

Transpiration and Water Stress

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I. INTRODUCTION

During the years that have passed since the publication of the first edition of this book, noticeable developments have taken place in the research of plant-water relations, including the processes occurring in harvested organs. Approaches of molecular biology have been extended to this sphere and have shed new light on the mechanisms of water transport in plant cells (Chrispeels and Maurel, 1994) and on the molecular basis of water stress adaptation (Bray, 1993; Zhu et al., 1997). The reevaluation of universal thermodynamic concepts of water status is discussed in food science (Chirife and Buera, 1996; Slade and Levine, 1991). In the applied sphere, new approaches to controlled-humidity storage, such as different versions of active packaging, have emerged (Ben-Yehoshua et al., 1995; Rooney, 1995; Shirazi and Cameron, 1992). These new developments in understanding postharvest water relations have not yet been adequately reviewed, with the exception of the specific subject of cut flowers, which was comprehensively surveyed recently by Van Doorn (1997). Certain aspects of the modern state of the art in postharvest water relations of fruits and vegetables have been discussed in relatively brief but informative and stimulating reviews by Woods (1990), Patterson et al. (1993), and Joyce and Patterson (1994). Several books on the postharvest handling and physiology of agricultural commodities also deal with this subject, among others (Hardenburg et al., 1986; Kader, 1992; Kays, 1991; Wills et al., 1998). Notable in this area is Burton's (1982) work, which thoroughly reviewed the data inventory and contributed much to it. This chapter attempts to cover the topic of water status in harvested commodities with an emphasis on postharvest water loss and its control, with special attention to recent developments in this field.

II. WATER AND POSTHARVEST LIFE

Due to its specific molecular structure, water possesses unique physicochemical properties (for details, see, for example, Benson and Siebert, 1992; Kramer and Boyer, 1995; Stilling, 1980), which made it the basis for the existence of life on our planet. Plants depend more on the availability of water than on any other single environmental factor (Kramer and Boyer, 1995). The pivotal physiological importance of water is attributed to its functions as major plant constituent, universal solvent, and active reagent (for example, in various hydrolytic reactions or in photosynthesis) as well as its role in the maintenance of cell/organ turgidity. The transportation and thermoregulatory functions of water are of major significance as well.

The significance of moisture loss in determining the shelf life and quality of harvested plant organs is hardly surprising, since the organ severed from the parent plant cannot replenish water lost by transpiration. Harvested produce remains fresh only as long as it retains water. Transpiration is thus one of the main processes that affect commercial and physiological deterioration of fruits and vegetables. It induces wilting, shriveling, and loss of firmness, crispness, and succulence, all components of freshness.

The desiccation resulting from moisture loss reduces the commercial value of the product, adversely affecting its appearance, texture, flavor, and weight—factors that determine the price of the commodity. The sales appeal of produce may be affected by the loss of a mere 1% to 2% of its weight, as is the case with grapes (*Vitis vinifera* L.), which show drying and browning of the stem and pedicels at this point. Most commodities become unsalable after losing 3% to 10% of their weight. Table 1 (edited by Burton, 1982) shows the percentage weight loss at which commodities were judged to become unsalable. These percentages were subjectively determined but nevertheless indicate the significance of transpiration in determining the shelf life of each commodity. Equally important, water loss induces physiological stress, which has been shown in many studies to accelerate senescence, as indicated by faster rates of membrane disintegration and leakage of cellular contents (Ben-Yehoshua, 1983).

The commercial life span of various commodities may be brought to an end by a number of processes: (a) transpiration; (b) decay; (c) overmaturity and other undesirable physiological processes (off-flavor, sprouting, rooting, elongation, and/or undesirable color changes); (d) metabolic processes leading to undesirable compositional changes; (e) chilling injury in cold storage and physiological disorders in general; and (f) mechanical injuries. The relative importance of these causes of deterioration depends on the commodity. Transpiration is the major cause of postharvest loss and poor quality in leafy vegetables such as lettuce (*Lactuca sativa* L.), chard [*Beta vulgaris* L. var. *flavescens* (Lam.) Lam.], spinach (*Spinacia oleracea* L.), cabbage (*Brassica oleracea* L. Capitata group), and green onion (*Allium cepa* L.).

Transpiration is second in importance after overmaturity at harvest in losses of immature fruit-type vegetables such as cucumbers (*Cucumis sativus* L.), summer squash (*Cucurbita pepo* L.), eggplant (*Solanum melongena* L.), pepper (*Capsicum annuum* L. Grossum group), okra [*Abelmoschus esculentus* (L.) Moench.], and snapbeans (*Phaseolus vulgaris* L.). It is third in importance after bruising and overripeness, for mature fruits and vegetables such as tomatoes (*Lycopersicon esculentum* Mill.), melons (*Cucumis melo* L.), bananas (*Musa* spp. AAA genomic group), mangoes (*Mangifera indica* L.), and apples [*Malus sylvestris* (L.) Mill. var. *domestica* (Borkh.) Mansf.], and fourth in importance for root vegetables, following mechanical injuries, improper curing, sprouting, and rooting

Table 1 Water Loss (Original Fresh Weight Basis) at which Commodities Become Unsalable^a

Commodity and cultivar	Maximum permissible loss (%)
Asparagus	8
Beans, broad	6
Beans, runner	5
Beetroot, storing	7
Beetroot, bunching with leaves	5
Blackberries, "Bedford Giant"	6
Brussels sprouts	8
Cabbage, "Primo"	7
Cabbage, "January King"	7
Cabbage, "Decema"	10
Carrot, storing	8
Carrot, bunching with leaves	4
Cauliflower, "April Glory"	7
Celery, white	10
Cucumber, "Femdam"	5
Leek, "Musselburgh"	7
Lettuce, "Unrivalled"	5
Lettuce, "Kordaat"	3
Lettuce, "Kloek"	3
Onion, "Bedfordshire Champion"	10
Parsnip, "Hollow Crown"	7
Potato, maincrop	7
Potato, new	7
Peas in pod, early	5
Peas in pod, maincrop	5
Peppers, green	7
Raspberries, "Malling Jewel"	6
Rhubarb, forced	5
Spinach, "Prickly True"	3
Broccoli, sprouting	4
Strawberries, "Cambridge Favourite"	6
Sweetcorn	7
Tomato, "Eurocross BB"	7
Turnip, bunching with leaves	5
Watercress	7

^a Approximate value from Robinson et al., 1975.

Source: Burton, 1982.

(Kader, 1983). In *Citrus* fruits, transpiration is the major cause of commercial and physiological deterioration (Ben-Yehoshua, 1969).

The dependence of postharvest life and quality on water loss rate is illustrated in numerous publications dealing with various commodities (e.g., Aharoni, 1994; Aharoni et al., 1993; Ben-Yehoshua et al., 1983b; Feher, 1994; Hrushka, 1977; Lazan et al., 1987; Lester and Bruton, 1986; Lownds et al., 1994; Lurie et al., 1986; Rajapakse et al., 1992;

Watada et al., 1987) as well as fruits (Bower et al., 1989; Cutting and Wolstenholme, 1992; Hrushka, 1977; Landrigan et al., 1996).

Not only loss of moisture but also excess water can place a harvested commodity in a stress situation and shorten its storage life. Surplus turgor pressure, caused either by absorption of external water (Glenn and Poovaiah, 1989) or by water redistribution within different fruit tissues (Paull, 1996), may cause fruit to crack or split. The water-excess stress is most common when moisture is allowed to remain or collect on the surface of the product, usually as a result of water condensation. Patterson et al. (1993) have described in detail the determinants and negative consequences of water condensation on the fruit surface. The latter include leakage of solutes from the damaged areas, inhibition of gas exchange (see Burton and Wiggington, 1970), and enhancement of microbial growth. The presence of condensed water on the surface of the produce enhances the development of postharvest pathogens (Eckert, 1978; Grierson and Wardowski, 1978), especially species such as *Erwinia* (Lund and Nichols, 1970) and *Botrytis* (Jarvis, 1977). On the other hand, excessive water loss and wilting also increase the susceptibility of vegetables to *Botrytis* and other pathogens (Eckert, 1978).

In order to reach the maximal postharvest life span, moisture content in the produce should be maintained at an optimal level, which varies considerably with different commodities. In some cases, prestorage adjustment of water content may be needed. Many cut flowers and foliage crops require the reintroduction of liquid water after harvest (Van Doorn, 1997). An attempt at replacement of postharvest moisture loss in carrots (*Daucus carota* L.) by rehydration in water was reported by Shibairo et al. (1998). On the other hand, sometimes the keeping quality of fresh produce may benefit from temporary enhancement of water loss. For example, "wilting" treatment is traditionally practiced with *Citrus* fruits in the Far East, where fruit is kept at ambient conditions immediately after harvest until it loses at least 3% of the initial weight, and only afterwards is it transferred to cold storage. It is interesting that this treatment was reported not only to extend postharvest life by reducing decay and storage injury (Kawada and Kitagawa, 1992) but also to result in eventual lower total weight loss of the fruit at the end of 3 to 6 months of storage (Murata and Yamayaki, 1992). However, the beneficial effects of wilting were not evident in experiments conducted in Israel (Ben-Yehoshua, Rodov, Peretz, unpublished data). Reduction of excessive turgidity of *Citrus* fruits is known to be a measure for alleviating physiological disorders (Grierson and Ben-Yehoshua, 1986). With apples, a similar method reduces the incidence of low temperature breakdown (Wills et al., 1998).

Once the product is at or near optimum moisture content, it is desirable to minimize any further change in moisture concentration by maintaining the appropriate microenvironment (such as air humidity and temperature). The postharvest life span of most fresh, succulent horticultural products benefits from high air humidity (usually 90% to 95%) unless there is a risk of liquid water condensation on the produce. With lower-moisture products such as roots, tubers, nuts, and corms, lower storage humidities are required in order to avoid moisture absorption by the commodity. The effects of the postharvest environment on water loss during storage are discussed in more detail in later sections.

III. BIOPHYSICAL BASIS OF WATER RELATIONS IN HARVESTED COMMODITIES

The physics of water relations in plants is well established, although a few awkward points are still unclear. The books by P. Nobel (1974, 1991) serve as an invaluable source of

information on the biophysical basis of physiological processes in plants. Transpiration of fresh fruits and vegetables, as of all higher plants, is a mass transfer process in which water vapor moves from the surface of the plant organ to the surrounding air. To better understand this phenomenon, Fick's law, the physical law that governs the diffusion processes, should be dealt with. The simplified version of Fick's law for the case of gas diffusion from a plant organ to the atmosphere can be written as:

$$J = (P_i - P_a) A_i / (R_D T) r$$

where P_i and P_a are the steady-state gas partial pressures in the intercellular spaces and in the ambient atmosphere at a substantial distance from the organ's surface, respectively; A_i is the organ's surface area; R_D is the gas constant per unit mass; T is the absolute temperature; r is the resistance; and J is the gas flux. According to Fick's law, the movement of any gas in or out of the plant tissue is directly proportional to the partial pressure gradient ($P_i - P_a$) across the barrier involved and the surface area of the barrier; and is inversely proportional to the resistance of the barrier to diffusion. Therefore, the driving force of transpiration is the gradient of water vapor pressure (WVP) between the tissue and the surrounding air. The water vapor pressure deficit (VPD) of the air is the difference between the WVP of air and that of saturated air at the same temperature.

The SI (Système International d'Unités) unit for expressing WVP is the pascal (Pa; newton meter⁻²), but the millibar (mbar = 100 Pa) is still frequently used. Standard atmospheric pressure is equivalent to 101.325 kPa, 1.01325 bar, 760 mmHg, or 29.92 in. Hg. The wide variety of units used in postharvest studies hampers understanding and operation of the data and needs unification. An attempt to elaborate a rationalized system of units for postharvest gas exchange research was made by Banks et al. (1995).

Relative humidity (RH) is probably the most popular term for expressing the water content of air. It is defined as the ratio of actual WVP in the air to the saturation WVP possible at a given temperature, expressed in percent. This definition makes clear that RH is a function not only of the amount of water vapor in the air but also of temperature. Thus, for the same RH, air at higher temperature has higher VPD than air at lower temperature. Using RH data without considering temperature effects can result in grave errors (Lipton, 1993). Still, in this review we often refer to RH as this unit is most frequently provided in publications and used in postharvest practice.

Another important characteristic of air humidity is the dew point, the temperature at which air with a given moisture content becomes saturated (100% RH). If air is cooled below its dew point, condensation can occur. The importance of this parameter is easily understood in considering the negative consequences of water condensation on the postharvest life of fruits and vegetables, as mentioned in the previous section.

In order to estimate the driving force of transpiration, let us consider the WVP value within plant tissue. The amount of solutes in the tissues affects the WVP in the plant organ. The effect of solutes is directly proportional to their molar concentration. A tissue with a fairly typical osmotic pressure of 1 MPa (10 bars) would have a depressed WVP of 20 Pa (0.2 bar) at 20°C. Tissue with such tonicity would be in equilibrium with RH of over 99%. However, the solute concentration in water exposed for evaporation is lower than that inside the cells, since in part it passes through the semipermeable plasmalemma as well as the cell walls and cuticle outside the protoplast. This water is held within the cuticle or the interfibrillar spaces in the cellulose walls by surface tension and absorptive forces; it is also in dynamic equilibrium with the cell content and dependent on the turgor pressure. Due to turgor effects, the equilibrium RH in real plant tissues is higher than that

predicted for a free solution of the same concentration (Patterson et al., 1993). Taking these interactions into account, Nobel (1974) calculated the value of intercellular RH as 99.4%. Rooke and Van den Berg (1985) determined a very similar value (99.5%) experimentally for whole carrots. In other words, the WVP of intercellular spaces in fresh plant organs is very close to saturation. In this case, the transpiration rate is proportional to the vapor pressure deficit (VPD) of the ambient atmosphere.

The temperature effect on the WVP of plant tissue is even more critical than that of solutes. A logarithmic plot of WVP against the reciprocal of temperature (K) is almost linear (Nobel, 1974). An increase of 0.5°C, which is below the expected fluctuation of tissue temperature in most refrigerated stores, would affect the WVP more than tissue tonicity. It is therefore important in this kind of measurement to carefully record both air and tissue surface temperatures. The following example illustrates the effect of temperature on water loss. If vegetables are harvested during warm weather (25°C) and are placed under conditions of 20°C and 70% RH, the WVP of the internal atmosphere at 25°C would be 3.17 kPa and that of the storage atmosphere at 20°C would be 1.64 kPa. Thus, the driving force of transpiration (VPD) is a high 1.53 kPa, and the vegetables will lose water at a high rate. When the internal temperature reaches 20°C, the driving force will be 1.48 kPa. However, if the vegetables were stored at 90% RH and 5°C and rapidly cooled, the WVP gradient between the air and the internal atmosphere would be as low as 0.09 kPa; thus there would be little water loss.

In order to quantitatively describe the water flow within the system, attention should be directed to thermodynamic analysis of this process. The most suitable parameter for specifying the state of water in any system is the free energy or chemical potential of the water. Water flow is governed by the gradients of chemical potential in the direction of decreasing potential, which in the case of passive diffusion of water is the same as that of decreasing concentration. Accordingly, for this case, the concept of chemical potential is still implicit in Fick's law.

It is customary to express the difference in chemical potential in units of energy per unit volume; thus, the water potential Ψ_w is a practical measure of the free energy status of water in a given system. The term water potential is identical to the older terms *suction pressure* or *diffusion pressure deficit* and is now universally used in biology and other disciplines.

Water potential can be measured unambiguously by, for example, measuring the vapor pressure of water in equilibrium with the system. Methods of water potential measurement have been reviewed by Boyer (1995). Many of these methods are based on the application of either pressure chambers or thermocouple psychrometers. Both methods have certain difficulties when applied to fruits and vegetables; for example, the psychrometer can only be used with small pieces of tissue. Recently, a new nondestructive method for measuring the water potential of fruits and vegetables was proposed by Jobling et al. (1997) based on the measurement of water exchange between the produce and pads containing a salt solution of known water potential attached to the surface of the organ.

For proper understanding of the physics of water in plants, it is necessary to break the water potential into its components, even if there are some doubts about the analysis (Nobel, 1974). Thus, water potential is composed of (a) the osmotic potential, due to the presence of dissolved solutes; (b) the pressure potential, due to the turgor pressure acting outward on the cell walls and internal membranes in plants; and (c) the matric potential, due to capillary and molecular imbibitional forces associated with cell walls and colloidal surfaces that bind some of the water. Thus, water potential Ψ_w can be presented as follows:

$$\Psi_w = \Psi_\pi + \Psi_p + \Psi_m$$

where Ψ_π is the osmotic potential, Ψ_p the pressure potential (turgor), and Ψ_m the matric potential. Except for Ψ_p , these values are negative. The water potential of pure water is zero. In fully turgid tissue, water potential will be a function of osmotic and turgor pressures since the matric potential approaches zero as the colloids and matric surfaces become saturated. When the tissue is under water stress, the osmotic and matric effects increase and the turgor pressure approaches zero.

IV. WATER MOVEMENT WITHIN THE HARVESTED COMMODITY

The water potential of the ambient atmosphere is much lower than that of the fresh plant organ. For example, the fall of water potential on the plant-air interface at 25°C is about 0.85 MPa for an atmospheric RH of 99% and 93.5 MPa for a RH of 50% (Nobel, 1974). In addition, factors such as temperature differences between the sunny and shady sides of the plant organ may cause a gradient of water potential within the organ itself (Jobling et al., 1996). These gradients determine the water movement within the harvested commodity. In this section, we consider the main pathways of this movement, as well as some factors affecting the rate of water flow within the commodity.

A. Routes for Water Transmission

In harvested fruits and vegetables severed from the parent plant, the xylem vessels are usually occluded with air and their operation is greatly impeded if not arrested altogether (Burton, 1982). Therefore, water has to use different routes to move through the tissue continuum. The following major potential pathways for water movement are present in the tissues of harvested plant organs.

1. Symplast

The cytoplasm of neighboring cells is interconnected by plasmodesmata, filled with protoplasm and lined with the plasmalemma. Hence, a virtually continuous cytoplasmic system, the symplast, is formed throughout the interior of a plant organ. Water and dissolved solutes move through the symplast system from cell to cell by diffusion, in response to energy gradients. For a review of plasmodesmata and symplast function, see Lucas et al. (1993).

2. Apoplast

The cell walls surrounding the symplast also form a continuous system, termed the *apoplast*. The apoplast offers an alternate avenue for the movement of liquid water by hydrostatic pressure gradient through the interfibrillar spaces in the cell walls (Woods, 1990).

3. Intercellular Atmosphere

The plant also contains a system of intercellular gas-filled spaces that form a continuous lattice and serve as a main pathway for the transfer of O₂, CO₂, and other fixed gases. This continuum of air space is responsible for adequate gas exchange in bulky organs (Ben-Yehoshua, 1969; Burg and Burg, 1965; Burton, 1982; Devaux 1891). In "Red Delicious" apples, the porosity may reach an average of 25% of the total fruit volume, while in the potato (*Solanum tuberosum* L.) tuber it accounts for only 0.6% to 1.3% of the tissue

volume (Marcellin, 1963). Like those of other gases, water vapor molecules can diffuse through these air channels down a partial pressure gradient toward the surface of the produce. However, as shown in the previous section, the WVP inside plant tissues is very close to saturation. This practically saturated air is found not only around the interior cells but also in the more exterior regions of the produce. As a result of an extremely small difference in WVP between the interior and exterior cells, the contribution of intercellular air spaces to water transport within the plant organ is minor (Woods, 1990). It may therefore be concluded that water moves to the surface of the product predominantly in the liquid phase, although some movement may occur in the vapor phase as well (Burton, 1982). Extending the calculations by Briggs (1967), Burton (1982) concluded that hydrostatic, apoplastic flow offered the path of least resistance for liquid water movement compared to the cell continuum. However, the dominant role of the apoplastic route in water transport has been disputed in several works (see Kramer and Boyer, 1995). Michael et al. (1997) reported that the protoplasts served as the dominant route for osmotically driven water transport through living slices of potato tuber, whereas the liquid-filled intercellular spaces were the dominant pathways for pressure-driven volume fluxes.

B. Water Flow Within the Commodity

The actual flow of water within harvested commodities calculated by Burton (1982) shows the great difference between leafy vegetables and potato tubers: 1.4×10^{-7} vs. 1.0×10^{-8} cm s⁻¹, respectively. Spinach leaves were reported to lose water about 200 times as fast as mature potato tubers (Robinson et al., 1975). In spite of such a significant difference between the two commodities in the rate of water flow, neither demonstrated serious internal resistance that impeded the water flow from the internal parts of the organ to the evaporating periphery. Accordingly, in most cases we can consider harvested crops as being internally uniform with a saturated intercellular atmosphere and resistance to water movement located predominantly in the surface layer.

C. Internal Barriers and Water Redistribution Within the Commodity

Some commodities contain internal barriers that impede water flow within the harvested organ. For example, the multilayered structure of onions and cabbages offer a tortuous route for water flow via the dwarf stem, with a high resistance to direct water transfer between the leaf layers (Burton, 1982; Woods, 1990). This block in the path of water causes an unequal water loss from different parts of the commodity. The external scales of the onion dry and shrink while the rest of the bulb remains succulent. In addition, water may be redistributed within the commodity itself. An example of water redistribution within the commodity is found in the case of sweetcorn (*Zea mays* L. var. *rugosa* Bonaf.) (Showalter, 1963, 1967). After detachment from the plant, water loss occurs primarily through the outer husk leaves of sweetcorn. This in turn draws water from the cob and kernels, resulting in kernel denting. A similar situation occurs in carrots, beets (*Beta vulgaris* L. ssp. *vulgaris*), radishes (*Raphanus sativus* L.) etc. when these commodities are marketed with intact tops, and their shelf life is considerably extended by trimming (Hardenburg, 1951; Lewis, 1957; Lutz et al., 1954)

When seeds mature, it is common for them to dehydrate as part of the maturation process. How can this process take place in the nearly saturated conditions of fleshy fruit? Based on their research with muskmelon (*Cucumis melo* L. *Reticulatus* group), Welbaum and Bradford (1988) and Bradford (1994) concluded that the seed in this case is dehydrated

osmotically, due to the high solute concentrations and, accordingly, low osmotic potential of the apoplast solution.

It has also been found that application of different temperatures to two sides of some fruits (apples, tomatoes) elicits cross movement of water from the warm to the cool side (Curtis and Clark, 1950).

V. THE COMMODITY SURFACE: A MAJOR EVAPORATION SITE

As shown above, the surface-exterior interface is a predominant site for water evaporation from plant organs. Plants evolved their systems of gas exchange by adjusting to conflicting demands: provision must exist for an effective route for the exchange of CO₂ and O₂, while minimizing transpiration to prevent desiccation. Thus, the system has to be a compromise between maintaining an adequate flux of O₂ and CO₂ while minimizing the flux of water vapor.

There are three major routes for moisture loss from harvested commodities to the atmosphere: (a) through the outer layer that forms a surface for evaporation (cuticle and epicuticular wax; periderm) while resisting water movement; (b) through the apertures in the surface connecting the internal and external atmosphere (stomata, lenticels); and (c) through the stem scar or pedicel, sometimes with adjacent sepals. The relative contribution of these components varies in different commodities and in many cases is still the subject of debate. In the following sections, the anatomical basis for surface resistance to water vapor diffusion is dealt with.

A. Stomata

In the case of leaves, the regulation of transpiration through the stomata is well understood. In mature leaves, before harvest, most of the evaporation occurs from the undersides via stomatal guard cells and adjacent subsidiary cells (for detailed reviews, see Mansfield, 1986; Kramer and Boyer, 1995). After harvest, the stomata close and the role of cuticular transpiration in leafy commodities increases (Woods, 1990). However, even in this case incomplete stomatal closure may considerably contribute to leaf water conductance (Kerstiens, 1996). The significance of stomatal transpiration in plant organs other than leaves is still to be determined, particularly in mature fruit after harvest.

The occurrence of stomata in fruits and their density varies among different species and depends on the age of the fruit. Stomata occur in many fruits at early stages of development (Blanke, 1986), but sometimes they are not found in mature fruit of the same species—for example, in the grape berry (Possingham et al., 1967), blueberry (*Vaccinium corymbosum* L.) (Eames and McDaniels, 1947), tomato (Clendenning, 1941), bell pepper (Lownds et al., 1993) and chili pepper (*Capsicum annuum* L. Longum group) (Blanke and Holthe, 1997). In contrast, mature pea pods had 24 to 26 stomata per square millimeter (Blanke and Lenz, 1989). Orange was found to have the greatest stomatal density reported so far for any fleshy fruit, with continuous development of new stomata until the start of maturation (Blanke, 1995, 1996). However, it was still at least one order lower than the corresponding leaf stomatal density.

Stomata usually function less effectively as fruit mature (Blanke and Leyhe, 1988; Wardlaw and Leonard, 1936). The stomata of maturing oranges, particularly their upper vestibular chambers, were reported to be plugged by various materials such as wax deposits, hyphal growth, and unidentified objects (Albrigo, 1972; Albrigo and Brown, 1970;

Turrel and Klotz, 1940). However, recently Blanke (1995) has disputed the credibility of these early findings and reported that fruit picked without touching the surface and examined by scanning electron microscopy (SEM), without using fixatives, showed large number of open unplugged stomata. While Moreshet and Green (1980) described functional stomata with regulatory guard cells in the orange fruit prior to harvest, their data showed clearly that the stomata on citrus fruit stop functioning after harvest. The differences between these observations may be related to the difference in the environmental conditions on the sites of the fruit growth. However, the rate of postharvest weight loss did not correlate with stomatal density either in citrus (Haas and Klotz, 1935), plantain (*Musa* spp. AAB genomic group), or cooking banana (*Musa* spp. ABB genomic group) (Burdon et al., 1993, 1994b).

In conclusion, it may be summarized that stomatal transpiration, while relatively active at early stages of fruit development on the plant, is in most cases is greatly reduced with maturation and is usually of minor importance for fruit water loss during the postharvest period.

B. Lenticels

The importance of lenticular transpiration varies from commodity to commodity but is more important in fruit, in which lenticels arise after the stomata stop functioning early in fruit development, through breaks caused by the complete removal of hairs or by skin expansion (Clements, 1936). Lenticels may become cutinized or suberized, thus preventing gas exchange; in other cases, they may remain open. Burton (1982) calculated the rate of water vapor movement through the lenticels of potato tuber to be less than 3% of the total moisture loss. He suggested that a similar situation holds true for other commodities with lenticels, such as taproots and pome fruits.

C. Trichomes and Hairs

Unicellular or multicellular projections develop on the epidermis of all parts of plants. The exact function of these protuberances is still obscure, but they are considered to reduce water loss (Cutter, 1976). The presence of trichomes can decrease the driving force of transpiration by reducing the surface temperature and increasing the boundary layer resistance. However, observations on the ecological role of trichomes led Johnson (1975) to the conclusion that pubescence cannot be regarded as a simple adaptation to an arid environment. In beans, broken hairs were shown to be an important avenue of water loss, increasing the overall rate of transpiration (Hoffman, 1967).

D. Periderm

Many commodities have a corky peripheral tissue called periderm. Typically, this tissue consists of several layers of cells that become corky as a result of deposition of suberin and waxes on their walls, and they ultimately lose their living contents. Potato tubers have a typical periderm with visible lenticels. The periderm is not readily permeable to water and is permeable to gases only through the lenticular pores, which replace the stomata of the original epidermis. About 97% of the total water lost from the potato tuber migrates through cell walls to the periderm, where it evaporates (Burton, 1982). In some other subterranean crops (e.g., carrot and parsnip, *Pastinaca sativa* L.), the surface is covered

with only a thin layer of lightly suberized living cells, with lower barrier properties to water transfer than the typical periderm.

E. Cuticle and Epicuticular Wax

Resistance to water movement is derived mainly from the cuticular layer (Ben-Yehoshua, 1969; Burg and Burg, 1965; Horrocks, 1964). This layer, which lines all interfaces between the plant and the atmosphere, protects the plant from its relatively dry environment. The cuticle comprises a matrix of cellulose, polyuronic acids, proteins, and phenolic compounds. These are combined with varying amounts of waxes embedded in the polymer matrix and deposited superficially over its surface (Kolattukudy, 1980). The importance of the cuticle and epicuticular wax varies among different types of fruit. The data on water permeabilities of cuticles in various plant species and organs have been summarized by Becker et al. (1986). For more detailed and extensive information on plant cuticles, we recommend the book edited by Kerstiens (1996).

Waxes, especially soluble ones, constitute the major barrier to water movement through the cuticle (Albrigo, 1972; Horrocks, 1964; Possingham et al., 1967; Schonherr, 1981). These natural waxes are deposited as overlapping hydrophobic platelets separated by air-filled pores and microcapillaries. The structural arrangement of wax platelets, together with their hydrophobic surfaces, impedes movement of water vapor through the capillary canals formed by the overlapping wax platelets. Transpiration is controlled by the hydrocarbons, long-chain alcohols, and aldehydes, which make up most of the "soft wax" component. The "hard wax" (oleonic acid) comprises 70% of the total cuticle (Possingham, et al., 1967).

Permeability to water usually depends more on the amount of wax than on the thickness of the cuticle (Kramer and Boyer, 1995). For example, the water-loss rate in bell pepper cultivars was positively correlated with cuticle thickness and negatively correlated with epicuticular wax content (Lownds et al., 1993). The effects of waxy bloom of several cultivars of *Brassica oleracea* (i.e., cabbage, broccoli, Brussels sprouts, cauliflower, collards, and kale) were investigated by comparing the stomatal and cuticular transpiration of glaucous and nonglucous cultivars (Denna, 1970). The glaucous characteristic is a waxy bloom on the surface of leaves and stems that imparts a bluish, whitish, or grayish cast to the foliage. Both the cuticular and the stomatal transpiration values of the glaucous cultivars were lower than those of the nonglucous ones. However, no correlation was found between the quantity of wax per unit area of leaf and the loss of water in glaucous or nonglucous plants. The water-loss rate in these commodities may be determined by the content of a certain hydrophobic fraction rather than by the total amount of wax. In all cultivars, the cuticular transpiration was about 9% of the stomatal transpiration (Denna, 1970).

After studying detached cuticular membranes devoid of chloroform-soluble wax, Schonherr (1981) concluded that water and hydrophilic solutes move through the cuticle in polar, water-filled pores, while the lipophilic molecules move in relation to their oil-water partition coefficients. Although it is difficult to extrapolate the behavior of the native intact cuticle from this artificial system, the hypothesis of water-filled pores in the cuticle has some indirect support. As stated previously, water is transported to the evaporating surface in the liquid phase. Evaporation at the outer cuticular surface creates a suction force that draws liquid water by mass flow from the epidermal cells through the liquid water phase of the cuticular membrane to the air-water interface (Ben-Yehoshua et al.,

1983a, 1985). This water phase in the cuticle is probably the same phase that Schonherr (1981) demonstrated in his studies of detached extracted cuticles. The discovery of aquaporins—special proteins responsible for facilitated water movement through plant cell membranes (Chrispeels and Maurel, 1994)—may be relevant to this problem as well.

F. Stem Scar and Sepals (Calyx)

The contribution of the stem scar as an avenue for water loss was investigated by comparing fruit with plugged and open scars. Cameron (1982) showed that the contribution of the calyx to the passage of water vapor varied in different fruits. In the "Golden Delicious" apple, the calyx provided only 2% of the total fruit water loss, while in tomato, the percentage was as high as 67%. In our experiments (Ben-Yehoshua, Rodov, and De la Asuncion, unpublished data), the stem scar of "Maor" bell pepper was shown to have minimal resistance to water vapor movement compared to sepals and cuticle (3 vs. 26 vs. 95 s cm⁻¹, respectively). Considering the area of the three, the cuticle was calculated to conduct about 69% of the total transpiration from the bell pepper fruit, while the remainder was divided almost equally between the stem scar and the sepals (15% and 16%, respectively).

G. Transpiration vs. Gas Exchange: Separate Pathways

Summarizing the above data, we can conclude that in most of the harvested commodities (especially the nonleafy ones), the surface water-resistant layers (cuticle, periderm) play the major roles in postharvest transpiration. Water is transported to these layers as a liquid and evaporates from their surface. Transpiration through the apertures connecting the internal and external atmospheres, such as stomata, may be considerable during the early stages of the organ's development on the mother plant. However, with the organ's maturation, the importance of these apertures (stomata, lenticels) in water loss declines because of their sparse distribution on the surface. The role of the apertures in transpiration further diminishes after harvest, when the stomata tend to close and to lose their activity.

This situation differs from that of the transfer of fixed gases, which does take place in the air phase through the apertures. The resistance values of fruit surfaces to the passage of different gases (ethylene, CO₂, and O₂) were found to be similar and to greatly exceed their resistance to water vapor: 100 times for apples (Burg and Kosson, 1983), 60 times for orange (Ben-Yehoshua et al., 1985), and 50 times for tomato (Shirazi and Cameron, 1993). If passage was limited by a liquid phase (either water or lipid), the resistance to different gases would be inversely proportional to their solubility in that phase. Since the three gases have widely differing air/water and air/oil partition coefficients, it is difficult to conceive of a route other than passage through the air phase that could transfer them through the fruit's surface with equal ease. Accordingly, different pathways for gases and water were suggested, assuming that H₂O runs through the liquid water phase, while O₂, CO₂, and ethylene pass through the surface apertures (lenticels and stomata) and diffuse in the air phase of the internal atmosphere (Ben-Yehoshua et al., 1983a, 1985).

A limited diffusion area can therefore explain the high resistance of the surfaces of bulky plant organs to the passage of gases. Burg and Kosson (1983) hypothesized that the lenticels in apple fruit are partially occluded with water, which would decrease even more the pore area available for mass transfer of all gases except water molecules. Similarly, stomatal closure may explain the high resistance of harvested plant organs to gas transfer. Based on diffusivity of O₂, CO₂, and ethylene in air, the resistance of open stomata

to these gases would be as low as 21 s cm^{-1} , compared with 6000 s cm^{-1} after harvest in *Citrus* fruits (Ben-Yehoshua et al., 1983a, 1985). Only 0.4% of the initial fully open pore area is needed to account for the observed residual gas-exchange capacity. The slightly opened stomata on harvested *Citrus* fruit, as mentioned previously, could account for this 0.4% opening.

The presence of separate pathways for water and gas exchange enables a compromise to be found between the two conflicting demands: maintaining an adequate flux of O_2 and CO_2 while minimizing water loss. Examples of successful realization of this compromise using suitable plastic packages are described in a later section.

VI. FACTORS THAT AFFECT TRANSPIRATION

A. Commodity Peculiarities

The variation in rate of transpiration among different commodities is enormous. Sastry et al. (1978), Burton (1982), and Van den Berg (1987) compiled the reports of many researchers on weight-loss rates from various fruits and vegetables (see Tables 2 to 5). Sastry et al. (1978) discussed the difficulties in preparing such a table, primarily because the experiments were not specifically designed to determine a transpiration coefficient, which could be defined as the mass of moisture transpired per unit VPD per unit time. The list begins with leafy vegetables and ends with potato tubers and shows a difference between the two of several hundredfold or even thousandfold (at comparable environmental conditions). Additional information on transpiration coefficients of various fruits and vegetables can be found in Romero et al. (1986) and Chadwick and Hellickson (1989).

The tremendous variation in the transpiration rates reported can be explained by many factors, such as the wide range in the ratio of surface area to volume of various commodities. Burton (1982) compared these ratios (see Table 6), showing that leafy vegetables have a surface/volume ratio of 50 to 100 cm^{-1} , whereas a densely packed head of cabbage or a large turnip (*Brassica rapa* L. Rapifera group) has a ratio of 0.2 cm^{-1} . The size of a fruit or vegetable has a significant effect on its transpiration. Large commodities have a lower surface/volume ratio than small ones and hence lose less moisture on a unit-weight basis. The shape of vegetables also affects the ratio of surface area to volume. Long, thin, cone-shaped carrots lost more weight than thick, cylindrical ones in a given environment (Sastry et al., 1978). The longer, thinner carrots shriveled faster at the tips because of the greater surface area per unit volume. The close relationship between transpiration rate and the surface/volume ratio has also been reported for oranges, tomatoes, papayas (*Carica papaya* L.), watermelons [*Citrullus lanatus* (Thunb.) Matsum. & Nak.] (Leonard, 1941) and peppers (Lownds et al., 1993).

Differences in surface permeance to water vapor is another source of broadly varying transpiration rates of various commodities. Table 7 presents transpiration from various types of plant surfaces expressed as absolute weight loss per unit surface area per unit VPD per unit time. Table 7 clearly demonstrates the effect of water-resistant layers (periderm, cuticle) on commodity transpiration rates.

B. Genetic Factors

An interesting study describing the possibility of reducing transpirational weight loss through a breeding program was reported for beans by Hoffman (1967). In an extended selection, carried out with 49 cultivars over 18 years, properties that affect weight loss

Table 2 Postharvest Water Loss from Leafy Vegetables Including Swollen Leaf Bases, Stems, and Inflorescences

Commodity and cultivar	Conditions of determination ^a		
	Temperature (°C)	Relative humidity (%)	Water loss (FW basis) (% day ⁻¹ Pa wvpd ⁻¹)
Leafy material with isolated or loosely arranged leaves			
Lettuce, "Unrivalled"	15	45-65	750 ^b
Spinach, "Prickly True"	15	45-65	1100 ^b
Watercress	15	45-65	3500 ^b
Leafy material, moderately compact			
Brussels sprouts	15	45-65	280 ^b
Cabbage	0-2	85	50 ^b
Cabbage, "Primo"	10	60-75	100 ^b
Leafy material, very compact			
Cabbage, "Decema"	10	60-75	10 ^b
Leaf bases, moderately compact			
Leek, "Musselburgh"	15	45-65	90 ^b
Leaf-bases, very compact			
Onion, "Bedfordshire Champion"	10	60-75	2 ^b
Stems and petioles			
Asparagus	10	60-75	360 ^b
Celery, white	15	45-65	280 ^b
Rhubarb	10	60-75	230 ^b
Young inflorescences, loose			
Calabrese, green	15	45-65	240 ^b
Sprouting broccoli	15	45-65	750 ^b
Young or aborted inflorescences, compact			
Cauliflower, "April Glory"	15	45-65	190 ^b
Cauliflower	0-2	85	120 ^c

^a The wide range of humidities given includes those measured for many experiments. Humidity was approximately constant in any one experiment.

^b Data from Robinson et al., 1975.

^c Data from Singh et al., 1952.

Source: Burton, 1982.

were determined. Surprisingly, density of stomata; thickness of cuticle; hair length; endocarp, mesocarp, and exocarp depth; or cell size of these tissues were not found to be related to the rate of transpiration. The only properties found to affect transpiration were the number of hairs and, more specifically, the number of broken hairs. Accordingly, Hoffman selected cultivars that were glabrous or relatively free of hair. In a later study, he found that by breeding more fibrous cultivars he could delay the appearance of flaccidity of the pods despite their water loss.

Several other examples of genotype-related variation in transpiration rates have been reported. The presence of waxy bloom in "glaucous" cultivars of *Brassica oleracea*, associated with a single Mendelian factor, reduced both stomatal and cuticular transpiration in these cultivars (Denna, 1970). Significant intervarietal variations in postharvest water-loss rates were revealed between different cultivars of the following fruits: mango

Table 3 Postharvest Water Loss from Fruits and Seeds^a

Commodity and cultivar	Conditions of determination ^b		Water loss (FW basis) (% loss day ⁻¹ Pa wvpd ⁻¹)
	Temperature (°C)	Relative humidity (%)	
Leguminous fruits			
Beans, broad	15	45–65	210 ^c
Beans, runner	15	45–66	180 ^c
Peas in a pod, "Onward"	15	45–65	130 ^c
Fresh leguminous seeds and immature cereals			
Peas, shelled	15	80	270 ^d
Sweetcorn, on cob	15	45–65	140 ^c
Soft fruits			
Blackberries, "Bedford Giant"	10	60–75	50 ^c
Raspberries, "Malling Jewel"	10	60–75	250 ^c
Strawberries, "Cambridge Favourite"	15	45–65	70 ^c
Other fruits			
Apple, Boskoop	0	85–90	9
Apple, Bramley's Seedling	0	90	3
Apple, Golden Delicious	0	85–90	7
Apple, Jonathan	0	85–90	4
Apple, Ontario	4	85–90	3
Apples, Worcester Pearmain	0	85–92	9–12
Banana	12.5	90	6
Banana, Cavendish, green	11–13	85–90	30
Cucumber	15	45–65	40 ^c
Eggfruit, Eerangeri	11–13	87–90	60
Guava, Safeda	8–10	85–90	30
Mango, Totapuri	6–7	85–90	10
Orange, Valencia	3.3	82–92	6
Orange, Valencia	8.9	80–88	4
Pear	0	85–92	5
Pepper, green	10	60–75	6
Plum, "Victoria," ripe	5	80	10
Plum, "Victoria," unripe	5	80	20
Sapodilla, "Oblong"	2–3	85–90	30
Tomato, "Eurocross BB"	10	60–75	10

^a Data from Burton, 1982.^b The wide range of humidities given includes those measured for many experiments. Humidity was approximately constant in any one experiment.^c Data from Robinson et al., 1975.^d Data from Singh et al., 1952.

Source: Burton, 1982.

Table 4 Postharvest Water Loss from Roots and Tubers^a

Commodity and cultivar	Conditions of determination ^b		Water loss (% day ⁻¹ Pa wvpd ⁻¹)
	Temperature (°C)	Relative humidity (%)	
Beetroot, storing	10	60-75	160 ^c
Beetroot, storing	0-2	85	90 ^d
Beetroot, bunching, with leaves	15	45-65	160 ^c
Carrot, storing	10	60-75	190 ^c
Carrot, bunching, with leaves	15	45-65	280 ^c
Cassava (tapioca), sweet	0-2	80-90	80 ^d
Parsnip, "Hollow Crown"	15	45-65	240 ^c
Potato, "King Edward," mature	10	83	2
Potato, "Majestic," mature	10	83	1
Potato, "Majestic," immature	10	84	10-30 ^e
Sweet potato	8-10	89	60 ^{d,f}
Turnip, young white	10	60-75	110

^a Data from Burton (1982) other than where marked.

^b See corresponding footnote in Table 2.

^c Data from Robinson et al., 1975.

^d Data from Singh et al., 1952.

^e After 5 days; during the first day after harvest it was 0.4%-2.1%.

^f Average over the first 2 weeks of storage, but fell to an average of about 0.2% during weeks 7 and 8.

Source: Burton 1982.

(Dietz et al., 1989), plantain and cooking banana (Burdon et al., 1993), blueberry (Makus and Morris, 1993), and peppers (Lownds et al., 1993, 1994). In mango cultivars the transpiration rate was correlated with lenticel density, while in peppers and cooking bananas it was correlated with epicuticular wax content.

C. Horticultural Factors

In many cases, the transpiration rate shows wide variation within the same crop and even within the same cultivar. Maguire and Banks (1996) have analyzed the contribution of various sources to total variation in estimates of fruit water-vapor permeance of "Braeburn" apple. About 50% of the total variation was found to be related to harvest date: there was about a twofold increase in fruit transpiration rate from the first to the second harvest. Interaction of harvest and orchard effects was also found, causing fruit from different orchards not to respond in the same way to the advancing harvest. Fruit-to-fruit variability accounted for as much as 22.3% of the total variation, probably reflecting different microenvironmental conditions and the developmental "history" of each individual fruit.

Excess irrigation increased the rate of fruit weight loss in "O'Henry" peaches [*Prunus persica* (L.) Batsch] (Crisosto et al., 1994) by affecting the structure of the fruit's ectoderm (lower trichome density and thinner cuticle compared with fruit from deficit and optimal irrigation). Preharvest foliar sprays of 2,4-D and/or GA on "Ruby Red" grapefruit reduced water loss during storage (Fucik, 1981).

Table 5 Transpiration Coefficients of Certain Fruits and Vegetables

Product	Transpiration coefficient ($\text{mg kg}^{-1} \text{ s}^{-1} \text{ mPa}^{-1}$)	Range of coefficients reported in literature
Apples	42	16–100
Brussels sprouts	6150	3250–9770
Cabbage	223	40–667
Carrots	1207	106–3250
Celery	1760	104–3313
Grapefruit	81	29–167
Grapes	123	21–254
Leeks	790	530–1042
Lemons	186	139–229
Lettuce	7400	680–8750
Onions	60	13–123
Orange	117	25–227
Parsnips	1930	1094–2771
Peaches	572	142–2089
Pears	69	10–144
Plums	136	110–221
Potatoes	25	15–40
Rutabagas	469	—
Tomatoes	140	71–365

Source: Sastry et al., 1978.

Table 6 Examples of Surface/Volume Ratios of Edible Plant Material

Surface/volume ratio ($\text{cm}^2 \text{ cm}^{-3}$)	Commodity
500–1000	Edible leaves (intercellular surface)
50–100	Individual edible leaves (exposed surface); very small grains (e.g., teff)
10–15	Most cereal grains
5–10	Leguminous seeds; smaller soft fruits (e.g., currants)
2–5	Leguminous fruits; nuts (except coconut); larger soft fruits (e.g., strawberry); rhubarb; shallot
0.5–1.5	Tubers; tuberous roots (except e.g., large yams); tap roots (except e.g., large Swede turnips); pome, stone and citrus fruits; cucurbitous fruits (except e.g., large marrow); banana; onion
0.2–0.5	Densely packed cabbage (e.g., cv. "Decema"); large Swede turnips and yams; coconut

Source: Burton, 1982.

Table 7 Relative Rates of Evaporation from Various Types of Plant Surfaces

Nature of evaporating surface	Where found	Estimated evaporation rate (mg cm ⁻² Pa ⁻¹ h ⁻¹)	Basis of estimate
Water-permeated walls (uncuticularized) of living cells	Lining the intercellular spaces (operative only in stomatal transportation)	330–390	Measured loss from peeled potato tubers (cv. Majestic) during the 2.5 h after peeling. ^a Surface area 87–124 cm ²
Water-permeated walls (lightly suberized) of living cells	Surface of some tap roots	100	Measured loss from parsnip roots ^b
		60	Measured loss from carrot roots ^b
Water-permeated walls of living cells, covered with waxy cuticle of varying thickness	Surfaces of leaves and herbaceous stems, flower buds, fleshy fruits, fresh leguminous seeds, etc.	35	Measured loss from rhubarb petioles ^b
		20	Measured loss from runner bean pods ^b
		17	Measured loss from cucumber fruit ^b
		10–15	Measured loss from fresh shelled peas ^b
		10	Measured loss from spinach leaves ^b
Suberized walls of dead cells in layer 5–15 cells thick	Surface of mature potato tuber	4	Measured loss from tomato fruit ^b
		1.5	Measured loss from unripe Baldwin apples
		1	Measured loss from King Edwards potato tubers
		0.7	Measured loss from Majestic potato tubers

^a Burton, unpublished work.

^b Results of Robinson et al. (1975) converted on the basis of approximate surface areas. Loss from rhubarb too high, because uncorrected for cut ends.

Source: Burton, 1982.

D. Maturation and Ripening

Wardlaw and Leonard (1936, 1939, 1940) carried out the earliest research on the relationship of ripening and transpiration in bananas and other tropical fruits. Ripening "Gros Michel" bananas kept at 29°C and 85% RH transpired at a constant rate during the preclimacteric period, but this rate rose at the beginning of the climacteric period (Leonard, 1941). After the climacteric, a steady state was attained, but at a rate twice as high as before the climacteric. Mangoes and papayas also underwent a similar sequence of changes in transpiration rates. In contrast, the rate of water loss from apples (Smock and Neubert, 1950) and from several avocado (*Persea americana* Mill.) cultivars did not change with ripening (Aharoni et al., 1968). Furthermore, plums (*Prunus x domestica* L.) were found to lose more water when unripe than when ripe (Sastry et al., 1978). However, Cutting and Wolstenholme (1992) showed that the rate of water loss in cold-stored avocado depends on its maturity at harvest and is lower in very mature, tree-stored fruit than in less mature, early-harvested fruit.

E. Respiration

In the respiratory process, the commodity produces CO₂, water, and heat. The water produced remains within the tissue, but the CO₂ escapes and accounts for part of the weight loss of the harvested organ as a result of the mass balance between the intake of O₂ and the release of CO₂. This carbon loss rate is directly proportional to the respiration rate and is usually a minor part (3% to 5%) of the total weight loss (Burton, 1982; Pantastico, 1975) except in cases where rates of moisture loss are low. Generation of heat within the tissue may lead to additional loss of weight. This heat is dissipated through direct heat transfer to the environment and through evaporation of water. The heat of respiration raises the tissue temperature, which in turn creates a VPD, thereby increasing evaporation. Lentz and Rooke (1964) showed that apples lost weight even in water-saturated air that was presumably at the same temperature as the fruit. They attributed this loss to the effect of the heat of respiration. Burg and Kosson (1983) reported that produce in hypobaric storage dissipates most of its respiratory heat via transpiration, since convection of heat is restrained by the lack of air.

Gaffney et al. (1985) calculated the weight-loss rates of three different commodities (apples, peaches, and Brussels sprouts) as affected by factors usually considered negligible, such as respiration. They showed that in certain conditions (high RH, relatively high temperature, and low air-flow rate), practically the whole of the weight loss of the produce, or at least the most significant part, is due to respiration effects, such as respiratory heat generation and carbon loss. These factors should be taken into account in evaluating the weight loss of commodities stored in water-saturated environments—for example, within plastic packages.

F. Environmental Factors

Environmental factors—such as humidity, temperature, pressure, and air movement—determine the magnitude of the transpirational driving force, i.e., the gradient of water potential between the produce and its environment. They therefore have a direct influence on the water loss.

1. Humidity

The effect of air humidity on vegetable water loss is self-evident. Even relatively small differences in RH at a given temperature may cause significant VPD and, accordingly, a significant difference in weight-loss rates. For example, when the RH values inside bell pepper packages stored at 8°C were stabilized by hygroscopic inserts at 99% to 100%, 96% to 98%, 92% to 95%, or 87% to 90%, the weight-loss levels were about 0.7%, 2%, 4%, and 6%, respectively (Rodov et al., 1995b).

In order to maintain constant water content in the commodity, its water potential should be as close as possible to its environment. Most fresh horticultural products contain 85% to 95% water. In practice, the highest storage RH achievable without the risk of water condensation (usually 90% to 95%) is beneficial for such commodities (for information on recommended storage conditions for various commodities, see Hardenburg et al., 1986). With lower-moisture products, lower storage RH is often required. For example, RH as low as 40% to 50% is recommended for the storage of dry beans, which contain only 15% moisture, while green or snap beans (88.9% moisture) require 95% RH in storage at a similar temperature. For garlic (*Allium sativum* L.), with a reported water content of 61.3%, storage RH of 65% to 70% is recommended (Hardenburg et al., 1986).

2. Temperature

Evaporation involves the escape of water molecules from the surface and depends on their free energy. Assuming other factors are held equal, raising the product temperature increases the free energy of the water molecules and, accordingly, their potential for evaporation. Enhancement of water loss by an increase in the commodity surface temperature has been described in Sec. VI.E above, in the example of respiratory heat.

The water-holding capacity of air depends on its temperature and decreases with temperature reduction. Fluctuations in temperature can result in a much greater water loss from stored products than a constant temperature. This may happen in particular when the air temperature reaches the dew point and part of the water vapor is converted into liquid, causing some atmospheric dehydration. The subsequent temperature increase then raises the water-holding capacity of the air and, accordingly, results in higher VPD, causing increased water loss from the produce. Small temperature changes that occur as the thermostat of the refrigeration system goes on and off can result in significant fluctuations in RH and increased moisture loss from the produce (Grierson and Wardowski, 1975; Koca et al., 1993). Because of temperature fluctuations and water-phase transitions within the coolroom refrigeration system (vapor condensation, icing, defrosting), this system acts as a water pump, removing moisture from the produce (Joyce and Patterson, 1994; Van den Berg, 1981).

3. Pressure

Elevated atmosphere pressure is relatively rare in postharvest practice, occurring to a certain extent only during controlled atmosphere storage, and its influence on the water loss rate of harvested commodities is usually insignificant (Kays, 1991). However, reduced air pressure can greatly affect the rate of water loss. In general, a partial vacuum reduces the number of water molecules in the air and thus increases the driving force of transpiration. At a given air humidity level, the rate of evaporation is inversely proportional to the pressure. Reduced pressure in the cargo areas of airplanes results in enhanced water loss during air transportation (Kays, 1991). Hypobaric storage of fruits and vegetables enables

the withdrawal of ethylene and control of both O₂ and CO₂ concentrations in the storage environment. During hypobaric storage, weight loss is minimized by using water-saturated air. However, even with air humidification, the large VPD in hypobaric storage may enhance weight loss (Burg and Burg, 1966; Burg and Kosson, 1983).

Stimulation of water evaporation from the commodity by reduced pressure provides the basis for vacuum cooling of produce. The escape of water molecules during evaporation represents an endothermic process and causes loss of energy (the latent heat of vaporization) and attendant drop of surface temperature. This method is most suitable for commodities with high surface volume ratios which inherently have high water loss rates. Leafy vegetables such as lettuce are very good examples of suitable commodities. The evaporation of 1 g of water from 1 kg of produce lowers the produce temperature by 0.61°C. During vacuum cooling, evaporation takes place not only from the outer surface, as in forced-air cooling, but about equally from the inner tissues because the vacuum removes air and water vapor from all of the surfaces. Water loss and cooling are thus reasonably uniform. In order to achieve the required cooling without excessive wilting of the external tissues, water may be added to the produce before the application of vacuum, so that some of the cooling is carried out by the evaporation of the added water. This practice also allows vacuum cooling to be used successfully for other, less obviously suitable products, such as sweetcorn and even carrots.

4. Air Movement

Air movement has conflicting effects on the transpiration process. In leaves, the role of wind and of the boundary diffusion layer is well known and has been intensively studied. In still air, the RH near the evaporating surface is higher than that of the ambient air, and thus there is less movement of water vapor from the leaf to the air. Air currents greater than 0.84 m s⁻¹ disturb this boundary layer (Nobel, 1974) and decrease its RH, so that transpiration increases. A similar boundary layer effect also takes place with harvested fruits and vegetables (Gaffney et al., 1985).

On the other hand, intensive air circulation within a closed, refrigerated storage environment makes the temperature more uniform and minimizes the amount of water removed from the produce by the refrigeration coils, decreasing the VPD between the produce and the air. In addition, better heat transfer reduces the respiratory heat effects on transpiration.

Therefore the overall effect of air flow on water loss may vary depending on the commodity's peculiarities and surrounding conditions, such as RH, temperature, air velocity, etc. According to calculations by Gaffney et al. (1985), the water-loss rates of apples were not significantly influenced by air velocity except at very high RH, when an increase of air flow reduced weight loss. These calculations were in good agreement with early experimental data on apples (Pieniazek, 1944). On the other hand, for peaches and Brussels sprouts, air velocity had a significant effect at all humidities, enhancing water loss at low RH levels and reducing it at high ones (Gaffney et al., 1985). Optimal air flow under refrigerated storage conditions should be a compromise between these conflicting effects.

G. Postharvest Handling

Rough postharvest handling may harm the integrity of the produce surface and thus may enhance the rate of water evaporation from the commodity to the environment. Avoiding abrasions and cuts during harvest and handling is recommended as one of the basic mea-

tures to minimize water loss. Abrasion was shown to shorten the postharvest life of cooking bananas by accelerating water loss and thus triggering their ripening (Ferris et al., 1994). In sweet potatoes (*Ipomoea batatas*, L.), skin injury increased the weight loss at different RH levels, especially at a relatively low level (80%). In turn, this high weight loss resulted in high spoilage during storage and was highly and positively correlated with the subsequent development of decay (Kushman, 1975).

Damage caused by suboptimal temperature is another factor affecting water loss (Purvis et al., 1985). The development of chilling injury (CI) in *Citrus* was accompanied by the appearance of large cuticular cracks that were probably responsible for the enhanced water conductance observed (Cohen et al., 1994; Rodov et al., 1994). On the other hand, McDonald et al. (1993) have shown that reduction of water loss in *Citrus* is not necessarily accompanied by reduction of CI, and vice versa. They proposed that permeability of the peel to gases other than water vapor may also influence the appearance of CI.

Hot water treatment was demonstrated to repair the minor cuticular cracks naturally occurring on the surface of *Citrus* fruits and to markedly reduce sensitivity to CI (Rodov et al., 1995a, 1996). Similar closure of surface cracks by softened epicuticular wax was observed in heat-treated "Golden Delicious" apples (Lurie et al., 1996). The rate of weight loss was significantly lower in hot water-treated kumquat [*Fortunella margarita* (Lour.) Swingle] fruit than in nontreated fruit (Rodov et al., 1995a; Schirra et al., 1995). This weight-loss reduction was evident only within the optimal temperature range (53 to 58°C), while the injurious temperature (above 60°C) sharply enhanced kumquat weight loss (Rodov and Ben-Yehoshua, unpublished data).

In conclusion, optimal postharvest treatment often tends to reduce the rate of water loss from the commodity, while enhanced weight loss usually indicates possible postharvest injury. Measurement of the weight-loss rate was proposed and applied by Ben-Yehoshua et al. (1970) for monitoring the effectiveness of packing plant operations.

VII. MEANS TO CONTROL WATER LOSS

This section will survey the technological approaches to control water loss during storage and transportation of agricultural commodities. In accordance with the basic principles described in previous sections, water loss may be reduced either by increasing the WVP in the ambient atmosphere and thereby reducing the VPD, or by increasing the surface resistance of the commodity to the movement of water vapor.

A. Reducing the Water-Vapor Pressure Deficit in the Atmosphere

1. Optimizing the Refrigeration System

Lowering its temperature reduces the water-holding capacity of air, which brings the atmosphere closer to saturation and leads to an increase in RH and a reduction of VPD (the latter assuming the produce is at or near the air temperature). However, in a conventional cold-storage facility, where the air is continuously passed over finned cooling coils and returned to the conditioned space, it is difficult to maintain high RH due to the dehumidifying action of the coils related to inherent temperature fluctuations. This difficulty may be diminished by proper design of the cold store—taking into account its thermal insulation, orientation, and heat exchange parameters (Schwarz, 1994)—and by optimal management of the cooling facility's performance (Scheer, 1994). According to Schwarz (1994), these "passive" measures are sufficient to maintain RH at a desirable level of 90% to 95%

even without additional "active" air humidification. A microcomputer system for controlling RH in horticultural stores has been developed (Adam and Pritchard, 1994).

Special refrigeration systems were designed for achieving and maintaining high RH levels in cold stores and overcoming the above-mentioned disadvantages of the conventional coil system. One of these systems is the Jacketed Storage System, in which refrigerated air is circulated through an air space surrounding the storage room, rather than within the room itself (Lentz et al., 1971, Van den Berg, 1981). This prevents the cold dry air of the evaporator from coming into direct contact with the stored produce and makes the RH in the room independent of the performance of the refrigeration and insulation system. Based on this system, Van den Berg and Lentz (1978) developed the concept of high-humidity storage of vegetables and fruits and verified its advantages in numerous experiments. According to data obtained with 10 different vegetables, a RH of 98% to 99% resulted in the highest quality and minimum decay during long-term storage (varying between several months for celery [*Apium graveolens* L. var. dulce (Mill.) Pers.] and up to a year for carrots and potatoes). Weight loss was sharply reduced in comparison with conventional cold storage, and wilting, softening, and yellowing were negligible. In cabbage, carrots, celery, and parsnips (*Pastinaca sativa* L.) but not in onions, the decay incidence at 98% to 100% RH was less than or about the same as at RH 75% to 95%.

Another high-humidity system, the Humifresh system, was designed by Meredith (1973). The air in a Humifresh system is humidified and cooled by chilled water in a special Filacell unit containing filaments of special packing. This air supply assures that the coldest air at maximum humidity goes over the stored product before the temperature increase due to heat gained from various sources. The advantages of Humifresh include, among others, maintenance of ultra-high humidities of 99% RH and above, minimum risk of condensation on the cold produce when adding warmer produce during loading, no defrost cycles, and avoidance of the problem of dry containers absorbing moisture from the produce during early stages of the storage cycle by providing moisture from a secondary refrigerant. The disadvantages of the Humifresh system are higher construction, operating, and maintenance costs compared with conventional cold storage systems.

2. Air Humidification

Whenever "passive" means (cooling management) are insufficient for maintaining a desirable humidity level in the cold store, additional water has to be supplied to the atmosphere by "active" means. The active option consists of a moisturizing system that generates minute water particles to be circulated in the room. Air humidification is of particular importance during the defrosting period of the cooling cycle, when the increasing temperature causes the air VPD to increase (Scheer, 1994). In the absence of air humidification, this VPD increase would cause enhanced water loss from the produce.

The following types of humidification systems were specified by Schwarz (1994):

a. Vaporization

The vapor is generated by a water boiler. The system is efficient and advantageous in respect to its high output and the fineness of the released particles. However, it is particularly energy-demanding and requires decalcification of the water.

b. Spray

A mechanical device (for example, a spinning disc) is used for spattering water droplets. The system is inexpensive and not very demanding with regard to water quality. It is limited to temperatures above 0°C because of icing hazards.

c. Induction

Droplets are spattered using compressed air. In controlled-atmosphere rooms, the compressed air comes from the room itself. The system is efficient and relatively inexpensive but prone to icing and clogging.

Afek et al. (1996) described an ultrasonic technique for moisture generation in potato stores. The system created 97% to 99% RH without leaving free water droplets on the tubers. The droplets produced by the ultrasonic device were as small as 5 μm in diameter, compared with ≥ 30 μm produced by spinning-disc humidifiers. Avoiding free water on tubers minimized the development of pathogens, and the high storage humidity reduced weight loss after 5 months of storage at 8°C to 1.5% compared to 5% with a spinning-disc humidifier (90% to 92% RH) and 10% without supplemental humidification.

The higher construction, operating, and maintenance costs are the disadvantages of active air-humidification devices. In addition, there is a risk of local excess in moisture supply, which may cause damage to the stored produce.

B. Increasing Surface Resistance to Water Vapor

1. Preharvest Application of Antitranspirant Materials

The possibility of reducing transpiration by increasing the surface resistance of a plant organ to water vapor is attractive. Most antitranspirants (such as abscisic acid) act by causing stomatal closure and others by covering the transpiring surface with a substance that decreases water-vapor diffusion. Preharvest application of Pinolene, a liquid polyterpene that forms a continuous plastic coating on the surface of fruit, resulted in less peel dehydration and aging in oranges even after 9 weeks of storage (Albrigo and Brown, 1970). However, since the plant carries on many activities besides transpiration, the effectiveness of a preharvest antitranspirant is determined not only by its water-saving capability but also by the way in which it alters other aspects of plant performance, such as gas exchange and, in particular, photosynthetic CO_2 consumption.

The inhibitory effect on photosynthesis seems to be an inherent problem of preharvest application of antitranspirants. Therefore their successful use is restricted mainly to the cases where photosynthesis is not important. Preharvest application of antitranspirants increased fruit size in peach, delayed harvest in grape, increased size and reduced shriveling of olive (*Olea europaea* L.), and increased the size of Bing cherry (*Prunus avium* L.) fruit (Davenport et al., 1973).

2. Postharvest Coating

Postharvest handling often removes the natural barrier from the produce surface—the cuticular and epicuticular layers—thus hastening water loss (Ben-Yehoshua, 1967). The purpose of coating fruits and vegetables is basically to enhance the natural barrier function and to restore it in those cases where washing and handling have partially removed or altered it. In addition to controlling water loss, coatings can perform other functions, such as delaying ripening by modification of internal atmospheres, improving shiny appearance and marketability, and providing a carrier for fungicides and other additives.

The practical application of coatings to produce after harvest has a long history. In China, as early as the twelfth or thirteenth century, oranges, mandarins (*Citrus nobilis* Lour.) and persimmons (*Diospyros kaki* L.f.) were dipped in molten waxes. Nevertheless,

coatings did not attain commercial use in storage of perishable produce until the 1930s. Many coating formulations have since been applied commercially for different commodities. Commercial use of coatings (mostly as wax preparations) is rather extensive for some fruits, especially *Citrus* and apples, and several vegetables such as tomatoes, rutabagas (*Brassica napus* L. Neobrassica group), melons, and cucumbers. More limited use has been noted for other vegetables: asparagus (*Asparagus officinalis* L.), beets, carrots, eggplant, kohlrabi (*Brassica oleracea* L. Gongyloides group), parsnips, peppers, potatoes, radishes, squash, sweet potatoes, and turnips. For additional information, see, for example, Baldwin (1994).

Fruit coatings should be prescribed according to the physiological requirements of the produce. The formulation selected should permit desirable gas exchange through the coating. The thickness of the coating and its uniformity are important. Too thick a coating may cause deterioration by creating partly anaerobic conditions, leading to fermentation and ethanol off-flavor, too thin a coating may not be effective enough to achieve the desired water loss results. All components of the formulation must be approved by the relevant health authorities.

Results of coating application in the packinghouse can be greatly improved by utilizing a scale that is capable of rapidly evaluating the adequacy of the coating procedure. Rate of weight loss of a sample of fruit could serve as a criterion of measurement. Data can be gathered during the week the coating is applied; measurement of the effects of coating on storage life may require more than 1 month (Ben-Yehoshua et al., 1970). The optimal rate of weight loss, as determined experimentally, provides a basis for regulating coating application. Measurement of the weight loss helps uncover any malfunction in the coating process (as well as other operational problems in the packinghouse) that increases the rate of weight loss, such as an injury-causing conveyer. A monitoring network utilizing this technique has been organized for all packinghouses in Israel. Too thick a coating can be detected by measuring the O₂ and ethanol concentrations inside the produce tissue. High ethanol levels correlate well with the presence of off-flavors. Optimal coating will maximally reduce weight loss without creating an injurious internal atmosphere.

C. Reducing Postharvest Transpiration by Use of Plastic Film

The use of plastic-film packaging is a simple and very efficient way to reduce transpiration (Hardenburg, 1971). The resistance of plastic films to water-vapor diffusion usually far exceeds the barrier properties of the fruit surface itself (Ben-Yehoshua, 1978). Accordingly, most of the water molecules evaporated from the produce do not escape through the film and remain within the package atmosphere, lowering the gradient of water potential between the fruit and its microenvironment and thus greatly reducing further water loss. In many cases, when transpiration control is the only expected effect of plastic packaging, the packages should be perforated or not tightly closed, because the respiratory activity of the fruit may alter the microatmosphere in the package by O₂ depletion and CO₂ accumulation. These changes may cause "off" flavors, especially at warm temperatures. However, some kinds of produce may benefit from these modified atmospheres. The latter are reviewed in a separate chapter of this book.

The advantages of plastic packaging as a means of minimizing water loss and associated produce deterioration have been demonstrated with various fruits and vegetables,

such as *Citrus* (Albrigo and Miller, 1992; Ben-Yehoshua, 1978; Kawada and Kitagawa, 1988); lettuce (Harris, 1980), persimmon and tomato (Kawada and Kitagawa, 1988), muskmelon (Mayberry and Hartz, 1992), bell pepper (Ben-Yehoshua et al., 1983c), asparagus (Raynal and Baccaunaud, 1995), eggplant (Fallik et al., 1995), grapes (Ben-Arie et al., 1995), and various herbs (Aharoni et al., 1997). Different kinds of plastic film packages (bags, wraps, liners, bulk-box covers) are applied during storage, transportation, and wholesale and retail marketing of fresh produce. Using plastic films, however, may have the adverse effect of increasing the risk of decay. Since the RH is high within plastic film packages, even minor fluctuations of storage temperature result in the precipitation of condensed water droplets, which accumulate on the film and/or produce surface, thus forming favorable conditions for pathogen development. Furthermore, in a plastic bag holding several fruits or vegetables, the decay of one causes secondary infection and spoilage of adjacent ones, often rendering the whole package unsalable.

Consequently, further testing of plastic-film packaging aims to find solutions for minimizing water loss without the risk of condensation. In the following paragraphs, some of these approaches are surveyed.

1. Seal-Packaging for Individual Produce (Unipack)

A special adaptation of film packaging has been developed for individual produce, in which each fruit or vegetable is sealed in plastic film and then passed through a hot-air tunnel to shrink the film (Ben-Yehoshua, 1978, 1985). This method is also called Unipack (Kawada, 1982). The technology that produced better plastic films and suitable machinery to apply the film to individual produce items facilitated this development. The technique is based on using bilaterally oriented polymer films stretched in two dimensions after extrusion. When such films are heated above a critical temperature, they shrink. Due to the tight contact between the produce surface and the film, the latter attains the temperature of the fruit or vegetable by conduction. Absence of a temperature gradient between the produce and the film diminishes the chance of water condensation within the inner space of the individually shrunk package. Thus, this method best satisfies the criterion of maintaining water content without increasing condensation (Ben-Yehoshua et al., 1981; Joyce and Patterson, 1994). This is the reason that Unipack does not increase decay, although the RH in the microatmosphere is saturated. In addition, individual seal packaging reduces decay by preventing secondary infection. This technique has been applied both manually and automatically. In labor-rich China, the manual technique became the routine method to store *Citrus* for long periods. However, in the developed world, automatic machines have been developed for the application of this technology to various commodities.

The method has been shown to double and, at times, triple the life of produce as measured by appearance, firmness, shriveling, weight loss, and other keeping qualities without any deleterious effect on flavor. Seal-packaging delayed various parameters of physiological deterioration in *Citrus*, tomatoes, and bell peppers better than cooling to optimal storage temperature (Ben-Yehoshua et al., 1981, 1983c). Moreover, it reduced chilling injury in various *Citrus* cultivars (Ben-Yehoshua et al., 1981) and thus could be combined with cooling in order to further extend the storage life of the fruit.

2. Mode of Action of Seal-Packaging

Control of deterioration of fruit by placing many fruits in a plastic bag was generally explained by Hardenburg (1971) on the basis of modification in the concentrations of CO₂,

O₂, and ethylene. These factors also affect individual seal packaging, but to a lesser extent. Changes in gas exchange were not large enough to account for the dramatic extension of fruit and vegetable life (Ben-Yehoshua, 1985, 1983c). Endogenous concentrations of CO₂, O₂, and ethylene were similar in both sealed and nonsealed *Citrus* fruit, but the rate of their physiological deterioration was altogether different (Ben-Yehoshua et al., 1983c).

An important effect of sealing is that the produce microatmosphere becomes water-saturated. This may be one of the controlling factors delaying deterioration. After all, a major effect of harvesting produce is the cutoff of the water supply from the mother plant. The plant organ is a reservoir of various nutrients and substrates but, because it has no water supply and transpiration continuously evaporates moisture from the surface, the cytoplasm dries, and the matrix, in which all life processes occur, is destroyed. The importance of transpiration as a major process leading to physiological deterioration of *Citrus* fruit has already been demonstrated (Ben-Yehoshua, 1969) and the hypothesis that sealing delays deterioration of lemon [*Citrus limon* (L.) Burm.] and bell pepper fruits by alleviating water stress was proposed (Ben-Yehoshua et al., 1983c). Results substantiated that the mode of action of seal packaging in delaying senescence and maintaining firmness of these fruits lies in the provision of a water-saturated atmosphere, which alleviates water stress. Figure 2 shows a very high correlation between weight loss, firmness, water potential, and amino acid leakage for bell peppers. The same correlations were also found in lemons. The effects of sealing on fruit deterioration and water deficit are at least parallel. Two independent measurements of tissue water status, water saturation deficit, and water potential correlated highly with weight loss. The correlation coefficient between weight loss and firmness of bell pepper was 0.97 and between water potential and amino acid leakage was 0.91. Placement of bell peppers in water-saturated atmosphere (Table 8) delayed both softening and disintegration of membranes, which water stress accelerated; furthermore, the firmness of bell peppers could be partially restored by immersing soft fruit in aerated water. Reducing the RH of the microatmosphere of sealed fruit by CaCl₂ canceled the effects of sealing in delaying the disintegration of membranes and the softening process. By introducing hygroscopic CaCl₂ to sealed peppers, the RH inside the bags was reduced and stress could be produced. The reduction of the humidity within the enclosure of sealed fruit caused the expected changes; that is, the rate of weight loss and water saturation deficit were increased and water potential was lowered, similar to changes occurring in nonsealed peppers. In addition, both firmness and membrane integrity were affected by the RH changes. Firmness was maintained in water-saturated atmosphere and reduced by lowering humidity around the seal-packed peppers. The leakage of both electrolytes and free amino acids was decreased in water-saturated atmosphere and promoted by reduction of RH, although the differences were not always statistically significant. In general, treatments that preserved higher water potential in the pepper tissue—i.e., seal-packaging and water-saturated atmosphere—reduced membrane leakage. Whereas treatments that induced tissue water stress, as evidenced by lower water potential—i.e., non-sealed packaging and seal packaging with hygroscopic material—enhanced membrane leakage.

The slowing of membrane disintegration was less marked than the inhibition of softening. Thus, pepper fruit held sealed for 4 weeks was as firm as freshly harvested fruit, but the membranes had already permitted leakage of amino acids at a higher rate than for fresh fruit. However, the extent of delay varied among different fruits. The greatest differences between fruits were in softening: while lemons and peppers remained firm

Table 8 Effect of RH and Seal-Packaging in High-Density Polyethylene (HDPE) Film on Firmness, Membrane Integrity, Water Potential, and Water Saturation Deficit of Green Bell Pepper Fruit Kept 4 Weeks at 17°C

Treatment	Weight loss (%)	Firmness (mm deformation)	Amino acid leakage (%)	Electrolyte leakage (%)	Water saturation deficit (%)	Water potential (MPa)
Water-saturated atmosphere	1.76b ^a	4.6b	14.4ab	21.6ab	11.5a	-0.52a
Sealed in HDPE	1.2a	3.3a	11.3a	19.2a	12.7a	-0.52a
Nonsealed	15.9d	12.5d	21.5b	22.7b	24.4b	-0.80b
Sealed in HDPE + CaCl ₂ ^b	10.5c	9.9c	17.3ab	22.3ab	29.9ab	-0.7b

^a Mean separation by Duncan's Multiple Range Test, 1% level.

^b Each fruit sealed in a plastic bag containing 5 g of CaCl₂ crystals.

Source: Ben-Yehoshua et al., 1985.

practically until they rotted, tomato softening was only slightly inhibited. Thus, the ripening process prevailed over the sealing action. The increase in ethylene production accompanying the climacteric in the tomatoes raised the ethylene concentration in the sealed enclosure up to 1 to 2 $\mu\text{l L}^{-1}$, which probably negated the inhibitory action of sealing with respect to ripening.

These data suggest that water stress and its alleviation are more important with pepper and lemon than with tomato in controlling deterioration. With tomato and possibly other climacteric fruits, however, ethylene, O_2 , and CO_2 may play a more important role than water stress. (Ben-Yehoshua et al., 1983b).

3. Effects of Individual Seal-Packaging and Waxing on Water Loss and on Gas Exchange

The various effects that seal-packaging and waxing have on gas exchange and keeping quality are not easily explained by morphological studies concerning the distribution of applied waxes (Ben-Yehoshua, 1967, 1969). While the commercial practice of waxing produce reduces transpiration inadequately, it is effective in restricting O_2 and CO_2 transport. Conversely, sealing fruits or vegetables individually in high-density polyethylene (HDPE) film (about 10 μm thick) reduces water loss by a factor of 10 without changing the endogenous O_2 , CO_2 , or ethylene content. Consequently, seal-packaging is more effective than waxing in preventing shrinkage and extending storage life. This difference was explained by studying the effects of waxing on the surface of *Citrus* fruit with a scanning electron microscope and by computation of the gas exchange (Fig. 1). Commercial waxing results in a new surface layer with a structure different from the natural extracuticular wax platelets (Ben-Yehoshua et al., 1985). The synthetic layer not only has many pits and breaks but is also far more effective than the natural extracuticular wax and other occlusions in clogging the stomatal pores, presumably because it flows into them as a liquid.

The explanation for the differences between the effects of waxing and seal-packaging was found by computing the resistance to diffusion of the various gases involved (Ben-Yehoshua et al., 1985). Waxing decreased water conductance by only 25%, but it increased the resistance to ethylene, O_2 , and CO_2 by 100%, 250%, and 140%, respectively. Waxing hardly affects transpiration because of the many pits and breaks in the new surface layer, but it specifically retards gas exchange by plugging the stomatal pores (Fig. 1). In contrast, seal-packaging increased resistance to water vapor by 1375% and to ethylene, O_2 , and CO_2 by 25%, 233%, and 72%, respectively. This result did not depend on the film's selective permeability, because polyethylene is more permeable to H_2O than to CO_2 , O_2 , and ethylene. Instead, the success of the plastic film in preventing water loss without substantially hindering gas exchange was mainly due to the fruit's selective permeability, allowing water to go through, but impeding gas transport. "Valencia" orange and "Duncan" grapefruit have relatively high resistance to CO_2 , O_2 , and ethylene (6000 cm^{-1}), but low resistance to water (about 100 cm^{-1}). Thus, the thin film's resistance to water provides a much greater barrier to transpiration than the resistance of the fruit's surface to the passage of water vapor. This study illustrates the usefulness of visualizing separate pathways for gas and water-vapor transport in harvested produce. This concept, discussed in a previous section on paths for gas exchange, helps to explain the observation that the 1 μm -thick skin coating formed by commercial waxing is more effective in impeding transport of O_2 and CO_2 than a 10 μm -thick HDPE film.

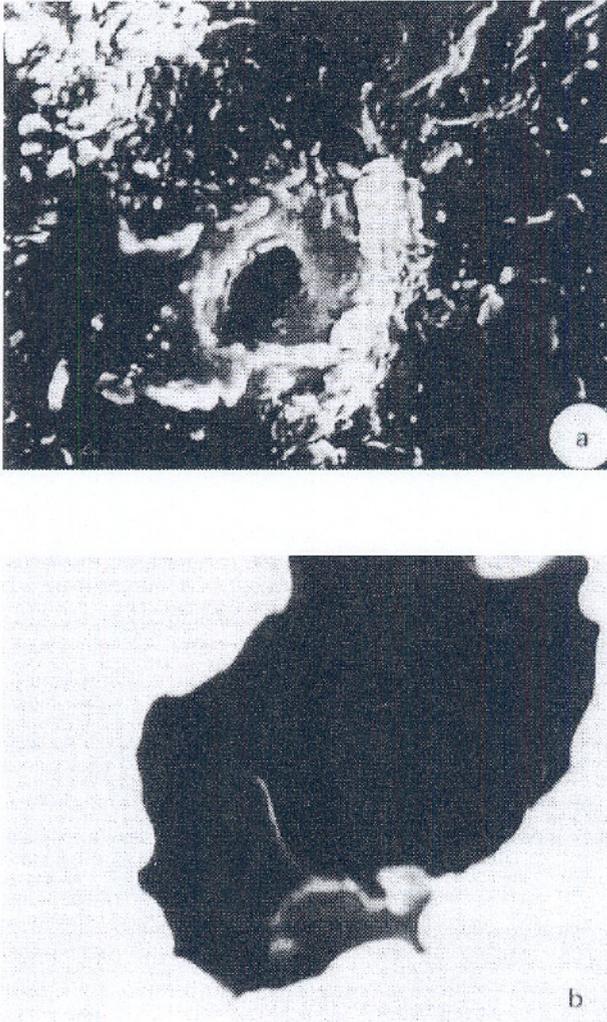


Figure 1 a. Scanning electron microscope (SEM) view of fruit surfaces of untreated grapefruit showing a stomata, wax platelets, and other irregular bodies of natural wax deposited over the cuticular surface ($\times 1600$). b. Stomatal pore. A greater magnification probes deeply into the pore, showing its partial opening, the various protrusions into the pore, as well as the cuticular walls at the surface opening of the pore ($\times 10,000$). c. Wax surface formed after waxing with FMC solvent wax ($\times 1600$). d. Stomatal pore partially clogged by the applied wax ($\times 1600$). e. Stomatal pore completely covered by the new wax layer ($\times 1600$). (From Ben-Yehoshua et al., 1985.)

4. Modified-Humidity Packaging (MHP)

Recent progress in the field of food packaging has resulted in the concept of "active packaging." Packaging is "active" when it performs a desired role other than just providing an inert barrier to external conditions, and is designed to correct intrinsic deficiencies of conventional ("passive") packaging (Rooney, 1995). In the sphere of postharvest water

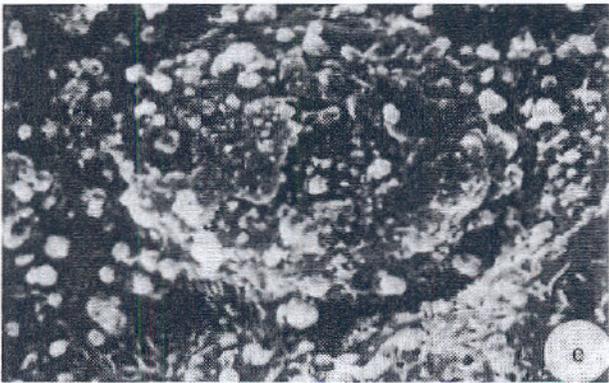
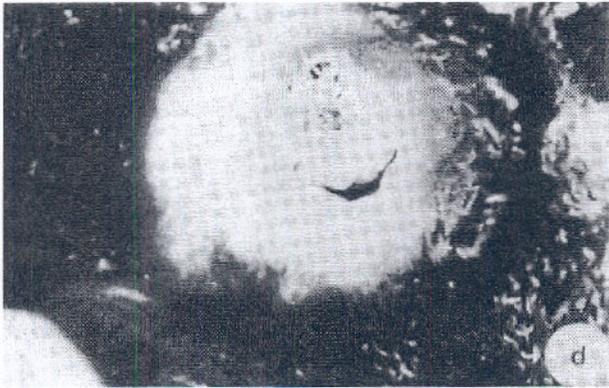
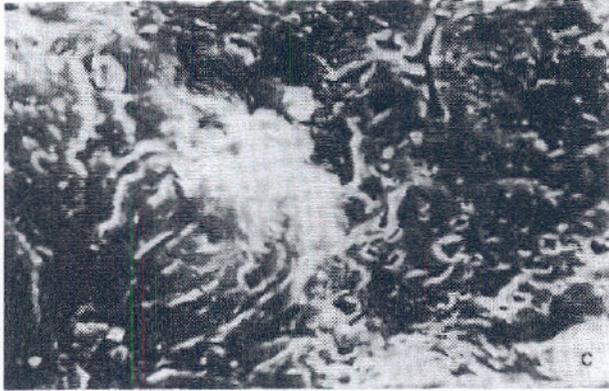


Figure 1 Continued.

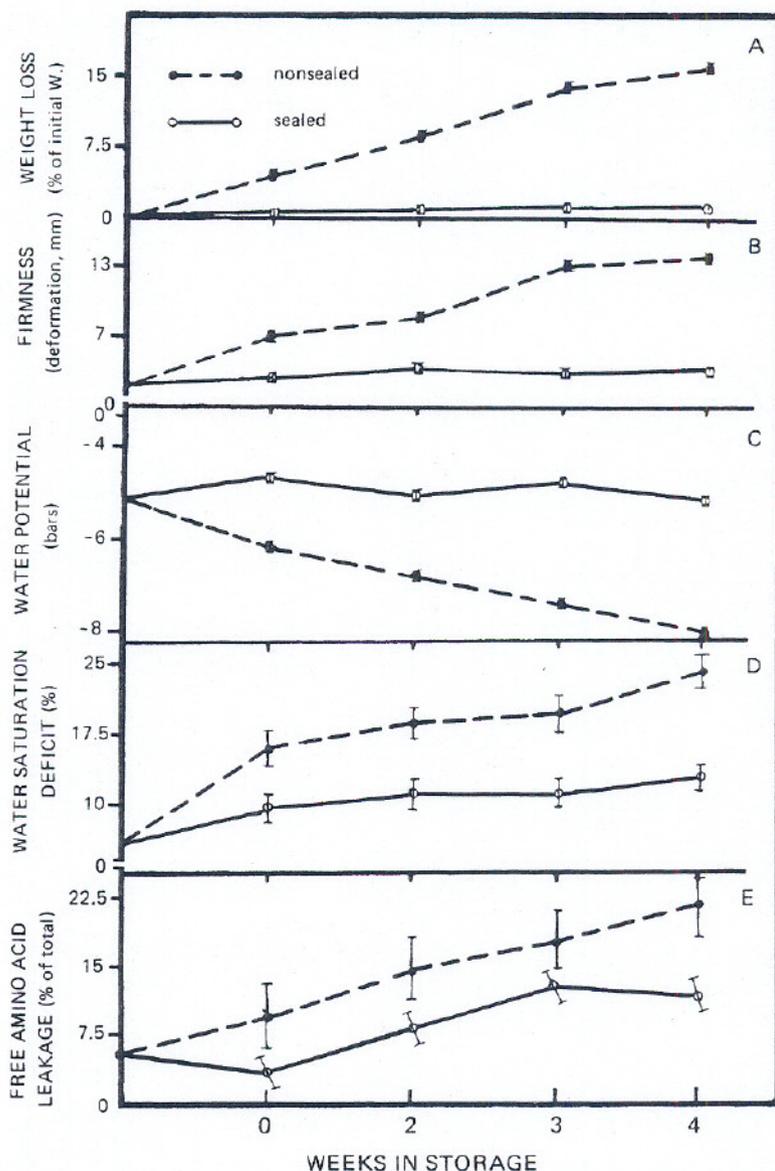


Figure 2 Effect of seal-packaging in HDPE on peppers stored at 17°C and 85% RH for 4 weeks. A. Weight loss. B. Firmness. C. Water potential. D. water saturation deficit. E. Leakage of free amino acids. Standard deviation is indicated. (From Ben-Yehoshua et al., 1985.)

relations, active packaging aims to solve the contradictory demand of simultaneously controlling water loss and water condensation.

The ideas suggested in this area can be combined under the term of *modified-humidity packaging* (MHP), introduced by Shirazi and Cameron (1992) as an extension of the widely used term *modified-atmosphere packaging* (MAP). The concept of MHP is based on the compromise that condensation is avoided by allowing limited water loss. By stabi-

lizing the in-package RH at an optimal level, higher than the ambient RH but lower than the saturation level at a given temperature, the commodity desiccates less than the unsealed product and is less damaged by condensation than one kept in a conventional plastic package. Below is a survey of several approaches used in the design of MHP.

a. RH Buffering

The RH in a package can be buffered with hygroscopic materials such as salts and polyols. The approach of controlling in-package RH by using microporous sachets of substances exhibiting type III sorption isotherm behavior—such as sorbitol, xylitol or sodium chloride—was proposed by Shirazi and Cameron (1992), who demonstrated that this method extended the storage life of packaged tomatoes mainly by retarding surface mold development. In our own experiments, we buffered the in-package RH by using sachets containing NaCl; these reduced the decay of red bell pepper sealed in low-density polyethylene and stored for 2 or 3 weeks (Rodov et al., 1995b). Humidity levels varied from about 88% with 15 g NaCl to about 97% with 5 g NaCl for a package containing 0.5 kg fruit; without hygroscopic material, the in-package RH was close to saturation, and free water was present both on the fruit and on the inner film surfaces. Depending on the amount of NaCl, condensation was prevented or significantly reduced. Adding hygroscopic material increased the VPD in the packages and, accordingly, the weight loss of the fruit. However, peppers packaged with NaCl still had lower weight loss and better quality than the non-sealed fruit. The water regime formed in the presence of 10 g NaCl (92% to 95% RH, VPD 65 to 77 Pa) enabled optimal balance between reduced fruit desiccation and inhibited pathogen development, thus extending the postharvest life.

Special packaging materials like Pichit film manufactured in Japan (Rooney, 1995), which includes a built-in hygroscopic substance(s) within its structure, represent a somewhat different approach to humidity buffering. Pichit film is described as containing an alcohol, presumably propylene glycol, and a carbohydrate, placed between two layers of a plastic film that is highly permeable to water vapor. Pichit is marketed as a wrapping material for home use, aimed at delaying the spoilage of foodstuff by controlling the RH in its proximity. Patterson (1991) developed another humidity buffer made up of a hygroscopic, water-insoluble polymer and a mixture of a nonvolatile hydrophilic liquid and water. The buffer helps to maintain the RH in a sealed container at a predetermined level and may be produced either as free-flowing granules or in the form of a sheet.

b. Perforation

The use of perforated film is a simple approach to modulating in-package RH, which depends on the ambient RH level. Holes placed in the plastic barrier of a produce package dramatically affected the in-package O₂ and CO₂ concentrations but had only a mild influence on the in-package RH level (Ben-Yehoshua et al., 1996a; Fishman et al., 1996a,b). For example, at ambient RH of 60%, the RH level inside the polyethylene package containing two mango fruit was reduced from 99.7% in a nonperforated package and to 93.2% in a package having as many as 40 holes 2 mm in diameter. Further experiments confirmed the above calculations. This slightly decreased RH level was enough to control condensation and at the same time to maintain low fruit weight loss and to prevent shriveling (Ben-Yehoshua et al., 1996a). In a similar way, bell pepper packages made from perforated polyolefin films allowed the beneficial combination of reduction of both condensation and *Botrytis* decay and satisfactory weight-loss control (Ben-Yehoshua et al., 1996a).

A variety of perforated plastic films are available commercially. The degree of perfo-

ration should be chosen to match the particular situation. Ben-Arie et al. (1995) provided a good example of empirical optimization of the degree of perforation in polyethylene grape packages by finding a compromise between the need to control decay development, desiccation, berry splitting, and SO₂-caused bleaching.

c. Water-Permeable Films

Hydrophilic plastics such as regenerated cellulose and polyvinyl alcohol have high permeability to water vapor and allow hardly any accumulation of condensed water droplets. This benefit is naturally associated with increased water loss as compared with less water vapor-permeable films. The mechanical strength of films based on cellulose and other highly hydrophilic materials may be reduced at RH higher than about 90%.

A series of water vapor-permeable plastic films is being marketed under the trade name Xtend (StePac, Tefen Israel). These films are microperforated in order to control in-package CO₂ and O₂ concentrations. Good results in preserving produce quality using Xtend films have been claimed by the manufacturer with a range of fresh vegetables, such as broccoli, green onion, cucumbers, strawberries, and sweetcorn (Aharoni et al., 1997). However, the polymer used in these films—and consequently the films themselves—is several times more expensive than those in other major films on the market.

A nonperforated polyamide film that possesses a relatively high water-vapor permeability compared to polyolefin films was tested by Ben-Yehoshua et al. (1996b) as a lining for telescopic cartons used in bell pepper shipping. The performance of polyamide-lined cartons was similar to that of those lined with a perforated polyolefin film. Both package types enabled about twofold reduction of fruit weight loss without increasing *Botrytis* decay, which flourished in cartons lined with nonperforated polyolefin as a result of profound water condensation.

d. Drip Absorption

Condensed water tends to collect as droplets on packaging films, wetting the produce surface and hindering observation of the product. The formation of droplets can be reduced by the use of surface-active antifog additives, which cause the condensed water to form a continuous transparent film on the plastic surface. However, antifog technology does not prevent the negative consequences of condensation. Moreover, the condensate on antifog films drains more easily and may accumulate as puddles in the bottom of the package unless additional means of drip absorption are applied.

Several companies manufacture drip-absorbent sheets aimed at preventing the accumulation of liquid inside the package. Basically, they consist of two quilted layers of a microporous or nonwoven polymer, such as polyethylene or polypropylene, between which is inserted a superabsorbent polymer in the form of free-flowing granules. The preferred polymers used to absorb the water are polyacrylate salts, although graft copolymers of starch can also be used (Rooney, 1995). These polymers are capable of absorbing 50 to 500 times their own weight in liquid. The drip-absorbents are used in pads or large sheets, mainly in packaging meat, poultry, or seafood. Examples of such materials include Toppan Sheet, manufactured in Japan and Thermarite, manufactured in Australia (Rooney, 1995). The use of the superabsorbent polymer Stocksorb (Stockhausen, Stockhausen, Germany) was successfully tested in MHP of bell pepper (Ben-Yehoshua et al., 1996a; Rodov et al., 1998). In many other cases, free water in produce packages was absorbed by paper inserts (Ben-Arie et al., 1995; Meir et al., 1995). Another way to immobilize the condensed water may be provided by the use of the surface alloy of a hydrophilic polymer on the bulk hydrophobic surface described by Noda (1991).

One of the recent developments in this area is a condensation-control carton designed by Patterson and Joyce (1993). The design comprises a fiberboard carton with multilayer structure that acts as an internal water buffer capable of collecting the condensed free water in an internal wick-like layer and releasing this water in vapor form in response to lowering of RH. More details on the structure of the condensation-control carton and on its performance in vegetable storage are given by Patterson et al. (1993) and Rooney (1995).

e. Mathematical Modeling of MHP

The application of MHP requires the tuning of various elements of the package system, such as film permeability, extent of perforation, produce amount, inserts, etc. This task may be simplified by the use of mathematical modeling. As shown earlier, the process of transpiration is based on relatively simple physical fundamentals such as Fick's law and can be described mathematically. The work of Gaffney et al. (1985) shows both advantages and limitations of such an approach to the description of postharvest water loss, the major limitation being the variability of biological objects. The variability of steady-state O₂ levels in MAP has been taken into account by Talasila et al. (1994). Unfortunately, the modeling of MHP has been given less attention than the modeling of in-package CO₂ and O₂ concentrations. Labuza et al. (1972) proposed a model predicting moisture gain or loss by food products packaged in flexible films. The effects of plastic wrap on the steady-state RH level and produce water loss were briefly addressed in the MAP model described by Cameron et al. (1995). Fishman et al. (1996a,b) developed mathematical models describing the effects of film perforation on O₂ concentration and RH in the atmosphere of a package containing fresh fruit. The model allows prediction of in-package RH dynamics as affected by the produce specificity, package parameters such as perforation level, and the ambient air humidity. In addition, the expected weight loss of the fruit may be evaluated by its use. Our recent experiments with MH-packaged mango fruit have confirmed the model's adequacy (Fishman et al., 1996a).

VIII. PHYSIOLOGICAL ASPECTS OF POSTHARVEST WATER STRESS

Transpiration not balanced by a water supply from the mother plant often results in water deficit stress in harvested commodities. In the present section, an attempt is made to describe some physiological and molecular implications of this situation. The physiological basis of plant responses to water deficit has been studied extensively at different levels. For more information, see the books edited by Close and Bray (1993), Smith and Griffiths (1993) and Bellhassen (1997).

Water deficit directly or indirectly affects practically all the physiological processes in plant tissues. According to Hsiao (1973), of all the physiological processes in leaf tissues, cell growth appears to be the most sensitive to water stress. Rate of cell elongation is affected by even a small reduction of tissue water potential (less than 0.1 MPa). High sensitivity to water stress has also been reported for protein and cell-wall synthases and for nitrate reductase. Moderate water stress (reduction of water potential by 0.5 to 1.5 MPa) causes changes in abscisic acid and cytokinin concentrations in leaf tissues, stomatal closure, and a sequential drop in the rate of photosynthesis. The respiration pattern in harvested avocado fruit was shown to be markedly altered by water stress (Akkaravessapong et al., 1996). The processes of proline and sugar accumulation are relatively resistant

to water deficit and are disturbed only by more severe stress, e.g., reducing water potential by 1 to 2 MPa.

A. Water Stress and Physiology of Harvested Plant Organs

1. Water Stress and Senescence

Boyer (1976) suggested that water stress affects tissues in the same way as senescence. The physiological changes occurring in harvested green and red bell pepper fruit were investigated by Lurie et al. (1986) in relation to the development of water stress. The decline in tissue water potential was accompanied by softening, decreased insoluble pectin, increased soluble pectin (Lurie et al., 1986), and increased electrolyte leakage (Ben-Yehoshua et al., 1983c), all processes attributed to senescence. When water stress was alleviated by keeping peppers in a water-saturated atmosphere, all of these physiological changes were prevented or markedly slowed. The authors proposed that in the case of bell pepper fruit, water stress hastens and possibly triggers the onset of senescence in harvested fruit. The common mechanisms of water stress and senescence may be related to deterioration of cell membranes by increased formation of free radicals (Ben-Yehoshua et al., 1983c; Leopold et al., 1981; Leshem et al., 1981; Lurie and Ben-Yehoshua, 1986; Nir and Poljakoff-Mayber, 1967).

2. Water Stress and Ripening

In the same way that water stress hastens senescence (see the previous section), it has a similar effect on ripening. Littmann (1972) found, with bananas and other climacteric fruits, that the greater the weight loss, the shorter the period from harvest until ripening and until the peak of the climacteric. Acceleration of ripening in water-stressed bananas and avocados has been confirmed recently by several researchers (Akkaravessapong, 1996; Burdon et al., 1994a, Ferris et al., 1994). In durian (*Durio zibethinus* L.) fruit kept at relatively low humidity, water was lost mainly from the rind rather than from the pulp (Ketsa and Pangkool, 1994). Accordingly, the developing water stress was found to accelerate rind degreening but had no significant effect on pulp ripening involving changes in starch and sugar contents, firmness, etc.

Fukushima et al. (1980) have tried to correlate postharvest changes in water potential, osmotic pressure, and turgor pressure of several fruits and vegetables. They applied standard methods to measure water potential and osmotic pressure and calculated turgor pressure by subtracting osmotic pressure from water potential, probably assuming that the matric potential is negligible. The rate of respiration and the turgor pressure rose in parallel several days after harvest, i.e., during the climacteric. They proposed to explain this phenomenon by the often concomitant rise in osmotic pressure as fruits ripen.

3. Water Stress and Hormonal Balance

Water stress acts to bring about changes in hormonal balance similar to those caused by senescence: a marked drop in endogenous levels of gibberellins and cytokinins and a marked rise in the level of abscisic acid and ethylene (Aharoni et al., 1975a,b, 1977; Itai and Benzioni, 1976; Morgan et al., 1977; Wright, 1978). These effects were reversed upon removal of stress by placing plant organs (orange fruit and leaves, lettuce leaves) in a water-saturated atmosphere.

In keeping with the above-mentioned effects of water stress on senescence and ripening, moisture deficit was shown to hasten ethylene synthesis in detached leaves (Apelbaum

and Yang, 1981; Ben-Yehoshua and Aloni, 1974) and fruits (Adato and Gazit, 1974). The physiological mechanisms underlying these phenomena in water-stressed bananas have been investigated by Burdon et al. (1994a). These authors showed that water stress affects banana ripening by increasing the ethylene production of the peel through an increase in 1-aminocyclopropane-1-carboxylic acid (ACC) content and ACC-oxidase activity.

In recent decades, much attention has been paid to the role of abscisic acid (ABA) in plant reaction to water stress. High ABA levels cause stomata to close (Kriedemann et al., 1972) and can be inhibitory to shoot growth but stimulatory to root growth (Creelman et al., 1990; Saab et al., 1990). The induction of gene expression by ABA during water deficit is discussed in the next section.

B. Molecular Responses of Plant Tissues to Water Deficit

Plant response to water deficit begins with stress perception, which initiates a signal transduction pathway(s) and is manifest by changes at the cellular, physiological, and developmental levels (for more detailed reviews, see Bray, 1993; Zhu et al., 1997). However, current understanding of molecular mechanisms underlying these phenomena is still limited, especially regarding harvested commodities. Because of the restricted information available, we refer in this section to data not necessarily obtained with harvested produce but also with other plant organs (detached and attached leaves, seeds, seedlings, etc.) and whole plants, assuming that in most of the cases the basic mechanisms would be similar.

1. Water-Stress Perception and Signal Transduction

It is currently assumed that loss of turgor or change in cell volume permits the detection of water loss on the cellular level (Bray, 1993). Turgor was demonstrated by Zimmerman (1978) to be a major control mechanism of membrane transport. He described the biphasic osmotic regulatory response of plants to salt and water stress. In the first phase, cells swell or shrink rapidly and markedly if exposed to hypobaric or hypertonic solutions, respectively. In the second phase, plant cells adjust their osmotic pressure in response to environmental stress and a reverse volume regulation is observed. The evidence that turgor pressure affects transport processes in the membranes led to a search for a mechanism involved in the sensing of turgor pressures. The possibility of a chemical reaction being involved in the primary step of turgor sensing was rejected, since the pressures required to reverse the direction of a chemical reaction in condensed phases are much too high to play a role. Alternatively, Zimmerman (1978) suggested that the basic step of the turgor-sensing mechanism might be electromechanical. In fact, Coster et al. (1977) showed that significant changes in the thickness of a cell membrane can occur as a result of direct compression due to the turgor pressure, indirect effects due to the stretching of cell walls, or stresses induced by the electrical field in the membrane. These changes can stimulate stretch-activated channels or cause alterations in the cell wall/plasma membrane continuum (Ding and Pickard, 1993), thereby triggering a signal-transduction pathway(s) required for osmoregulation and other responses. However, Zimmerman's (1978) final remark, that we are still far from understanding the individual steps in the transformation of a pressure signal into cell response, is still valid.

Further long-distance translocation of water stress signal within the plant may require other, poorly understood mechanisms. It was suggested that ABA may act as a translocated signal triggering water stress-response mechanisms (see Davies and Zhang, 1991). However, this suggestion was disputed by Munns (1990). It is currently accepted

that gene expression in response to water deficit is controlled by multiple mechanisms, including ABA-dependent and ABA-independent pathways (Chandler and Robertson, 1994; Skriver and Mundy, 1990; Yamaguchi-Shinozaki et al., 1995). Experiments using mutants blocked in the ABA biosynthesis pathway demonstrated that several water deficit-induced genes require an elevated level of ABA for their expression during stress conditions (Bray, 1993; Cohen and Bray, 1990).

2. Genes Expressed During Water Deficit—Adaptive Mechanisms

The numerous responses of plant cells to water deficit are controlled by an array of genes with many different functions. Some of the gene products are involved in water stress signaling and regulation, such as a protein kinase (Conley et al., 1997). Others, such as proteases and ubiquitin, may be involved in the degradation of proteins that are denatured during cellular water loss. Counteracting these degrading mechanisms are chaperones and protease inhibitors that are also induced by water deficit (Bray, 1993). Certain water stress-induced proteins are thought to possess antifungal activity and to protect the stressed tissue from pathogen invasion; examples include osmotin (Kononowicz et al., 1993) and nonspecific lipid-transfer proteins (Plant et al., 1991; Terras et al., 1992).

Understanding the possible adaptive role of stress-induced gene products is important. Water stress triggers mechanisms that are believed to protect cellular structures from the negative effects of dehydration and/or to adjust cellular metabolism to the conditions of moisture deficit. The phenomenon of osmotic adjustment was mentioned in the previous section as the second phase of a cell's response to water deficit according to Zimmerman (1978). The subject has been reviewed in detail by Morgan (1984). Osmotic adjustment maintains cell water content by lowering the osmotic potential of the cytosol and thus increasing water uptake. The adjustment results from an accumulation of osmolytes (compatible solutes) such as sugars, glycerol, amino acids such as proline, sugar alcohols such as mannitol, and other low-molecular-weight metabolites. Some genes that encode enzymes for steps in the synthesis of these osmolytes have been induced by water deficit (Bray, 1993). Transgenic tobacco plants expressing a foreign gene leading to mannitol accumulation demonstrated improved stress tolerance (Tarczynski et al., 1993). Proteins with channel properties specific for water, ions, or solute molecules are also believed to be involved in the osmotic adjustment (Bray, 1993).

Another group of environmentally or developmentally inducible adaptive mechanisms protects the cellular membranes and enzymes from disorganization. It has been proposed that membrane integrity in desiccating seeds is protected by the accumulation of specific sugars, such as trehalose or sucrose, that form hydrogen bonds with cell membranes in a way similar to water (Koster and Leopold, 1988). A similar role has been proposed for hydrophilic proteins called dehydrins, embryo maturation (Em) proteins, or late-embryogenesis-abundant (LEA) proteins (Dure, 1993). The genes for these proteins (*lea* genes) were first identified as genes expressed during the maturation and desiccation phases of seed development (Baker, et al., 1988). It was later shown that these genes may also be induced in vegetative tissues by water loss or ABA (Close and Chandler, 1990). However, expression of *lea* genes in transgenic tobacco plants did not improve stress tolerance (Iturriaga et al., 1992).

3. Adaptation to Water Stress: Relevance to the Postharvest Situation

The question emerges, to what extent are the above-described adaptive mechanisms relevant to the case of postharvest water stress in fresh agricultural produce?

In general, one can expect that harvested plant organs, severed from the mother plant and undergoing senescence, will be limited in their adaptive potential compared with the intact organism. Indeed, detached organs cannot adjust to water deficit by the mechanisms available at the whole-plant level, such as reduced leaf growth, defoliation, and increase in root-shoot ratio, which often protect the cells of droughted plants from dehydration (Tardieu, 1996). On the other hand, the generative plant organs, such as fruit and seeds, are predisposed by their biological function to be separated from the mother plant at a certain developmental stage and, accordingly, to encounter water deficit. In order to secure the development of a new organism, these organs should have preformed mechanisms enabling them to withstand water stress for a certain period of time.

The developmentally triggered synthesis of LEA proteins in desiccating seeds, as well as the accumulation of solutes (sugars, etc.) during maturation and/or ripening of fleshy fruits, which decreases their osmotic potential, may serve as such preadaptational physiological mechanisms. Interestingly, these two adaptive mechanisms (accumulation of LEA proteins in desiccating seeds and accumulation of osmolytes in the fruit flesh) may be interrelated in the course of fruit development—in the phenomenon of osmotic seed dehydration inside maturing fleshy fruit.

Persisting plant organs such as bulbs, tubers, roots, and corms have many morphological and anatomical peculiarities that may be regarded as preadaptation to postdetachment water deficit: low surface/volume ratio, presence of water-barrier layer on the surface, stomatal closure, and gradual degradation of the stomata with maturation. These mechanisms have been considered in detail in the previous sections.

In conclusion, a number of adaptive mechanisms to deal with water deficit can be found in harvested commodities, particularly in those originating from persisting plant organs. These mechanisms are usually developmentally programmed as preadaptation to expected water stress. Plant organs not biologically predisposed to detachment (for example, most of the leafy vegetables) lack most of these mechanisms and are usually very sensitive to postharvest water loss.

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