# An overview of preharvest factors influencing mango fruit growth, quality and postharvest behaviour

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Mango, a tropical fruit of great economic importance, is generally harvested green and then commercialised after a period of storage. Unfortunately, the final quality of mango batches is highly heterogeneous, in fruit size as well as in gustatory quality and postharvest behaviour. A large amount of knowledge has been gathered on the effects of the maturity stage at harvest and postharvest conditions on the final quality of mango. Considerably less attention has been paid to the influence of environmental factors on mango growth, quality traits, and postharvest behaviour. In this paper, we provide a review of studies on mango showing how environmental factors influence the accumulation of water, structural and non-structural dry matter in the fruit during its development. These changes are discussed with respect to the evolution of quality attributes on the tree and after harvest. The preharvest factors presented here are light, temperature, carbon and water availabilities, which can be controlled by various cultural practices such as tree pruning, fruit thinning and irrigation management. We also discuss recent advances in modelling mango function on the tree according to environmental conditions that, combined with experimental studies, can improve our understanding of how these preharvest conditions affect mango growth and quality.

**Key words:** environmental conditions, fruit load, irrigation, shelf life, size, taste

Uma revisão dos fatores pré-colheita que influenciam o crescimento, qualidade e comportamento pós-colheita de frutos de manga: Manga, um fruto tropical de grande importância, é geralmente colhido verde e comercializado após um período de armazenamento. Infelizmente, a qualidade final da manga na prateleira é altamente heterogênea, em termos de tamanho do fruto, qualidade do paladar e comportamento pós-colheita. Tem-se obtido uma quantidade expressiva de informações sobre os efeitos do estádio de maturação e condições pós-colheita sobre a qualidade final da manga. Contudo, tem-se dado atenção consideravelmente menor à influência dos fatores ambientes sobre o crescimento da manga, características de qualidade e comportamento pós-colheita. Neste artigo, faz-se uma revisão dos estudos sobre manga, evidenciando-se como fatores ambientes afetam o acúmulo de água e de matéria seca estrutural e não-estrutural nos frutos durante o seu desenvolvimento. Discutem-se essas alterações com relação à evolução de atributos de qualidade dos frutos ainda nas plantas e após a colheita. Os fatores de pré-colheita abordados são luz, temperatura, disponibilidades de água e de carbono, raleio de frutos e manejo da irrigação. Discutem-se também recentes avanços sobre modelagem associada à função do fruto na planta, conforme as condições ambientes que, combinados com estudos experimentais, pode melhorar a nossa compreensão sobre como as condições de pré-colheita afetam o crescimento e a qualidade da manga.

Palavras-chave: carga de frutos, condições ambientes, irrigação, paladar, vida de prateleira

#### INTRODUCTION

Mango is a climacteric fruit generally harvested green, which ripens during the marketing process (transport, storage etc.) with an irregular storage period between harvest and consumption. In addition to these market constraints, we must also take the high variability of preharvest and postharvest factors into account, as well as the difficulty to harvest fruit at an optimal maturity stage. All of these factors are involved in providing strong heterogeneous batches of mangoes in the supply chain in terms of fruit size, gustatory quality and postharvest behaviour.

Studies on mango dealing with the factors that determine the final quality of fruit at the consumer level have generally focused on maturity at harvest (Jacobi et al., 1995; Lalel et al., 2003a) and on postharvest management (Hoa et al., 2002; Nunes et al., 2007). However, as is the case with other stone fruits, preharvest cultural practices, which affect the environmental conditions of fruit development, profoundly influence postharvest performance and final quality (Crisosto et al., 1995; Hewett, 2006). Few studies related to the effects of environmental factors on mango quality before harvest have been carried out, and even less have focused on the interaction between preharvest and postharvest factors, whereas it is necessary to take these factors into account in order to propose technical solutions to improve final mango quality.

Fruit quality consists of many attributes, both intrinsic, including texture, sweetness, acidity, aroma, shelf life and nutritional value, and extrinsic, such as colour or size.

Mango is a fleshy fruit containing more than 80% water (Lakshimnarayana et al., 1970). Its size depends on the accumulation of water and dry matter in the various compartments during fruit growth. The skin, the flesh and the stone have specific compositions that appear to accumulate water and dry matter at different rates, depending on environmental conditions (Léchaudel et al., 2002). Fruit growth after cell division consists in the enlargement of fruit cells characterised by a large accumulation of water that results from the balance between incoming fluxes such as phloem and xylem, and outgoing fluxes such as transpiration (Ho et al., 1987). Changing the balance between these various fluxes,

which have elastic and plastic components, leads to large variations in fruit volume. Mango dry matter mainly consists of carbohydrates, 60% of which are sugars and acids (Ueda et al., 2000), the main compounds contributing to fruit sweetness and acidity (Malundo et al., 2001). The amount of carbohydrates supplied to tree fruits depends on the amount produced by leaf photosynthesis, on sink demand and on the availability of the reserve pool. Also, from the point of view of fruit quality, it is essential to understand how preharvest factors influence source-sink relationships involved in fruit growth.

Fruit flesh taste is highly dependent on the balance between organic acids and soluble sugars, which are predominantly represented in mango by citric and malic acids, and sucrose, fructose and glucose, respectively (Medlicott and Thompson, 1985). The patterns of these compounds during mango development and maturation are well described, even if many studies deal with the evolution of fruit flesh composition during ripening according to harvest date. To our knowledge, only a few results of preharvest factor effects on mango taste have been reported.

Another quality trait for mango is its shelf life, which can vary with postharvest conditions, the best known of which is temperature. However, this attribute can be influenced by conditions during fruit growth that affect the supply of minerals to the fruit. In fact, relationships between minerals [the main one in mango is potassium, followed by magnesium and calcium; Simmons et al. (1998a)] and shelf life are often studied. In particular it appears that variations in calcium content or the ratio between calcium and the other two minerals delay ripening and senescence (Ferguson, 1984) or reduce storage disorders (Bangerth, 1979). Calcium is supplied by the xylem (Jones et al., 1983), and potassium and magnesium are phloem-mobile nutrients (Nooden, 1988). Special attention must also be paid to the influence of environmental factors on ingoing fruit fluxes as well as on the balance between mineral ions in mango, as has been done for other fruits (Ferguson et al., 1999). Moreover, shelf life can be discussed in terms of dry matter content, which is directly affected by carbohydrate and water fluxes at the fruit level during its growth.

Maturation of mango, a climacteric fruit, occurs in the final stages of fruit growth, resulting in a rise in

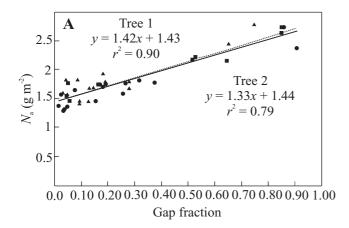
respiration rate and ethylene production (Akamine and Goo, 1973). Since mango is generally harvested green, the onset of the climacteric phase is studied during fruit storage according to the maturity stage at harvest (Lalel et al., 2003a). However, these processes involved in mango maturation have been studied in some cases during fruit development (Reddy and Srivastava, 1999) and presented other components of ethylene biosynthesis, such as its immediate precursor, 1aminocyclopropane-1-carboxylic acid (ACC) and a conjugated derivate, malonyl-ACC (Léchaudel and Joas, 2006). Moreover, changes in volatile aroma compounds, which are mainly produced during ripening, and in their precursors, such as fatty acids, have been reported to be related to ethylene production (Lalel et al., 2003b). Therefore, understanding the influence of preharvest conditions on mango maturation and the biosynthesis of secondary compounds (precursors or final products) is a necessary step to elucidate the determinism of nutritional and aromatic quality attributes.

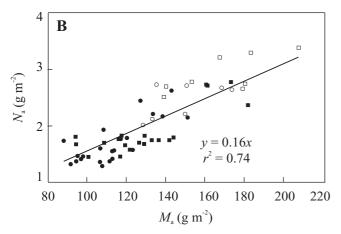
The fruit is a complex system and it is difficult to take all of the environmental factors that affect its growth into account in the same experiment. A recent approach proposed by researchers was to build a model of mango fruit growth that integrated preharvest conditions. The first model functions at the branch level and takes the effects of changing source-sink relationships on fruit growth in dry mass into account by simulating the main processes involved, i.e. source activity, mobilisation of reserves, respiration and fruit demand (Léchaudel et al., 2005a). The second model is based on a biophysical representation of mango fruit growth in water mass and takes account of both reversible elastic and irreversible plastic components of growth (Léchaudel et al., 2007). This model predicts diurnal and seasonal variations of fresh mass and fruit water relationships after the period of cell division on the basis of climatic data and fruit dry mass. By combining the two models, a global model of mango functioning was proposed to simulate changes in fruit size and flesh composition at the branch level in terms of sugar, acid and mineral content, for example, according to climatic data, environmental factors, and 'initial' fruit size (Léchaudel et al., 2006).

In this review, we emphasize the fact that final mango quality at the consumer level depends not only on the maturity stage at harvest and postharvest conditions during storage and marketing, but on environmental factors as well. These factors can be controlled by various cultural practices, i.e. light and temperature through tree pruning, carbon availability through fruit thinning, or water availability through irrigation management. The research on mango presented in this paper has been carried out to help us to develop an understanding of how environmental factors affect fruit growth and its quality on the tree, fruit postharvest behaviour and final fruit quality.

#### **ENVIRONMENTAL FACTORS**

Light environment: Light exposure is a factor that varies with the position within the canopy of the fruit-bearing branch and of the fruit itself. The effect of light on photosynthesis includes both a direct effect of the photosynthetic photon flux on the rate of electron flow (Farquhar et al., 1980) and an indirect effect of light on leaf photosynthetic capacity, since plants allocate nitrogen resources within the canopy to enhance photosynthetic capacity in portions of the tree receiving high irradiances (Hollinger, 1996). In a mango tree, photosynthetic acclimation to light is mainly determined by the mass-to-area ratio, M<sub>2</sub>, and, to a lesser extent at low irradiance, by changes in the allocation of total leaf nitrogen, whereas changes in leaf nitrogen on a mass basis, N<sub>m</sub>, play a minor role (Urban et al., 2003). In fact, on mango, leaf nitrogen on an area basis,  $N_{_{\rm a}}$  (calculated as the N<sub>m</sub>-to-M<sub>a</sub> ratio), which reflects photosynthetic capacity, was linearly related to the fraction of intercepted light (Figure 1). The lowest mass-to-area ratio and N<sub>a</sub> were observed in the shaded leaves (Table 1). These effects of light exposure lead to a lower carbon assimilation in shaded leaves. Fruit growth in dry mass depends on the partitioning of carbohydrates between maintenance of the system, i.e. the fruit-bearing branch, fruit growth and storage in leaves and stems. If the carbon supply decreases, fruit growth in terms of dry mass is reduced as well. It has been shown (Table 1) that fruit size and dry matter content decrease in 'Kensington' fruit from upper to lower positions in the canopy (Hofman et al., 1995). Another quality criterion, soluble solids content (Mendoza and Wills, 1984) and total sugars (Table 1), which can be related to dry matter content, were determined to be lower in mango fruit from the lower





**Figure 1.** Relationships between leaf nitrogen concentration per unit leaf area ( $N_a$ ) and either (**A**) the gap fraction for leaves in the crowns of 3-yr-old trees [measurements were performed on leaves less than 2-month-old ( $\bullet$ ), 8-month-old ( $\blacksquare$ ), 12- to 14-onth-old ( $\blacktriangle$ ) and 17- to 20-month-old ( $\spadesuit$ )], or (**B**) the leaf mass-to-area ratio,  $M_a$ , [measurements were performed on leaves of 3-year-old trees [Tree 1 ( $\bullet$ ) and Tree 2 ( $\blacksquare$ )], leaves far from (standard leaves,  $\bigcirc$ ) and close to ( $\square$ ) developing fruits of 11-year-old trees] [adapted from Urban et al. (2003)].

portion of the canopy. Using the modelling approach, especially through sensitivity analysis, it has been shown that the final fruit dry mass is sensitive to carbon assimilation parameters.

Another effect of light exposure on mango quality deals with its attractive trait, especially the red pigmentation of skin through the influence of light on anthocyanin production. Mangoes inside the canopy retain a greener skin colour due to the decrease of fruit exposure to sunlight (Simmons et al., 1998a). Bagging of fruit, a cultural practice used to reduce fruit disease,

**Table 1.** Effect of fruit position on the canopy on quality of 'Kensington' mango fruit. Fruits were harvested on the same day and ripened at 22°C [adapted from Hofman et al. (1995)].

Fruit	Fruit	Dry	Days to	Total sugars
position	mass (g)	matter (%)	eating soft	(°Brix)
Upper	360	13.1	13.4	11.6
Middle	370	13.0	14.5	11.6
Lower	346	11.6	15.9	10.5

diminishes light received on the skin and reduces the area of red colour on the peel and its intensity (Hofman et al., 1997).

Temperature: Simulations have shown that temperature influences processes involved in fruit growth at the sink level, i.e. fruit demand and growth rate. The contribution of temperature to fruit demand can be associated with the daily variation in degree-days used to compute fruit demand in the model of mango growth in dry mass (Léchaudel et al., 2005a). In this study, the model predicted the observed response of fruit growth to changes in temperature between seasons among controlling conditions of carbon and water supplies. An analysis of variance carried out on simulations from two sites and seven successive years indicated that the fruit growth rate was significantly affected by temperature. However, this effect was significantly less important than another source-sink factor, the initial fruit dry mass representing fruit size after cell division. This factor, which reflects the total number of cells in fruit flesh, can be influenced by temperature as well. It has been suggested in other species, including Satsuma mandarin (Marsh et al., 1999) and apples (Austin et al., 1999), that temperature may affect the rate of cell division. Other preharvest factors such as resource limitation during cell division due, for example, to carbon competition, can be a source of variation of the initial fruit dry mass.

Carbon availability: It is a recognised fact that fruit growth is mainly affected by the availability of carbohydrates. For mango, it would be useful to be able to determine the leaf-to-fruit ratio of a girdled branch or the crop load of a tree required to obtain optimum fruit size, since biennial bearing, which can be due to depletion of carbohydrates, occurs in many mango

cultivars (Chacko et al., 1982; Reddy and Singh, 1991). Several studies have shown that mango fruit size increased with increasing leaf-to-fruit ratio. In addition, to produce larger fruit at harvest on branches with the highest leaf-to-fruit ratio, changing carbohydrate supply to the fruit increased the proportion of fresh mass in the flesh to the rest of the fruit. This relationship between fruit size and the fraction of fruit mesocarp was observed at the tree level by effectively managing cultural practices that affect crop load (Spreer et al., 2007).

The amount of carbohydrates supplied to tree fruits depends on source size and activity and on sink demand, according to the simulation in the model of mango growth. Changing the number of leaves per fruit directly affected source size as well as source activity (Urban et al., 2004). Both leaf  $N_m$  and  $N_a$ , and non-structural carbohydrate concentration, were lower and higher, respectively, in the high leaf-to-fruit ratio (100 leaves per fruit) than in the low leaf-to-fruit ratio (10 leaves per fruit) treatment (Table 2). This suggests that carbohydrate content may become the driving force behind photosynthetic acclimation to changing source-sink relationships. Moreover, leaf-to-fruit ratio and the associated changes in carbon availability may have an additional effect on photosynthetic capacity by affecting the relationship between key parameters such as the maximal rate of carboxylation ( $V_{cmax}$ ), the light-saturated rate of photosynthetic electron transport (J<sub>max</sub>), and N<sub>a</sub>. Despite the increase in source activity (Urban and Léchaudel, 2005) and the mobilisation of both leaf and stem reserves (Léchaudel et al., 2005a), mango size was smaller in low leaf-to-fruit ratio treatments (Table 2). On the contrary, increasing the leaf-to-fruit ratio from 50 to 100 leaves per fruit increased source size and thus carbon availability, and lead to fruit with higher sugar contents in the flesh. However, there was no significant increase in fruit size. These findings at the source and sink levels confirm that, in the case of non-limiting carbon supply, mango growth rate is limited by sink size. The sink limitation is balanced by the buffer role of reserves, so that carbohydrates produced in excess of fruit demand were stored in leaves and stems, as indicated by both simulated and measured reserve concentrations (Table 2).

Changing carbon availability to fruit influenced both the dry mass and the water mass of its three main compartments: skin, pulp and stone (Léchaudel et al., 2002). A biophysical model of mango growth was able to accurately simulate the observed increase in fruit size with increasing availability of assimilate supply (Léchaudel et al., 2007). This model, based on water relations (water potential and osmotic and turgor pressures) at the fruit level and on reversible and irreversible components of fruit growth, was able to reproduce the shrinkage and swelling of fruit linked to elastic behaviour during the daytime, and the fruit expansion due to positive plastic and elastic growth during the night. Shrinkage was sensitive to the surface conductance of fruit skin, the elastic modulus and the hydraulic conductivity of fruit, whereas the fruit growth rate was highly sensitive to parameters linked to changes in wall extensibility and yield threshold pressure, regardless of assimilate supply.

Since dry matter accumulation is affected by the availability of assimilate supply, changes in its structural component, including cell walls, and its non-structural one, consisting of soluble sugars, acids, minerals and starch, have been investigated according to their sensitivities to leaf-to-fruit ratio treatments. The influence of dilution during fruit growth on quality traits such as flesh taste or shelf life has been considered by expressing concentrations of the main biochemical and mineral compounds per unit of fresh mass. Thus, Léchaudel et al. (2005b) have shown that total dry matter content and structural dry matter content of flesh were higher in fruit from high leaf-to-fruit ratio treatments, whereas structural-to-total dry matter ratio was not affected by changes in carbon availability. Therefore, carbon availability affects the concentration of a compound on a fresh mass basis by changing either the total dry matter content, the content of this compound per unit of structural dry mass, or these two components at once.

Expressed per unit of structural dry mass, the concentrations of calcium were higher in flesh from low leaf-to-fruit ratios. It has been suggested that small fruits have a higher surface area-to-volume ratio due to decreasing leaf-to-fruit ratio than large fruits from the high leaf-to-fruit ratio treatments, which can result in an increase in water loss per unit of fruit mass via transpiration, and in calcium accumulation through the xylem (Wilkinson, 1968). In treatments with low leaf-to-fruit ratios, it is possible that larger amounts of water may

**Table 2.** Nitrogen, carbohydrate contents, photosynthesis characteristics of leaves and final fruit mass of girdled fruiting branches with 10 and 100 leaves per fruit (high- and low-fruit load, respectively): gap fractions (GF), concentration of nitrogen per dry mass unit ( $N_m$ ), leaf mass-to-area ratio ( $M_a$ ), amount of nitrogen per unit leaf area ( $N_a$ ), and total non-structural carbohydrates (TNC<sub>a</sub>) per unit leaf area, net photosynthetic assimilation ( $A_{net}$ ), leaf diffusive conductance to water vapour ( $g_s$ ). Means are presented  $\pm$  SE. For each line, values with different letters differ significantly (P < 0.05) [adapted from Léchaudel and Joas (2006) and Urban et al. (2004)].

Parameters	High fruit load	Low fruit load
GF	$0.50 \pm 0.07 \mathrm{a}$	$0.51 \pm 0.07 \mathrm{a}$
$N_m (g N g^{-1} DM)$	$1.42 \pm 0.04 \mathrm{b}$	$1.31 \pm 0.02 \mathrm{c}$
$M_a (g DM m^{-2})$	$143.7 \pm 2.9 \text{ a}$	$142.4 \pm 2.6$ a
$N_a (g N m^{-2})$	$2.04 \pm 0.07 \mathrm{b}$	$1.87 \pm 0.05 \mathrm{c}$
$TNC_a(g m^{-2})$	$16.0 \pm 1.3 \mathrm{a}$	$32.9 \pm 2.7 \mathrm{b}$
$A_{net} (\mu mol CO_2 m^{-2} s^{-1})$	$8.17 \pm 0.50 \mathrm{a}$	$5.33 \pm 0.56 \mathrm{b}$
$g_{s} (\text{mol H}_{2}\text{O m}^{-2} \text{ s}^{-1})$	$0.13 \pm 0.01$ a	$0.07 \pm 0.01 \text{ b}$
Final fruit mass (g)	$218.5 \pm 11.9 a$	$420.2 \pm 15.3 \text{ b}$

be lost by the fruits during the day to compensate for the higher transpiration rate of the surrounding leaves of these treatments, since leaves from these treatments have the highest leaf diffusive conductance (Table 2). Lang and Volz (1998) reported a positive relationship between xylem sap inflow during the night and xylem sap outflow during the day. At night, in low leaf-to-fruit ratio treatments, larger amounts of water should come into fruits via the xylem to compensate for these water losses. These additional inflows of sap also provided additional imports of calcium into the fruit. Concentrations on a structural dry mass basis of other minerals, especially potassium and magnesium, were not affected by changes in carbon availability. The contents of these two minerals on a fresh mass basis were higher in the flesh of fruit from high leaf-to-fruit ratios, which reflected that leaf-to-fruit ratio has possibly influenced translocation to the fruit of carbohydrates, potassium, and magnesium in the same way. In fact, is has been shown that these cations are translocated to fruit with assimilates through phloem (Nooden, 1988).

The shortage of assimilate supply appeared to increase glucose and fructose content per unit of structural dry mass in mango flesh. This result indicates a possible role of these hexoses during fruit development in osmotic adjustment, even if this strategy to sustain growth during stress conditions was only reported for water stress (Wang and Stutte, 1992). Sucrose is the other

sugar that plays an important role in mango sweetness. It has been observed that the breakdown of starch mainly leads to an increase in sucrose content per unit of structural dry mass, rather than an increase in glucose content. Moreover, the rates of sucrose accumulation were higher when assimilate supply increased. This can be explained by a strong relationship between sucrose and the rate of assimilate inflow, and by an increase of enzyme activities related to sucrose accumulation, as suggested by the relationship found between sucrose-phosphate synthase activity and leaf area in muskmelon fruit (Hubbard et al., 1990).

Fruit flesh from lower leaf-to-fruit ratios accumulated more citric acid, as shown by its higher contents per unit of structural dry mass in flesh for this treatment (Léchaudel et al., 2005b). However, due to the opposite effect of carbon availability on dry matter content, citric acid content on a fresh mass basis was unchanged regardless of the leaf-to-fruit ratio treatment. Malic acid was affected by changes of carbon availability according to the period of fruit development.

To conclude about the effects of carbon availability on key components involved in the perception of mango flavour, measurements of useful indices such as total soluble solids and titratable acidity confirmed that an increase in leaf-to-fruit ratio had a positive effect on sweetness (Simmons et al., 1998a; Léchaudel and Joas, 2006) and a negative one on sourness (Léchaudel and Joas, 2006).

Fruit maturation, a crucial period of fruit development during which metabolic changes influencing the final quality of mango occurred, depended on changes in carbohydrate availability. The onset of a climacteric crisis represented by the strong rise in respiration rate and synthesis of the ethylene precursor, ACC, was previously observed in fruit from higher leaf-to-fruit ratio treatments (Léchaudel and Joas, 2006). The intensity of fruit respiration was also affected by changes in assimilate supply. In fruit from lower leaf-to-fruit ratio treatments, the observed higher content of malonyl-ACC (MACC) could correspond to a regulation of the ethylene biosynthetic pathway (Lelièvre et al., 1997). It has been demonstrated that MACC could be a stress indicator (Hoffman et al., 1983), suggesting that lower leaf-to-fruit ratios during fruit growth could represent stress conditions for mango.

Exogenous ethephon exacerbated the climacteric crisis by increasing the respiration rate and ethylene production, as well as fatty acid content (Lalel et al., 2003b). The production of total aroma volatiles, monoterpenes, esters and aldehydes was enhanced in fruits which have a more intense climacteric crisis. To our knowledge, no study has yet been carried out on mango that deals with the effect of preharvest factors able to affect the intensity of the climacteric crisis (i.e., carbon availability) on aromatic quality.

Water availability: The main effect of water stress on fruit growth according to the quantity of water shortage and the period when stress occurred was to alter the final mango size. Simmons et al. (1995) observed that if irrigation was cut off between flowering and the first half of the growing period, water stress occurred and affected fruit growth rate and final fruit size. However, for a water shortage close to harvest (1.5 weeks before harvest, for example), no effect on fruit size was observed. Early water stress influenced final fruit size through an effect on the cell number (Table 3). Even when water was withheld during the second month of its development, final fruit size was 34% smaller than from non-stressed trees. Water stress from the end of the first half of the growing fruit period altered final fruit size through an effect on the cell size (Table 3). This effect can be explained by the decrease in carbon assimilation and in water fluxes

entering the fruit, because of the lower leaf conductance and leaf water potential, respectively. In fact, as is the case for many plants, reducing water availability to mango trees by managing irrigation is characterised by measurements of lower leaf water potential at predawn (Schaffer et al., 1994). Plant roots under drought stress often produce ABA as a hormonal signal to the shoot to reduce the stomatal aperture (Hartung et al., 2002). Simmons et al. (1998b) observed that mango leaf diffusive conductance declined with the decrease in water supply. The reaction of the fruit to water stress conditions is to increase the thickness of its cuticle (Table 3). Another study under different irrigation regimes showed that irrigation at 7-d intervals resulted in the greatest yield with the largest fruit, compared to irrigation at 14-d intervals or no irrigation at all.

It has been observed that fruit drop on water-stressed trees was much greater (Schaffer et al., 1994). Spreer et al. (2007) found that partial root zone drying, an innovative irrigation technique that can be a way to increase water-use efficiency, tended to yield larger fruits, since the overall fruit size distribution was more favourable and the fraction of undesirable mangoes in the lower classes was reduced. The authors suggested that fruit drop had been increased on trees from partial root zone drying, resulting in a reduction in the total number of fruits per tree, and also in larger fruits. This relationship between fruit drop and water stress is consistent with Hartung et al. (2002) who proposed that higher levels of ABA were synthesized in response to water stress involved in fruit abscission in the early stages of mango development.

The effect of water shortage by the partial root zone drying technique on other quality traits was not significant, as shown by the total soluble solids-to-acidity ratio, or firmness measurements. Changing water availability by reducing irrigation (40% of the daily evapotranspiration) enhanced the increase of pulp dry matter content with fruit development (Diczbalis et al., 1995). Late water stress accentuated the decline in fruit Ca concentration (Simmons et al., 1995) and strongly affected fructose concentration on a fresh mass basis (Léchaudel et al., 2005b). The increased levels of fructose indicated that this soluble sugar may have contribute to osmotic adjustment of mango, as has been demonstrated for other fruits under water stress condition (Mills et al., 1997).

**Table 3.** Effects of water stress on 'Kensington' mango fruit cell number and size, cuticle thickness and fruit mass at harvest, and on quality either after ripening at 22°C (shelf life, % dry matter), or after four weeks storage at 10°C and one week ripening at 22°C (% internal or external chilling injury, % green skin). For each line, values with different letters differ significantly (P < 0.05) [adapted from Simmons et al. (1998b)].

		Water stress (time of application)			
Treatment	Control	Early After cell division Preharvest			
Cell Number	345.9 a	280.1 b	349.6 a	319.8 a	
Cell size (µm)	97.5 a	96.3 a	68.0 b	95.7 a	
Cuticle thickness (µm)	12.9 c	14.3 b	17.5 a	13.5 bc	
Fruit mass (g)	513.0 a	343.5 b	350.2 b	478.8 a	
Shelf life (days)	13.6 b	15.2 a	11.7 c	13.4 b	
% Dry matter	13.9 bc	12.7 c	17.4 a	14.4 b	
% internal chilling injury	7.2 b	0.0 b	37.7 a	5.0 b	
% external chilling injury	5.2 b	2.5 b	61.7 a	12.5 b	
Green skin (%)	2.7 b	9.8 a	12.2 a	3.2 b	

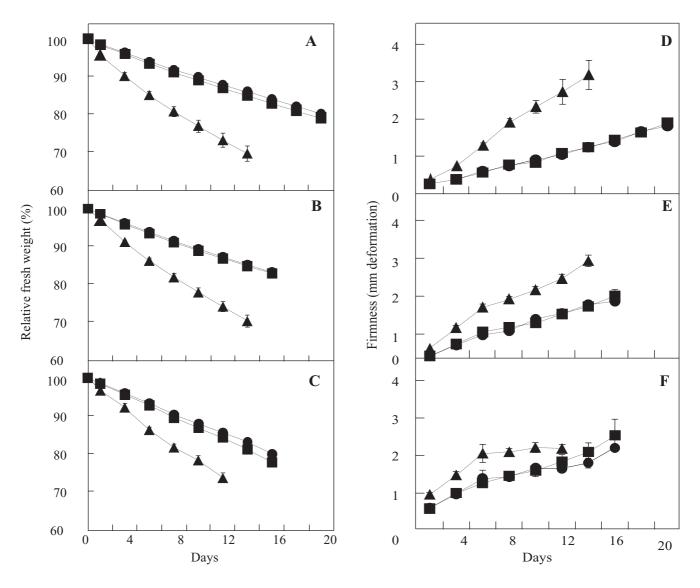
### POSTHARVEST BEHAVIOUR IN RELA-TION TO PREHARVEST FACTORS

The position of fruit in a mango tree affected the time between harvest and the climacteric crisis, as shown by the faster ripening of mangoes from the upper canopy (Hofman et al., 1995), which had the highest pulp dry matter content as well. A strong correlation between shelf life and pulp dry matter content has been observed by many authors, regardless of preharvest factors (position in the canopy, leaf-to-fruit ratio, water stress, etc.).

Bagging also influences mango quality to a small degree. However, fruit bagged with plastic softened faster than unbagged fruit. Shelf life, as measured in days to fruit softening, was significantly reduced by bagging fruit with plastic bags. Therefore, bagging fruit influenced postharvest behaviour of mango, especially water exchanges during storage. In fact, water loss of fruit during storage significantly increased (Hofman et al., 1997; Joyce et al., 1997) as a result of bagging with plastic bags during fruit development (Figure 2). Postharvest researchers are known to study water loss processes since these changes may affect fruit physiology during its ripening, i.e. earlier ethylene synthesis (Paull, 1999), or a rise in membrane deterioration (Ben-Yehoshua et al., 1983). It has been observed that fruit shrivelling was significantly higher at the end of storage, as shown measurements in fruit deformation (Figure 2). This increase in water loss during

storage may be due to the artificially higher humidity environment of fruit bagged with plastic, which may therefore influence structure and/or composition of the cuticle and/or lenticels. Schreiber et al. (2001) demonstrated that non-esterified, free carboxyl groups present in the cutin polymer matrix contributed to the effect of humidity on cuticular water permeability. This humidity-sensitive polar path of cuticular water permeability is arranged in parallel with the humidityindependent non-polar path formed by lipophilic wax components of the cuticle. Cuticular conductance can be affected by cuticle thickness (Knoche et al., 2001), which varies according to fruit growing conditions. It has been shown that cuticle thickness of some plants was reduced when growth occurred in high-humidity environments (Tribe et al., 1968). Another source of water loss is the increase in cuticle cracking, which can be influenced by a low vapour pressure deficit corresponding to high humidity (Moreshet et al., 1999).

Carbon availability affected visual quality and fruit storage potential. Simmons et al. (1998a) showed that increasing the leaf-to-fruit ratio decreased shelf life and increased the incidence and severity of disease (Table 3). Fruits from these treatments had the highest increase in fruit mass during growth on the tree, and the lowest calcium-to-potassium plus magnesium ratio, a source of cell structure weakening, which could favour postharvest disease.



**Figure 2.** Changes in (**A-C**) relative fresh mass [percentage of initial (harvest) fresh mass] and (**D-F**) firmness (mm deformation) during ripening of unstored 'Sensation' mango fruit (**A,D**), and of mango stored for 15 (**B,E**), and 30 (**C,F**) days at 10°C, for unbagged (●), paper bagged (■) and plastic bagged (▲) treatments [adapted from Joyce et al. (1997)].

Water availability influenced both postharvest behaviour and final mango quality. It was observed that fruit from early water stress treatment took significantly longer to ripen at 22°C, and had lower pulp dry matter content. After cold storage, these fruits had more internal and external diseases and stayed greener than the control (Table 3). When water stress was applied just before the end of the first half of the fruit growing period, fruits ripened earlier and retained more green skin colour. The fruit flesh had higher content in dry matter, calcium and magnesium, and no difference in K content. The chilling

injury susceptibility of mango from this treatment was not affected by cold storage (Table 3).

#### FINAL COMMENTS

Environmental factors are one of the main sources of variation of mango quality, as has been described in various studies and reviewed in this paper. These preharvest factors affect both fruit growth during its development by changing the accumulation of water and dry matter, including biochemical and mineral

compounds, and fruit behaviour during its storage. Having knowledge of and then being able to control changes in fruit quality in response to environmental conditions may be essential to adopting cultural practices that will provide high quality fruits and to defining optimal postharvest procedures that will take fruit production conditions into account. A way to improve final mango quality traits such as size, colour, taste, nutritional value and flavour is also to build an integrated approach that links the two categories of factors, preharvest and postharvest, which influence the various components of mango quality. This approach can combine experiments and models since fruit is a highly complex system.

#### **REFERENCES**

- Akamine EK, Goo T (1973) Respiration and ethylene production during ontogeny of fruit. J. Am. Soc. Hort. Sci. 98:286-291.
- Austin PT, Hall AJ, Gandar PW, Warrington IJ, Fulton TA, Halligan EA (1999) Compartment model of the effect of early-season temperatures on potential size and growth of 'Delicious' apple fruits. Ann. Bot. 83:129-143.
- Bangerth F (1979) Calcium-related physiological disorders of plants. Annu. Rev. Phytopathol. 17:97-122.
- Ben-Yehoshua S, Shapiro B, Chen ZE, Lurie S (1983) Mode of action of plastic film in extending life of lemon and bell pepper fruits by alleviation of water stress. Plant Physiol. 73:87-93.
- Chacko EK, Reddy YTN, Ananthanarayanan TV (1982) Studies on the relationship between leaf number and area and development in mango (*Mangifera indica* L.). J. Hort. Sci. 57:483-492.
- Crisosto CH, Mitchell FG, Johnson S (1995) Factors in fresh market stone fruit quality. Postharvest News Inf. 6:171-211.
- Diczbalis Y, Hofman P, Landrigan M, Kulkarni V, Smith L (1995) Mango irrigation management for fruit yield, maturity and quality. In: Proceedings of Mango 2000 marketing seminar and production workshop. Brisbane, Australia, pp.85-90.
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves in C<sub>3</sub> species. Planta 149:78-90.

- Ferguson IB (1984) Calcium in plant senescence and fruit ripening. Plant Cell Environ. 7:397-405.
- Ferguson IB, Volz R, Woolf A (1999) Preharvest factors affecting physiological disorders of fruit. Postharvest Biol. Technol. 15:255-262.
- Hartung W, Sauter A, Hose E (2002) Abscisic acid in the xylem: where does it come from, where does it go? J. Exp. Bot. 366:27-32.
- Hewett EW (2006) An overview of preharvest factors influencing postharvest quality of horticultural products. Int. J. Postharvest Technol. Innov. 1:4-15.
- Ho LC, Grange RI, Picken AJ (1987) An analysis of the accumulation of water and dry matter in tomato fruit. Plant Cell Environ. 10:157-162.
- Hoa TT, Ducamp M-N, Lebrun M, Baldwin EA (2002) Effect of different coating treatments on the quality of mango fruit. J. Food Qual. 25:471-486.
- Hoffman NE, Liu Y, Yang SF (1983) Changes in 1-(malonylamino)cyclopropane-1-carboxylic acid content in wilted wheat leaves in relation to their ethylene production rates and 1-aminocyclopropane-1-carboxylic acid content. Planta 157:518-523.
- Hofman PJ, Smith LG, Holmes R, Campbell T, Meiburg G (1995) Mango fruit quality at harvest is affected by production conditions. In: Proceedings of Mango 2000 marketing seminar and production workshop. Brisbane, Australia, pp.199-208.
- Hofman PJ, Smith LG, Joyce DC, Johnson GI, Meiburg G (1997) Bagging of mango (*Mangifera indica* cv. 'Keitt') fruit influences fruit quality and mineral composition. Postharvest Biol. Technol. 12:83-91.
- Hollinger DY (1996) Optimality and nitrogen allocation in a tree canopy. Tree Physiol. 16:627-634.
- Hubbard NL, Pharr DM, Huber SC (1990) Sucrose metabolism in ripening muskmelon fruit as affected by leaf area. J. Am. Soc. Hort. Sci. 115:798-802.
- Jacobi KK, Wong LS, Giles JE (1995) Effect of fruit maturity on quality and physiology of high-humidity hot air-treated 'Kensington' mango (*Mangiera indica* Linn.). Postharvest Biol. Technol. 5:149-159.
- Jones HG, Higgs KH, Samuelson TJ (1983) Calcium uptake by developing apple fruits. I. Seasonal changes in calcium content of fruits. J. Hort. Sci. 58:173-182.
- Joyce DC, Beasley DR, Shorter AJ (1997) Effect of preharvest bagging on fruit calcium levels, and

- storage and ripening characteristics of 'Sensation' mangoes. Aust. J. Exp. Agric. 37:383-389.
- Knoche M, Peschel S, Hinz M, Bukovac MJ (2001) Studies on water transport through the sweet cherry surface: II. Conductance of the cuticle in relation to fruit development. Planta 213:927-936.
- Lakshimnarayana S, Subhadra NV, Subramanyam H (1970) Some aspects of developmental physiology of mango fruit. J. Hort. Sci. 45:133-142.
- Lalel HJD, Singh Z, Tan SC (2003a) Maturity stage at harvest affects fruit ripening, quality and biosynthesis of aroma volatile compounds in 'Kensington Pride' mango. J. Hort. Sci. Biotechnol. 78:225-233.
- Lalel HJD, Singh Z, Tan SC (2003b) The role of ethylene in mango fruit aroma volatiles biosynthesis. J. Hort. Sci. Biotechnol. 78:485-496.
- Lang A, Volz RK (1998) Spur leaves increase calcium in young apples by promoting xylem inflow and outflow. J. Am. Soc. Hort. Sci. 123:956-960.
- Léchaudel M, Joas J (2006) Quality and maturation of mango fruits of cv. Cogshall in relation to harvest date and carbon supply. Aust. J. Agric. Res. 57:419-426.
- Léchaudel M, Normand F, Génard M (2006) Predicting harvest dates and quality of mango (cv 'Cogshall') fruit according to environmental factors. 8th International Symposium on Mango. Sun City, South Africa.
- Léchaudel M, Génard M, Lescourret F, Urban L, Jannoyer M (2002) Leaf-to-fruit ratio affects water and drymatter content of mango fruit. J. Hort. Sci. Biotechnol. 77:773-777.
- Léchaudel M, Génard M, Lescourret F, Urban L, Jannoyer M (2005a) Modeling effects of weather and source-sink relationships on mango fruit growth. Tree Physiol. 25:583-597.
- Léchaudel M, Joas J, Caro Y, Génard M, Jannoyer M (2005b) Leaf:fruit ratio and irrigation supply affect seasonal changes in minerals, organic acids and sugars of mango fruit. J. Sci. Food Agric. 85:251-260.
- Léchaudel M, Vercambre G, Lescourret F, Normand F, Génard M (2007) An analysis of elastic and plastic fruit growth of mango in response to various assimilate supplies. Tree Physiol. 27:219-230.
- Lelièvre JM, Latché A, Jones B, Bouzayen M, Pech J-C (1997) Ethylene and fruit ripening. Physiol. Plant. 101:727-739.

- Malundo TMM, Shewfelt RL, Ware GO, Baldwin EA (2001) Sugars and acids influence flavor properties of mango (*Mangifera indica*). J. Am. Soc. Hort. Sci. 126:115-121.
- Marsh KB, Richardson AC, Macrae EA (1999) Early- and mid-season temperature effects on the growth and composition of satsuma mandarins. J. Hort. Sci. Biotechnol. 74:443-451.
- Medlicott AP, Thompson AK (1985) Analysis of sugars and organic acids in ripening mango fruits (*Mangifera indica* L. var Keitt) by high performance liquid chromatography. J. Sci. Food Agric. 36:561-566.
- Mendoza DB, Wills RBH (1984) Changes in mango during growth and maturation. In: Wills RBH, Mendoza DB (eds), Mango: Fruit Development, Postharvest Physiology and Marketing in ASEAN, pp.21-38. ASEAN Food Handling Bureau, Kuala Lumpur.
- Mills TM, Behboudian MH, Clothier BE (1997) The diurnal and seasonal water relations, and composition, of 'Braeburn' apple fruit under reduced plant water status. Plant Sci. 126:145-154.
- Moreshet S, Yao C, Aloni B, Karni L, Fuchs M, Stanghellini C (1999) Environmental factors affecting the cracking of greenhouse-grown bell pepper fruit. J. Hort. Sci. Biotechnol. 74:6-12.
- Nooden LD (1988) Whole plant senescence. In: Nooden LD, Leopold A (eds), Senescence and Aging in Plants, pp.391-439. Academic Press, San Diego.
- Nunes CN, Emond JP, Brecht JK, Dea S, Proulx E (2007) Quality curves for mango fruit (cv. Tommy Atkins and Palmer) stored at chilling and nonchilling temperatures. J. Food Qual. 30:104-120.
- Paull ER (1999) Effect of temperature and relative humidity on fresh commodity quality. Postharvest Biol. Technol. 15:263-277.
- Reddy YTN, Singh G (1991) Further studies on the relationship between leaf number and area fruit development in mango (*Mangifera Indica* L.). J. Hort. Sci. 66:471-478.
- Reddy YTN, Srivastava GC (1999) Ethylene biosynthesis and respiration in mango fruits during ripening. Indian J. Plant Physiol. 4:32-35.
- Schaffer B, Whiley AW, Crane JH (1994) Mango. In: Schaffer B, Andersen PC (eds), CRC Handbook of Environmental Physiology of Fruit Crops, Subtropical and Tropical Crops, pp.165-197. CRC Press, Boca Raton.

- Schreiber L, Skrabs M, Hartmann KD, Diamantopoulos P, Simanova E, Santrucek J (2001) Effect of humidity on cuticular water permeability of isolated cuticular membranes and leaf disks. Planta 214:274-282.
- Simmons SL, Hofman PJ, Hetherington SE (1995) The effects of water stress on mango fruit quality. In: Proceedings of Mango 2000 marketing seminar and production workshop. Brisbane, Australia, pp.191-197.
- Simmons SL, Hofman PJ, Whiley AW, Hetherington SE (1998a) Effects of leaf:fruit ratios on fruit growth, mineral concentration and quality of mango (*Mangifera indica* L. cv. Kensington Pride). J. Hort. Sci. Biotechnol. 73:367-374.
- Simmons SL, Hofman PJ, Whiley AW, Hetherington SE (1998b) Effects of preharvest calcium sprays and fertilizers, leaf:fruit ratios, and water stress on mango fruit quality. In: Coates LM, Hofman PJ, Johnson GI (eds), International Workshop on Disease Control and Storage Life Extension in Fruit, pp.19-26. Australian Centre for International Agricultural Research, Chiang Mai.
- Spreer W, Nagle M, Neidhart S, Carle R, Ongprasert S, Müller J (2007) Effect of regulated deficit irrigation and partial rootzone drying on the quality of mango fruits (*Mangifera indica* L., cv.'Chok Anan'). Agric. Water Manage. 88:173-180.

- Tribe IS, Gaunt JK, Wills RBH (1968) Cuticular lipids in the Gramineae. Biochem. J. 109:8-9.
- Ueda M, Sasaki K, Utsunomiya N, Inaba K, Shimabayashi Y (2000) Changes in physical and chemical properties during maturation of mango fruit (*Mangifera indica* L. 'Irwin') cultured in a plastic greenhouse. Food Sci. Technol. Res. 6:299-305.
- Urban L, Léchaudel M (2005) Effect of leaf-to-fruit ratio on leaf nitrogen content and net photosynthesis in girdled branches of *Mangifera indica* L. Trees-Struct. Funct. 19:564-571.
- Urban L, Léchaudel M, Lu P (2004) Effect of fruit load and girdling on leaf photosynthesis in *Mangifera indica* L. J. Exp. Bot. 55:2075-2085.
- Urban L, Le Roux X, Sinoquet H, Jaffuel S, Jannoyer M (2003) A biochemical model of photosynthesis for mango leaves: evidence for the effect of fruit on photosynthetic capacity of nearby leaves. Tree Physiol. 23:289-300.
- Wang Z, Stutte G (1992) The role of carbohydrates in active osmotic adjustment in apple under water stress. J. Am. Soc. Hort. Sci. 117:816-823.
- Wilkinson BG (1968) Mineral composition of apples. IX. Uptake of calcium by the fruit. J. Sci. Food Agric. 19:646-647.