studies to delay or prevent the appearance of woolliness in peaches and nectarines have relevance to the storage industry. CA has generally been tried using formulas found successful for apples. Here we show that higher than normal CO_2 give the greatest benefit. Although it is unlikely that CA will be adopted widely for stone fruits because of the size of the commercial rooms and because extension of storage life is not months but weeks, these data can be used to develop modified atmosphere storage bags. Delayed storage (off the tree pre-ripening) is a very low-tech method of assuring better quality fruits after storage (provided that storage is 0°C). This technique has been found to be equally effective on Israeli and American cultivars and is currently being tested on a wide number of cultivars in the US to determine harvest parameters to be used for each cultivar.

References

Ben Arie, R., Lavee, S. 1971. Pectic changes occurring in Elberta peaches suffering from woolly breakdown. Phytochem. 10:531-538.

Ben Are, R., Sonego, L. 1980. Pectolytic enzyme activity involved in woolly breakdown of stored peaches. Phytochem. 19:2553-2555.

Buescher, R., Furmanski, R. 1978. Role of pectinesterase and polygalacturonase in the formation of woolliness in peaches. J. Fd Sci. 43:264-266.

Campbell, A., Huysamer, M., Stotz, H., Greve, L.C., Labavitich, J.M. 1990. Comparison of ripening processes in intact tomato fruit and excised pericarp discs. Plant Physiol. 94:1582-1589.

Dawson, D., Melton, L., Watkins, C. 1992. Cell wall changes in nectarines (*Prunus persica*). Plant Physiol. 100:1203-1210.

De Haan, I. 1957. Pectin conversions in peaches during cold storage. S. African Ind. Chem. 11:26-34.

Downs, C., Brady, C. 1990. Two forms of exopolygalacturonase increase as peach fruit ripen. Plant Cell Envir. 13:523-530.

Greve, L.C., Labavitch, J.M. 1991. Cell wall metabolism in ripening fruit. V. Analysis of cell wall synthesis in ripening tomato pericarp tissue using a D-(U-13C)-glucose tracer and GC/MS. Plant Physiol. 97:1456-1461.

Huysamer, M., Greve, L.C., Labavitch, J.M. 1992. Cell wall composition and synthetic capacity of the pericarp of ripening tomato. HortSci. 27:61.

Lill, R.E., Van der Mespel, G.J. 1988. A method for measuring the juice content of mealy nectarines. Scient. Hort. 36:267-271.

Lill, R.E., O'Donoghue, E.M., King, G.A. 1989. Postharvest physiology of peaches and nectarines. Hort. Rev. 10:413-452.

Lurie, S., Levin, A., Greve, L.C., Labavitch, J.M. 1994. Pectic polymers from normally and abnormally ripening nectarines. Phytochem. 36:11-17.

Pressey, R., Avants, J. 1973. Separation and characterization of endopolygalacturonase and exopolygalacturonase from peaches. Plant Physiol. 52:252-256.

Pressey, R., Hinton, D., Avants, J. 1971. Development of polygalacturonase activity and solubilization of pectin in peaches during ripening. J. Fd Sci. 36:1070-1073.

Shackel, K., Greve, L.C., Labavitch, J.M., Ahmadi, H. 1991. Cell turgor changes associated with ripening in tomato pericarp tissue. Plant Physiol. 97:814-816.

Shackel, K., Ahmadi, H., Greve, L.C., Labavitch, J.M. 1992. Influence of apoplastic solutes on the turgor of tomato pericarp cells. HortSci. 27:626.

Von Mollendorff, L.J., de Villiers, O.T., Jacobs, G. 1989. Effect of time of examination and ripening temperature on the degree of woolliness in nectarines. J. Hort. Sci. 64:443-447.

Von Mollndorff, L.J., Jacobs, G., de Villiers, O.T. 1992. Influence of different cold storage temperatures and periods on extractable juice, internal conductivity and woolliness in 'Flavortop' nectarines. J.S. African Soc. Hort. Sci. 2:14-18.

Von Mollendorff, L.J., de Villiers, O.T., Jacobs, G., Westraad, I. 1993. Molecular characteristics of pectic consitutents in relation to firmness, extractable juice and woolliness in nectarines. J. Amer. Soc. Hort. Sci. 118:77-80.

Publications

Sonego, L., Lers, A., Khatchitski, A., Zutkhi, Y., Zhou, H., Lurie, S. and Ben Arie, R. 1999. Ethylene delays onset of woolly breakdown in stored peaches. In: Biology, and biotechnology of the plant hormone ethylene II (eds. A. Kannellis, C. Chang, H. Klee, A. Bennett, J. Pech and De. Grierson) Kluwer Academic Publ., Dordrecht, The Netherlands, pp. 405-411.

Zhou, H.W., Sonego, L., Ben Arie, R. and Lurie, S. 1999. Analysis of cell wall components in juice of 'Flavortop' nectarines during normal ripening and woolliness development. J. Amer. Soc. Hort. Sci. 124:424-429.

Zhou, H.W., Lurie, S., Lers, A., Khatchitski, A., Sonego, L. and Ben Arie, R. 2000. Delayed storage and controlled atmosphere storage of nectarines: two strategies to prevent woolliness. Postharv. Biol. Technol. 18:133-141.

Lurie, S., Zhou, H.W., Sonego, L., Khatchitski, A., Ben Arie, R. and Lers, A. Cell wall enzymes and cell wall changes in nectarines (Prunus persica) mRNA abundance, enzyme activity and changes in pectic and neutral polymers during ripening and in woolly fruit. J. Amer. Soc. Hort. Sci., in press.

Zhou, H.W., Ben Arie, R. and Lurie, S. Pectin esterase, polygalacturonase and gel formation in peach pectin fraction. Phytochemistry, submitted.

Zhou, H.W., Li, D., Ben Arie, R. and Lurie, S. The role of ethylene in the prevention of chilling injury in nectarines. J. Plant Physiol., submitted.

Lurie, S., Sonego, L., Zhou, H.W., Greve, L.C., Labavitch, J.M., Ahmadi, H. and Shackel, K. Chilling injury in peaches. In preparation.