desirable warmer controlled temperatures. Proper decisions require information about the relative susceptibility of the commodity, knowledge of threshold chilling temperatures, duration of exposure that can be tolerated, and the effect of other factors, such as fumigation for insect control, that would influence susceptibility. The fact that low transit temperatures are not desirable for chilling sensitive commodities is fortunate from an energy-saving standpoint.

Some comments on vegetables

Since chilling injury of vegetables is not one of the specific topics covered in the symposium, I wish to make a few comments. The fact that many vegetables are susceptible to chilling injury has resulted in serious problems and losses in their handling. This relates especially to tomatoes, where the industry has recently mounted a program intended to inform both members of the trade and consumers concerning the proper temperatures for tomatoes. Tomatoes offer a good example of where field chilling, transit chilling, market chilling, and the home refrigerator all contribute to the potential losses of product and quality. All of the "warm-season" vegetables, except sweet corn, are subject to chilling injury. These warm-season vegetables are of tropical origin and all, except sweet potatoes, are fruits (in a botanical sense). In contrast, the cool season vegetables should be stored near 0°C. Asparagus and potatoes are exceptions.

Retrospect and prospect

An awareness that certain plants will not tolerate low temperatures has existed for many years. However, widespread interest in chilling injury research has occurred only during the past 30 years or so, and much of the work has taken place in the past 10 to 15 years. Perhaps my own introduction to this subject will give some focus. During the winter of 1937–38, I was a graduate student at Cornell University and my attention was called to a surface breakdown on greenhouse cucumbers shipped by truck from the Midwest to eastern markets. Inspectors certified the cucumbers to have been frozen and claims were filed against the trucker. This was of special interest to me since the trucking company involved belonged to my family. Preliminary investigations indicated that the injury was due to low, but non-freezing temperatures. However, it was evident that very little was known about the disorder. The problem became the subject of my Master's thesis and I have retained a general interest in chilling injury since that time. It is my opinion that 40 years ago the commercial horticulturists were more aware of the occurrence and importance of chilling injury than were horticultural scientists. Only during the past few years has the topic of chilling injury appeared in textbooks of plant physiology.

I am sure that interest in chilling injury will be maintained and that interesting and valuable results will be forthcoming. It is probably safe to predict that chilling injury will assume an importance not previously known in the developing countries as these countries adopt technologies of temperature control and attempt to develop their export markets. The necessity to meet quarantine requirements to move horticultural products from areas of insect infestation will place a new focus on chilling injury. The fumigation treatment may require a subsequent storage period at chilling temperatures. Since these stresses are additive, the implications are obvious. Alternative treatments may require a prolonged holding period in the chilling range. Descriptive research is needed to evaluate the tolerance of cold sensitive crops to various accepted quarantine procedures.

A positive note

Chilling injury is not necessarily all bad. We need to be alert to the possibilities of using to our advantage the alterations induced in the commodity by chilling temperatures. For example, slight chilling can result in improved sweetness and texture of stored sweet potatoes. A cold treatment improves the ripening of harvested pears. Night temperatures in the chilling range results in improved color of oranges. There are probably other examples where responses to chilling temperatures can be beneficial.

CHILLING INJURY OF CROPS OF TROPICAL AND SUBTROPICAL ORIGIN

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Information regarding chilling injury (CI) of tropical fruits may be found in recent texts and reviews (36, 27, 28). However, there is much additional information in widely scattered sources.[1]

Sensitivity to low temperature is a common property of living systems. Higher animals have elaborate temperature control systems and are damaged if the body temperature remains more than a few degrees below the optimum for any extended period. Many bacteria and fungi thrive only in a narrow temperature range (37). Fruit flies cannot survive more than a few days at less than 10°C and many algae are similar to higher plants in susceptibility to CI.

As in other stress conditions, some plants react temporarily to an abrupt lowering of temperature but have the capacity to recover and to protect themselves against its effects. Other plants or plant parts lack this capacity and are rapidly and apparently irreversibly damaged by even short exposure to chilling temperature. Most likely, only plants exposed to chilling temperature regularly and over evolutionary time select the structures or functions that protect against low-temperature stress. The protective systems utilized may turn out to be either constitutive or adaptive and may differ in plants of different origin. In tropical and subtropical plants, we might anticipate that chilling resistance might be either completely lacking or adaptive. It is probable that the overall sensitivity of the plant is reflected in the sensitivity of the fruit to chilling injury.

My primary interest is in the horticultural aspects of CI. Throughout the recent research relating CI to membrane dysfunction, there is little work relating the insights developed from that very excellent research to the horticultural problem of what can we do to alleviate chilling injury (28). Indeed, the only message I have discerned from this work is that the dysfunction is so deep-seated and so fundamental, that any search for ways to alleviate CI is probably doomed to failure. This may be true, but it is also apparent that a few hard researchers have not received that message and continue to study the environmental and biological factors which influence the development of CI.

Although CI is easily avoided in tropical fruits, there are reasons why low-temperature storage may be desirable. Low-temperature refrigeration is the most manageable way to control fruit ripening and thus may lead to exposure of CI-sensitive fruit to damaging temperatures. Postharvest fungus diseases such as *Rhizopus* may be controlled by low-temperature storage. Quarantine insect pests, such as fruit flies *(Ceratitis, Dacus, Anastrepha),* also may be controlled by low temperature. Obviously, CI severely limits these uses of refrigeration.

There are several ways to limit or reduce sensitivity to CI, some of which have rather broad application, while others are limited to certain fruits. Temperature and exposure time are the prime variables. For any fruit, at any temperature down to freezing, there seems to be some minimum time to induce irreversible injury. This time varies from a few hours to several weeks depending on the fruit and the temperature. In similar fashion, maximum temperatures depend upon the exposure time. If the cold period is interrupted, damage

[1]My thanks to Hilary Burton, Technical Information Specialist, ARS, USDA, for assistance in the literature survey.

is reduced or eliminated, and as climaceteric fruit ripens, it becomes less sensitive to chilling. Desiccation injury seems to be a natural consequence of CI, and a definite contributor to the damage. With many fruits, the control of moisture loss reduces symptoms of CI.

Avocado

CI in avocado has been described by several researchers; the following description is adapted from Hatton et al. (18): Chilling injury in avocados is characterized by several symptoms that may occur singly or in various combinations in different cultivars. The most common symptom is a grey-brown discoloration of the flesh, especially in the vascular tissue. The extent of discoloration may vary from almost inconspicuous trace areas in the flesh to severe cases where all the flesh is discolored. In severe cases, uneven ripening, development of undesirable flavors and odors, pitting, and scald-like browning or darkening of the skin commonly occurs. Sometimes fruit may appear satisfactory while in storage, but display chilling injury when allowed to soften at higher temperatures.

Existing avocado cultivars differ in sensitivity to CI and considering the wide range of climatic conditions prevailing in Central America where the avocado is native, additional genetic material may be available for continued improvement in resistance to CI.

Second, ripening of avocados tends to overcome chilling sensitivity (26). In the preclimacteric stage, sensitivity is relatively high, increasing to a maximum at the climacteric peak, decreasing rapidly as the fruit ripens, and reaching a minimum about 2 days past the climacteric. This information may be used to maximize the storage life of avocados (56). Fruit is first stored at a temperature of about 8°C for 3–4 weeks or until it reaches the point of ripening. Then, an ethylene treatment (500 ppm for 24 hr at 20°) is applied to ripen all of the fruit. Finally, the fruit is cooled to 2° where, experimentally, it may be stored for several weeks more; however, the authors do not recommend such a long storage period under commercial conditions.

Controlled atmospheres can be used to prevent CI. 'Fuchs' and 'Waldin' avocados stored at 7°C in 2% O_2 and 10% CO_2 for 3–4 weeks remained free of CI during ripening at 21°, although the controls were severely damaged. Storage for 8 weeks in sealed polyethylene bags at 4 to 8° in which O_2 and CO_2 reached 2 to 6% and 3 to 7%, respectively, also reduced CI (43).

Calcium affects ripening and susceptibility to CI in avocados (49, 9). Calcium not only delayed the onset of ripening (climacteric maximum) but, in an individual fruit, the portions having the lowest calcium levels were the most sensitive to chilling. Vacuum infiltration with $CaCl_2$ (7.5% wt/v) sharply reduced chilling damage when the fruit was held at 5°C for 3 weeks.

CI was avoided by storage under hypobaric conditions, but very low pressures were needed. Apelbaum et al. recommended 60 mm Hg at 6°C for 5 weeks, which is barely within the chilling range for 'hass' (6). Spalding and Reeder, using only slightly higher pressure and at 7.2°, showed that the hypobaric treatment was inferior to a high (10%) CO_2 treatment after 6 weeks. (45)

Banana

Bananas are extremely sensitive to CI. Exposure to 5°C for only 24 hr will induce obvious symptoms (20). Mild symptoms are a slight darkening of the vascular tissues and latex vessels. More severe symptoms are a dull yellow skin, browning of the skin, failure to ripen, loss of flavor, hardening of the central placenta, and increased susceptibility to mechanical injury (34). Unlike some of the tropical fruits, banana cultivars show little difference in susceptibility to CI, and there is little reason to hope that chilling resistant cultivars may be developed (1, 8). Ripe fruit is somewhat less sensitive to CI than mature-green fruit but, again, the difference is too small to be useful. Slow cooling, about 5°/3 days, reduces injury slightly, but does not seem to be a practical method for alleviating damage. Protecting the fruit against moisture loss will alleviate CI symptoms (34). Protection of the fruit by treating it with a small quantity of vegetable oil or dimethylpolysiloxane may act by reducing desiccation or by altering the composition of the cell membrane (20). Low-pressure storage (220 mm Hg) reduced symptoms of CI in bananas stored at 5° for 1 month (34). However, at 150 mm Hg and the non-chilling temperature of 14°, bananas could be stored successfully for 120 days (4).

Mango

Mango fruits are highly sensitive to CI. Chilling is characterized by a greyish, scald-like discoloration of the skin, failure to ripen, non-uniform ripening, poor flavor, failure to color, pitting, and increased susceptibility to postharvest decay (30, 47, 41, 2). Severe damage usually occurs when fruit is stored only a few days below 13 to 15°C and, in fact, some workers indicate that even these temperatures are too low if storage is extended beyond 3–5 days (51). On the other hand, other indicate that 7 to 8° (30, 32) is satisfactory, and a few recommended temperatures as low as 5° for certain cultivars (2, 30, 48). Some of these differences in recommendations are due to variations among cultivars and growing conditions, but mostly to differences in the criteria used in evaluating the fruit.

As in most chilling-sensitive fruits, partial ripening reduces the mango fruit's sensitivity to CI, permitting storage at 5°C for 8 to 12 weeks without commercially important damage (32). This result can be interpreted in light of the observation of Kane and Marcellin (23) that the fatty acid composition of mango mitochondria shifts as the fruit ripens. This observation is consistent with current theories on membrane structure and function and should receive more attention. CI may be avoided by storage under hypobaric conditions (5, 46). Mangoes, stored 3–4 weeks at 50 to 7 mm Hg and 13°, ripened at 21°, usually within 3–4 days. The highly colored varieties 'Haden' and 'Maya' did not develop their usual red-orange color but remained yellow.

Papaya

The symptoms of mild CI in papaya are a delayed ripening, uneven ripening, and increased susceptibility to otherwise non-prevalent decay fungi. More severe chilling causes increased delay in ripening, blotchy coloring, a scald-like symptom at certain seasons of the year and, ultimately, total failure to ripen, production of off-flavors and odors, and extreme susceptibility to decay fungi. Under low humidity, pitting may occur (21, 22).

Mild chilling may or may not occur during 5 to 7 days of storage at 10 to 12°C. Some evidence of mild chilling occurs during 2 to 3 weeks storage at 10°. Serious chilling always develops following storage at 5° for 7 to 14 days (13, 33).

Very little work directed toward alleviation CI of papaya has been done, although the fruit becomes progressively less susceptible to CI as it ripens (33, 3, 7). Unfortunately, no one has developed a commercially acceptable way to use this information. The use of modified atmospheres has been of little utility for papaya (3, 17).

Citrus

Grapefruit and limes are the most chilling-sensitive of the citrus fruits and considerable research has been done on methods to avoid or ameliorate CI in grapefruit, but relatively little work has been done on other citrus. Two types of symptoms are common on grapefruit; pits or depressions in the rind occur when the fruit is stored at about 4 to 5°C, and superficial brown-staining of the rind occurs at 0 to 1° (T.T. Hatton and R.H. Cubbedge, personal communication) (39). Hatton and Cubbedge have shown that prestorage conditioning of the fruit at 10, 16, and 21° greatly reduces the incidence of CI during 3 weeks subsequent storage at 1° (personal communication). Treatment with 40% CO_2 for 3 days at 21° controlled CI during subsequent storage at 1° for 3 weeks (16). Carbon dioxide at 10% during storage at 4.5° for 7 weeks also reduced CI to commercially acceptable levels (50). Benomyl and thiabendazole (42, 25, 54) reduced symptoms of CI in grapefruit during storage for 7 weeks at 4.5° or for 12 weeks at 8°. As in most other fruits, control of moisture loss by high relative humidity greatly alleviated the symptoms of CI (14, 53). Hypobaric storage at 220 mm of Hg also reduced symptoms of chilling in both grapefruit and limes held at 4.5° for 7 and 4 weeks, respectively (35). Warming at 7-day intervals at 21° for 8 hr reduced CI in 'Marsh' grapefruit stored at 5° (11, 12).

There is considerable evidence that grapefruit are predisposed to CI by factors associated with the physiology of the tree at the time of harvest. CI is least severe at midseason when the tree at harvest is least active (19, 40). Sensitivity to CI also coincides with fruit color. Green fruit during early harvest is susceptible, becoming least susceptible when little green is present (15). Late in the season, sensitivity to CI increased as the tree became active and the fruit regreened. Location of the fruit on the tree also affected incidence of CI (38). Grapefruit from the exterior canopy were more sensitive to CI than those from the interior of the tree.

At those times of the picking season when grapefruit is most sensitive to CI, the use of biphenylamine-treated pads in the shipping container increased the incidence and severity of the CI symptoms. At other times of the year, the biphenylamine had no effect (24).

Ethylene treatment for 48 hr at 29°C reduced susceptibility of early harvested fruit, which required degreening, during subsequent storage at 4.5°, but the same treatment applied later in the harvest season increased CI in fully colored fruit (15).

The available information suggest that losses from CI may be reduced whenever it is necessary to store grapefruit at low temperature. The control of temperature and humidity, applying wax, benomyl, or thiabendazole, and preconditioning the fruit at 10°C for 1 week all appear to reduce CI to acceptable levels. Increasing CO_2 during the preconditioning period may not be worth the additional risk or expense, but ethylene degreening may be useful for early-harvest fruit.

The use of packaging film box liners has been studied and, as anticipated, reduced CI; whether or not this practice can be controlled well enough to become a commercially acceptable practice is questionable (53, 14).

Conclusion

In most research on CI, subjective sensory evaluation of injury plays an important role. Objective measurements, such as changes in sugars, organic acids, fatty acids, respiration rates, volatile production, etc., have been made, although their relevance is often difficult to evaluate. Therefore, it is not always clear whether differences in published results are due to different evaluation methods, cultivars, growing conditions or handling methods.

In his 1973 review of CI (27), Lyons cited the few references then available about the effect of hypobaric conditions on development of chilling injury and suggested additional study. Since low pressure would remove the various volatile metabolites, such as acetaldehyde, ethanol and a-farnesene, that are implicated (55) in the CI syndrome, reduction in CI could be expected. However, since 1973, I have found very little work on hypobaric storage at chilling temperatures, although some work was done at marginally chilling temperature, and I conclude that removal of volatile metabolites has not effectively reduced CI.

What conclusions may we draw from these findings?

First, it seems that although refrigeration may not be essential for all fruits, it has such broad general utility that a concerted effort should be made to develop chilling-resistant cultivars of important tropical fruits (10). It seems very likely that chilling-resistant strains of various fruits might be found in mountainous regions near centers of origin. Standard plant-breeding techniques could be used to develop chilling-resistant commercial cultivars. Achieving a degree of chilling resistance in tropical fruits certainly should be worthy of some effort.

Second, we should search for specific plant growth regulators which influence membrane composition. Such materials might confer resistance to CI on otherwise chilling-sensitive fruits.

Third, we should continue to study alternatives to refrigeration and the use of moderate non-chilling temperatures in combination with controlled atmospheres, hypobaric conditions, and plant regulators to control ripening and postharvest behavior of chilling-sensitive fruits.

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CHILLING INJURY OF CROPS OF TEMPERATE ORIGIN

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We expect that a plant of tropical or subtropical origin is chilling sensitive. A corollary might be that a plant not of tropical or subtropical origin is not chilling sensitive. Although there are exceptions to such a corollary, which I shall be describing, this evolutionary distinction is largely true because even those temperate crops that are chilling sensitive have developed survival mechanisms to circumvent this genetic liability.

There is an obvious evolutionary advantage, if not necessity, for temperate crops to possess chilling resistance, since they must survive in a sometimes-chilling environment. However, there also must be some competitive advantage associated with chilling sensitivity, or else all plants evolving in non-chilling environments would not possess it. In other words, crops of temperate origin must have paid a price for their chilling resistance. A good case can be made that the price that was paid by green plants was a lower photosynthetic capacity quite possibly due to modified membrane properties (24). Thus, temperate-zone crops may have been forced to sacrifice growth potential for their ability to survive in chilling temperatures. This distinction in chilling susceptibility among plants of different evolutionary origin strongly suggests genetic control over chilling susceptibility or resistance; yet this genetic control is not distinct. To date, attempts to select for chilling-resistance among warm-season crops have not been very fruitful, and neither have been attempts to breed chilling resistance into them (24). The genetic control over chilling is very hard to isolate.

Variation in chilling sensitivity

Within species of warm-season crops, we find considerable variations in chilling sensitivity among cultivars (5). As I will demonstrate, we also can find wide variations in chilling sensitivity among cultivars of temperate crops. Some of this diversity is not genetic because environmental conditions affect the occurrence of chilling injuries. However, it must be borne in mind that effects of chilling on temperate crops are much more subtle than those on tropical crops, if for no other reason than that chilling-sensitive temperate crops are ones that have evolved as survivors in a chilling environment. Actually, temperate-zone crops carry only rudimentary chilling sensitivity, and the expressions arise only when the plant tissue is given added stress besides that of cold itself. One such added stress is senescence, and so postharvest physiologists are prominent among those who have to cope with temperate-crop chilling sensitivity.

What temperate-zone crops are chilling-sensitive? A survey of USDA Handbook 66 (9) turned up a mere handful of clear examples: apples, asparagus, cranberries, nectarines, peaches, plums, and potatoes. Potatoes pose a problem in semantics: is it a crop of temperate or subtropical origin? Since it probably originated at high altitudes, I have chosen to include it here, and in its expression of chilling injury, potato is similar to the others on this list. This brief list represents the crops known to be chilling-sensitive, but there prob-