# 10

# Fruit Transpiration: Mechanisms and Significance for Fruit Nutrition and Growth

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## 1. Introduction

Water and minerals transport in plant occur through the transpiration stream as triggered mainly by the environmental conditions. The transpiration of leaves has been studied in great detail over many years and the roles played by the various leaf structures (cuticle, stomata, lenticels etc) are well understood. Similarly well understood are the influences on foliar transpiration of meteorological variables such as temperature, radiation, vapour pressure deficit and wind, also, how these variables can be differently important to foliar transpiration depending on whether one is considering an isolated leaf or an entire canopy (Jarvis, 1985). In contrast with this, the transpiration of fruits has not been studied to nearly the same extent, neither with regard to skin structures and their associated functional properties nor with regard to the transpiration response of fruit to the various meteorological variables.

Most fruit-crop species (including apple, apricot, avocado, kiwifruit, capsicum and tomato), suffer from pre- and post-harvest physiological disorders. Higher incidences of these physiological disorders have many times been reported as being associated with lower concentrations of calcium (Ca) in the fruits (Faust et al. 1968, Tzoutzoukou and Bouranis 1997, Ferguson et al. 2003, Thorpe et al. 2003). Transpiration is the main driving force for the xylem stream (White and Broadley 2003) in which Ca seems to move relatively freely while this ion is also well known to be substantially immobile in the phloem (Buckowak and Wittwer 1957). Along with the observation that fruit are largely phloem fed, calcium's well know xylem mobility and phloem immobility explain in part why fruit are generally low-Ca organs and also why higher fruit transpiration rates are sometimes associated with increased fruit Ca levels (Cline and Hanson 1992, Tromp and Van Vuure 1993, Montanaro et al 2006 and 2010). It is therefore reasonable to hypothesise that for any particular fruit, the seasonal integral of fruit transpiration rate will predict fruit Ca content at harvest and thus (at least potentially) the incidence of Ca-related physiological disorders.

This chapter focuses the mechanisms behind fruit transpiration in some fruit tree species, its seasonal trend and discusses the significance of fruit water loss on mineral composition particularly on Ca accumulation.

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## 2. Understanding and measuring fruit transpiration

Based on the Fick's- or Ohm's-law analogy (Fiscus et al., 1982), specific fruit transpiration rate ($T_F$) (the water vapour efflux per unit area of skin surface) depends on the product of the conductance properties ($C$) of the fruit skin and the driving force ($V$):

$$T_F = C \times V \quad (1)$$

Fruit conductance depends on skin properties determining its permeance, hence it is species specific. In addition it varies along with the season. Smith et al (1985) showed that the skin conductance in kiwifruit berry decreases rapidly during the early two weeks after anthesis (Fig. 1), thereafter the conductance decreases again reaching the minimum at about 8 weeks after anthesis where remains relatively constant until harvest.

Back to the Eq. 1, the term $V$ is the difference in water vapour pressure between the airspaces inside the fruit and the air immediately outside it. The driving force depends on environmental conditions such as temperature, radiation, relative humidity, etc. Under most commercial training systems in most of fruits, their intercellular air (which is very close to saturation with relative humidity values close to ~99.4% (Nobel, 2005)) will have a water vapour pressure very close to the theoretical value for water at the temperature of this intercellular air. This means that transpiration will be driven substantially by a vapour pressure gradient whose value is numerically close to the water vapour pressure deficit ($VPD$) (Fig. 2) of the bulk atmosphere and this in turn is a reasonably exact function just of the surrounding air's temperature and of its relative humidity (Goudriaan and van Laar 1994). Based on Eq. 1, fruits under higher relative humidity are predicted to have a lower transpiration. Results presented by Li et al. (2002), even in a preliminary form, are in line with this prediction. In that study, it has been reported that an increase of relative humidity from 40 to 60% induced a reduction of fruit water loss by approximately 30-50% in two peach varieties under laboratory condition.

Measurement of fruit water loss could be performed in both attached and detached fruit.

Regular leaf gas exchange instrumentation equipped with appropriate chamber helps to measure fruit transpiration in attached fruit, particularly for those species (e.g. kiwifruit) with relatively long peduncle (Photo 1). Since such a instrument requires knowledge of the surface area being analysed, it is required to preliminarily determine an appropriate correlation with fruit area and some geometrical traits of fruit which could be easily measured in the field (e.g. length, diameter). For example, for estimates of fruit surface area in kiwifruit berry a fruit sample (×70) were carefully peeled during the growing season and their skin area measured using a portable area meter (Model Li-3000, LI-COR). For the same fruit, estimated fruit surface area ($E$s) was calculated as $E$S = L*W*3.14, where L was the fruit length and W the maximum fruit diameter. The fitted linear regression (y = 1.0078 * $E$S + 0.798; $R^2$ = 0.97) between estimated and measured fruit surface area was then used in the field for measurements of fruit transpiration (Montanaro et al., 2006).

Fruit transpiration could be inferred in the field also through the weigh loss of detached fruit (Lang 1990). In that case, the fruit water reservoir is able to sustain the transpiration for several hours (~10) (Li et al., 2002) despite the lack of the xylem/phloem supply by the parent plant. This valuable method is also used to assess in/out fluxes of fruit. Briefly, it is based on fruit diameter (and volume) changes occurring in fruits subjected to a sequence of

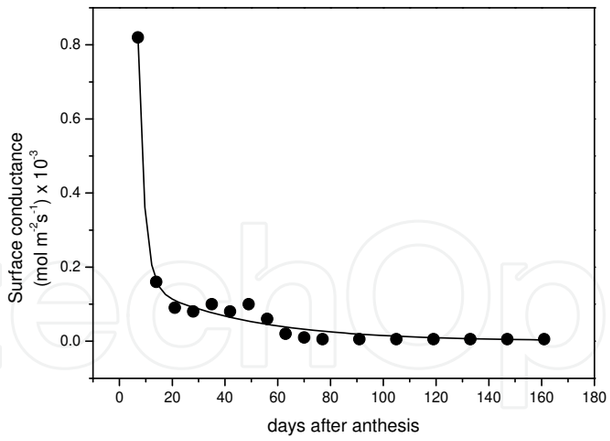


Fig. 1. Surface conductance to water vapour measured in detached kiwifruit. (Redrawn from Smith et al., 1995).

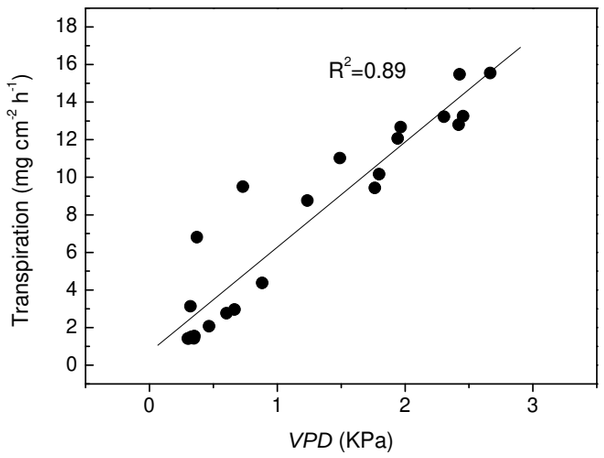


Fig. 2. Relationship between vapour pressure deficit (*VPD*) and fruit transpiration measured in detached kiwifruit berry in 3-week-old fruits. (Redrawn from Montanaro et al., in press).

Photo 1. Measurement of fruit transpiration in attached kiwifruit (left) and detached apricot (right) using a portable gas-exchange equipment (ADC-LCA4, ADC BioScientific Ltd, Hoddesdon, England).

manipulation as concern their vascular connections (Lang 1990). The diameter variations of fruit should be accurately determined using specific highly accurate gauge (Lang 1990). That method requires the measurement of diameter of "intact" (with normal vascular connections), "girdled" (with the phloem connection severed) and "detached" fruit (with all vascular connections severed). The method is based on a subtractive analysis to quantify separately the phloem, xylem and the transpiration contribution, under the assumption that volume growth integrates a fruit in/out fluxes.

## 3. Daily and seasonal changes in fruit water loss

The absolute value of fruit transpiration is inevitably related to the whole fruit surface area. Regular growing fruits show a rapid expansion of their surface area early after fruit set due to cell division (Fig. 3). Later in the season fruit surface further increases but at a lesser extent.

Specific fruit transpiration varies considerably over a 24-hour period taking relatively high values in the middle part of the day but reducing to almost nothing at night (Montanaro et al., in press). Figure 4 shows the daily variation of fruit water loss in two species (peach and kiwifruit) which is presumably due to diurnal variation in key variables of the fruit's aerial microenvironment (e.g. temperature, relative humidity). A noteworthy fact is that despite fruit transpiration was assessed with different method (weigh loss for peach, gas exchange for kiwifruit) it clearly shows a similar behaviour and a consistent absolute value.

Seasonal fruit transpiration usually shows a maximum rate just after fruit set, thereafter it declines quite promptly reaching a minimum at the half of the whole development stage (Fig. 5). In apricot fruit (cv Tyrithos) that maximum has been recorded to be close to 0.55 mmol $m^{-2}$ $s^{-1}$ in very young fruits (i.e. 6 days after fruit-set) (Fig. 5). During the following 4 weeks, transpiration rapidly decreased to approx. 0.35 mmol $m^{-2}$ $s^{-1}$ accounting for about 80% of the whole transpiration decline. Thereafter, transpiration again decreased but more slowly reaching 0.30 mmol $m^{-2}$ $s^{-1}$.

In kiwifruit, the rate of fruit water loss is similar even the absolute value significantly higher than stone fruits (apricot/peach). Fruit transpiration per unit of fruit area had a maximum value of 2.3 mmol $m^{-2}$ $s^{-1}$ in the first days after fruit set (Fig. 5). During the following 2 weeks transpiration rapidly decreased by 65% compared to the initial values. In the subsequent 30 days it reached very low values, approximately 10% of the initial rate. The substantial reduction in transpiration of fruit by day 50-60 after fruit set occurs at the same time as the permanent disfunction of the fruit vascular system as reported by Dichio et al. (2003).

There are evidences that the minimum rate of transpiration reached by fruit is species specific. The minimum transpiration rate recorded at the end of the grow period in *Prunus armeniaca*, was relatively high at 55% of the early value according to data on peach (Li et al., 2002). The transpiration profile is also in agreement with findings in grapevine and kiwifruit even though the extent of decline differed (Boselli et al., 1998; Montanaro et al., 2006). In these species, the lowest transpiration rate was about 10% (kiwifruit) and 20% (grapevine) of the initial values. In kiwifruit the large decline of fruit transpiration has been associated with the evolution of a suberised outer cell layers, and death of the outer cells associated with wax biosynthesis (Celano et al., 2009). It is likely that such changes are not so marked

in the case of apricot, leading the lowest transpiration rate to remain within about ½ of the initial values.

### 3.1 Changes in skin properties

Seasonal changes in fruit-skin conductance are probably responsible for the decline in transpiration during the season showed in Figure 5. Xiloyannis et al. (2001) the decrease in fruit transpiration in kiwifruit has been associated with the collapse of the surface tissues of the fruit and the development of a suberized periderm. That is, transversal freeze fractures of frozen-hydrated kiwifruit epidermis proved that the external layer of epidermal cells collapsed during fruit development (Photo 2), producing a bearing-like protection for the fully hydrated parenchymatic cells positioned below them. These epidermis structural changes are associated with the heavy reduction in transpiration rate recorded during fruit growth (Xiloyannis et al., 2001).

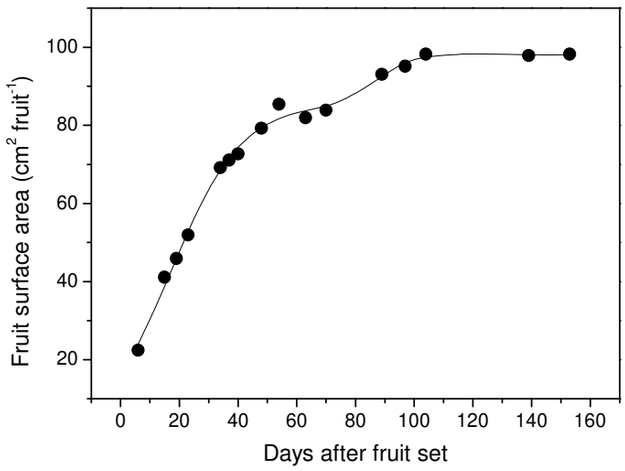


Fig. 3. Seasonal trend of fruit surface area observed in kiwifruit (cv Hayward).

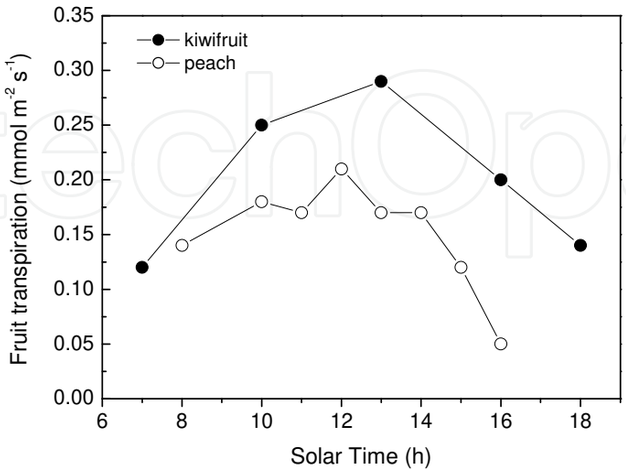


Fig. 4. Daily oscillation of fruit water loss measured 1-week after fruit-set in attached kiwifruit (cv Hayward) and detached peach fruit (cv Dixired). (Redrawn from Li et al., 2002 and Montanaro et al., 2006).

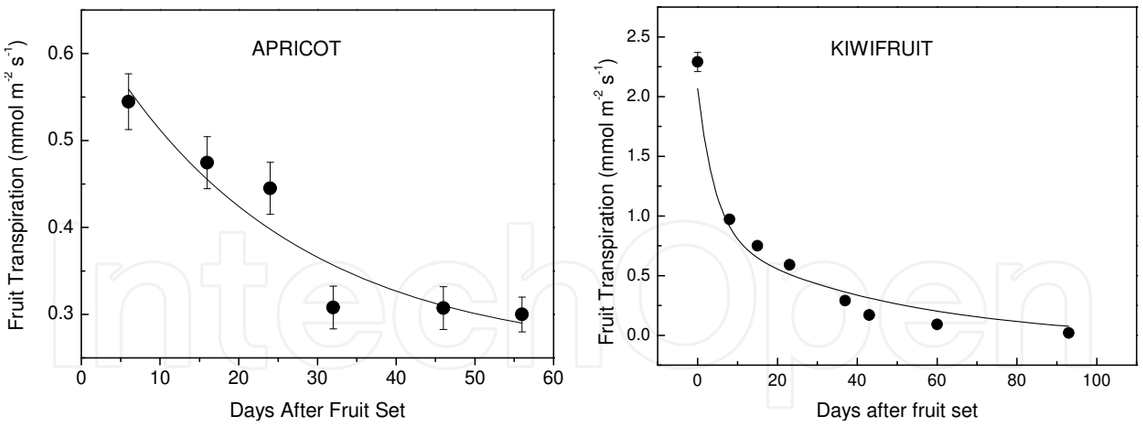


Fig. 5. Seasonal trend of specific fruit transpiration rate measured midday in apricot (left) and kiwifruit (right) as measured in detached and attached fruit, respectively. (Redrawn from Montanaro et al., 2006 and 2010).

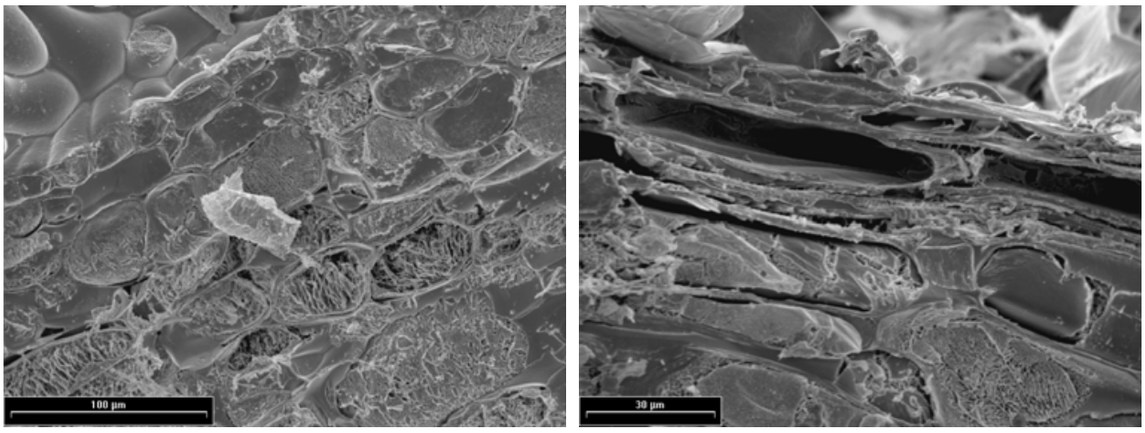


Photo 2. Low Temperature SEM images. Transversal freeze fractures of frozen-hydrated kiwyfruit epidermis sampled at the 4th (left) and at the 17th (right) week from fruit set. Note the collapse of the external layers of epidermal cells during the development of the fruit, which produces a bearing-like protection for the parenchimatic cells positioned below them. (From Xiloyannis et al., 2001).

### 3.2 Which role for hairs?

In some species, fruits have the skin with dermal structures (hairs) which inevitably are involved in skin conductance properties and in turn affect fruit transpiration. This is the case with some kiwifruit species (e.g. *Actinidia deliciosa*).

From an anatomical point of view the dermal hairs of kiwifruit have been reasonably well characterised (White, 1986) but, as yet no information exists as to their possible influence on the transpiration physiology of the fruit. It is therefore worthwhile at this stage to introduce to the discussion some relevant aspects of their development and physiology.

As previously reported in Xiloyannis et al., (2008), the juvenile kiwifruit already has a full set of hairs (trichomes) at bloom and no new hairs develop from this time on. The hairs are

also fully formed and are typically 2.5 to 3.0 mm long and their bases are about 0.1 mm in diameter giving them an aspect ratio (length/basal diameter) of about 25. In the very young fruit, the hairs are packed together so closely that their bases are almost touching. Subsequent surface expansion of the fruit moves the hairs apart so that they become increasingly isolated from one another during the growing season.

Hairs are of quite simple structure (Fig. 6) and contain no vascular tissue. This requires that any evaporative water loss occurring from the more apical cells must be made good by diffusion of water up from the skin through the more basal cells. This diffusion pathway (it is likely that it will be predominantly through the cell wall matrix, not through the protoplasts) is probably sufficient to maintain hair vitality early on when the hairs' close proximity to one another means that they will offer a degree of mutual protection from water loss. However, as they move apart with fruit growth, this protection will become less and less, and so the acropetal diffusion pathway will probably become limiting at some stage. This understanding fits with our observation that cell death (drying) is first evident in the most apical hair cell and this then progresses downwards (basipetally) through the hair eventually reaching the most basal ones last (Xiloyannis et al., 2008).

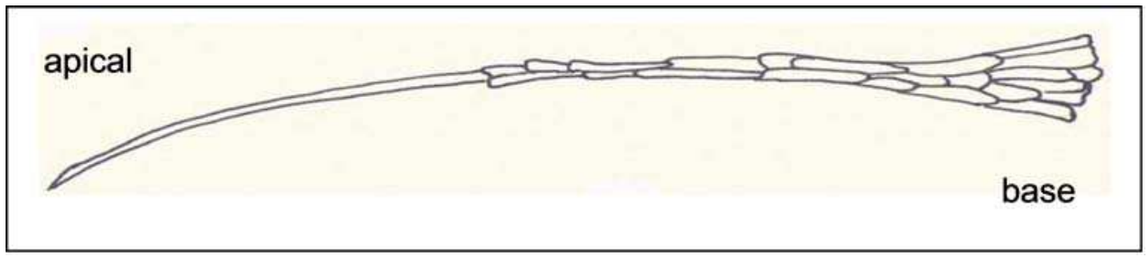


Fig. 6. Drawing of a dermal hair from cv. 'Hayward' kiwifruit. Cell death occurs basipetally, from left to right in this drawing (Redrawn from Xiloyannis et al., 2008).

A simple calculation based upon hair dimensions (the area of a hair ≅ π × base radius × hair length) and hair density (hairs $mm^{-2}$ of fruit surface) (data not shown) proves that, in a very young kiwifruit, the still-living hairs are sufficiently numerous as to increase the 'living' surface area of the fruit by a factor of around 40-times, compared with a hairless fruit of the same dimensions. This massive amplification of fruit surface area is almost certainly responsible for the very high surface conductance of a young kiwifruit. The amplification factor steadily decreases as the fruit surface area increases with growth (data not shown), but the hair dimensions and hair numbers per fruit remain the same (i.e. the hair density decreases). The proportion of living hairs (hairs with some live hair cells) falls from close to 100% at the time of fruit set to about 50% by 30 days after full bloom and by 60 days after full bloom all the cells of all hairs are dead (Fig. 7). We interpret the rather striking skin surface conductance results of Smith et al., (1995) and our own fruit transpiration results, not in terms of the development of a more complex dermal layer (although this too could be involved), but predominantly in terms of the basipetal progression of cell death in the dermal hairs. During this short period of early fruit growth, as hair cell death progresses, the 'hair effect' will change from one in which they *increase* water loss from the fruit skin to one in which they *decrease* it. The fully dead (dry) hairs will serve to reduce fruit water loss by entrapping a thick (c. 3 mm) boundary layer of still, moist air around the fruit. This effect is much the same as that of the layer of fur that reduces the rate of heat loss from the skin of

mammals. Moreover, this understanding is consistent with the behaviour, elsewhere reported (Dichio et al., 2007) that, under the influence of an increasing forced air stream, the kiwifruit's boundary layer resistance breaks down progressively and fruit transpiration increases very significantly. This in turn impacts the import of certain minerals (see below).

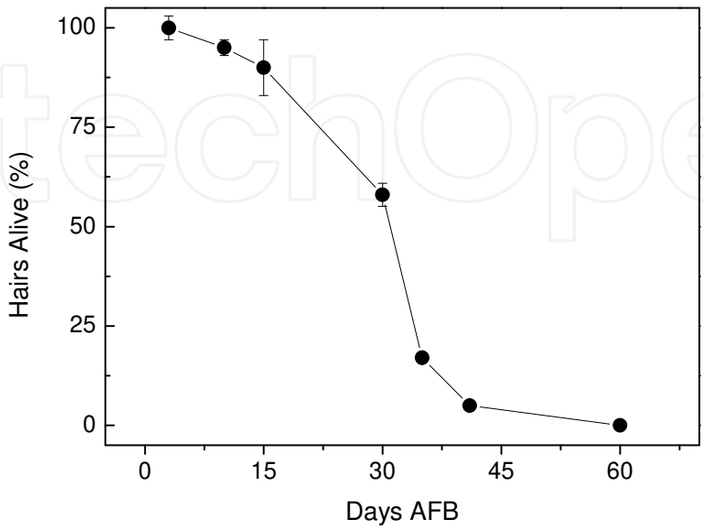


Fig. 7. Hair viability (% of hairs in the sample containing some live cells). Fruit were grown under normal commercial conditions in New Zealand and were not subjected to any special treatment. Each point is the average (± SE) of 100 observations. (Redrawn from Dichio et al., 2003)

### 3.3 The within-fruit resistances

Late season occurrence of anatomical changes of fruit epidermis produces a reduction of surface conductance (Smith et al., 1995; Celano et al., 2009) contributing to the transpiration decline previously observed during fruit development (Montanaro et al., 2006), this might strongly reduce the driving force of xylem inflow. Reduction of incoming xylem stream would be also the result of various co-occurring phenomena such as disruptions (or occlusions) localized either in the (tomato) pedicel (Van Ieperen et al., 2003) or in the (apple, kiwifruit) fruit tissue (Dichio et al., 2003; Dražeta et al., 2004). In fruit of Vitis sp the reduction of hydrostatic pressure gradients and the high phloem flows at the end of the season have been indicted to repress xylem inflow (Bondada et al., 2005; Keller et al., 2006; Choat et al., 2009). In some crops (e.g. apple, tomato and grape, kiwifruit) it has been argued that high hydraulic resistance inside fruits may be involved in phloem unloading processes and to protect the fruit from excessive backflow (Keller et al., 2006 and references therein; Morandi et al., 2010a).

Figure 8 shows the seasonal changes in the hydraulic conductance of fruit (berry+stalk) of kiwifruit. Within the first 35 days after full bloom, hydraulic conductance increased rapidly. This is presumably due to the differentiation of new xylem vessels as a result of a post bloom rise in the activity of the intrafascicular vascular cambium, probably stimulated by seed set (Dražeta et al., 2004). Conductance rose to about 0.22 $cm^3$ $MPa^{-1}$ $s^{-1}$ × $10^{-3}$. For about 20 days, conductance remained relatively stable but then decreased progressively after day

60 after full bloom, according to Dichio et al. (2003). In the late season, hydraulic conductance (measured using a pressure bomb) was very low (0.05 -0.1 $cm^3$ $MPa^{-1}$ $s^{-1}$ × $10^{-3}$) (Fig. 8). This result is in conflict with the data emerging from our dye studies (Dichio et al., 2003), which show a much earlier cessation of flow. This discrepancy will be addressed more thoroughly in a separate study and may have to do with the rather high axial pressure gradient applied to the xylem vessels resulting from the application of a bomb pressure of 1.3 MPa (this high bomb pressure is a requirement of our method in order to obtain measurable volumes of exuded sap). The problem is that the pressure is applied over a relatively short distance of about 70 mm between the fruit flesh and the proximal end of the fruitstalk – this is an unnaturally high gradient for the xylem that would normally experience axial gradients some 3-orders of magnitude less. An alternative explanation of the discrepancy (Bondada et al., 2005) could be a reduction in the available pressure gradients (the driving force of xylem sap flow), but this explanation requires confirmation through further experimentation and analysis. The picture emerging emphasises that physical alterations along the fruit xylem pathway do account for some of the reduction in xylem water inflow to the fruit in the late season and consequently the lowered rates of Ca import.

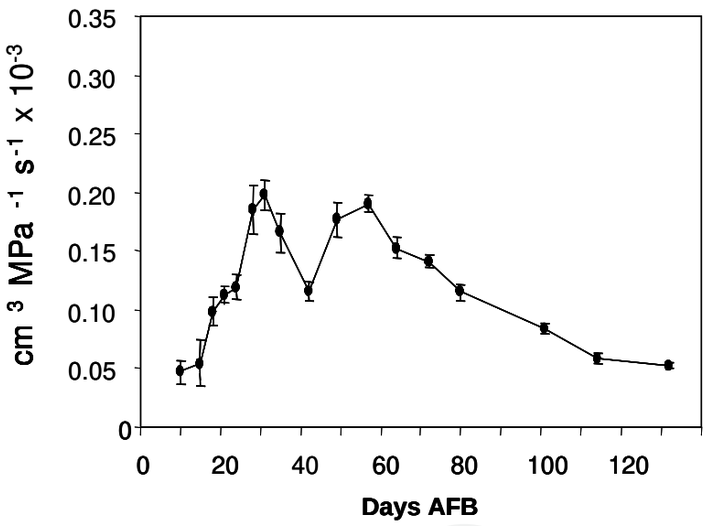


Fig. 8. Hydraulic conductance of kiwifruit fruit (berry + peduncle) measured using a pressure bomb method. Each point is the average of 12 fruit. (Redrawn from Xiloyannis et al., 2008).

### 3.4 Calculating diurnal fruit transpiration

The diurnal fruit transpiration could be calculated through the integration of the fitting curve of the daily measurements. By plotting the single diurnal values, the seasonal trend of the total fruit transpiration could be estimated. For example, in kiwifruit it has been observed a considerable increase in daily fruit transpiration during the early first 25 days after fruit set when a value of approx. 2 g of water per fruit per day was reached (Fig. 9). Subsequently, fruit transpiration decreased. In fact, at 43 day after fruit set, the reduction in fruit transpiration per day with respect to the peak value observed was 65%, later in the season (93 day) fruit transpiration was almost zero (Fig. 9). The increase in total fruit transpiration in the early part of fruit growth apparently contrasts with the reduction of the

rate of fruit water loss (Fig. 5) usually observed in that early stage. The rapid increase of fruit area occurring early of fruit development (Fig. 3) helps to explain such a raise of total amount of water lost by fruit. Measurements of transpiration flux (rate and seasonal trend) of kiwifruit are comparable with findings in stone fruit (detached peach, Li and co-workers 2002) measured in field by weight loss method.

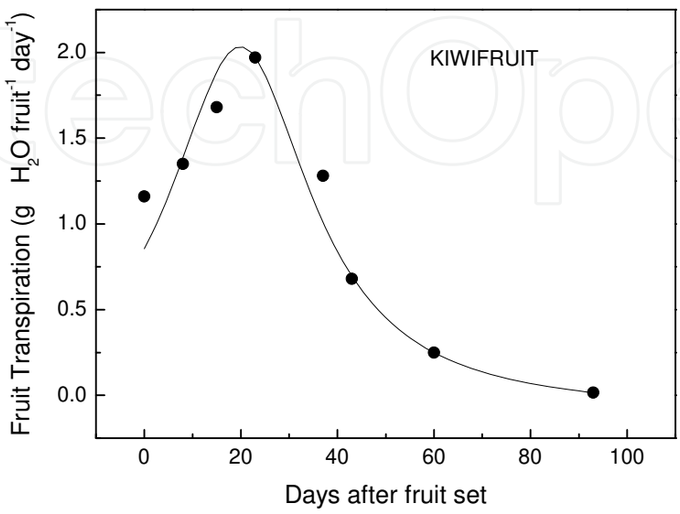


Fig. 9. Seasonal fruit transpiration calculated in kiwifruit (cv Hayward). Each point is the integral of 5 measurements recorded from 7 pm to 6 am.

## 4. Significance of transpiration on dry matter and minerals accumulation

Fruit transpiration represents the key driver for accumulation of xylem-born minerals, while the growth of fruit depends on phloem stream. However, recently a role of fruit water loss for the phloem unloading into fruit has been proposed. Water losses induce a decrease in fruit water potential (more negative) via an increase in the osmotic concentration and a decrease in the turgor pressure (Morandi et al., 2010b). In this physiological model, as more water is lost by a fruit, more water can be drawn from the phloem and the xylem streams into the fruit itself. However, other regulatory factors, like environmental conditions, related to time of the day, and stem/fruit water potential gradients, may affect fruit inflows. During the central part of the day, the xylem import to the fruit is low, likely due to the high amount of water directed to transpiring leaves, which reach lower water potentials (Morandi et al., 2010b). Xylem inflows cannot balance the high transpiration water losses, with the consequence that fruit shrink (Morandi et al., 2007), increase their concentration and decrease their turgor pressure. This may facilitate translocation and bulk flow phloem unloading into fruit tissues relating fruit transpiration to phloem import, hence transpiration may be viewed as important in determining fruit daily imports of water and dry matter (Morandi et al., 2010b).

Based on this idea, reduction of fruit transpiration would reduce accumulation of dry matter. The Figure 10 shows the effect of reduced transpiration (obtained through bagging which saturates the environment surrounding the fruit leading the relative humidity close to 100%) in apricot and peach fruits.

Optimal mineral nutrition represents a prerequisite for achievement and preservation of high quality plant product. Particular attention should be paid to calcium nutrition due to its involvement in determining tissue mechanical strength and tolerance to biotic and abiotic stresses (Hirschi, 2004). Calcium is a phloem immobile element (Bukovac and Wittwer, 1957), this implies that the amount of Ca reaching a fruit (or a leaf) is almost entirely dependent on supply trough the xylem. Xylem transportation of Ca depends on plant and environmental variables (and their interaction) which often are unfavourable and reduce Ca accumulation in fruit (White and Broadley, 2003).

In kiwifruit, it has been proved the positive effect of windspeed on Ca accumulation (Dichio et al., 2007. That is, for low average windspeeds (0–1.5 m/s), Ca remained almost constant, the level ranging from 18 to 24 mg/fruit. As windspeeds increased beyond this range, the level of mineral rose significantly. Applying a simple cubic model to the data ($y = a + bx^3$) the $r^2$ value obtained for this rise were 0.72 (Fig. 11). For the highest windspeeds of 3.3 m/s (about 12 km/h) the levels of Ca was almost double that for still air (see Fig. 11). In contrast with Ca, the accumulation of fruit K (mass per fruit) showed no evidence at all of any rise with windspeed. Instead K levels were about 300 mg/fruit (ranging from 212 to 380 mg/fruit) and this level was maintained regardless of windspeed. Applying the same cubic model to the K results gave an $r^2$ value of only 0.13.

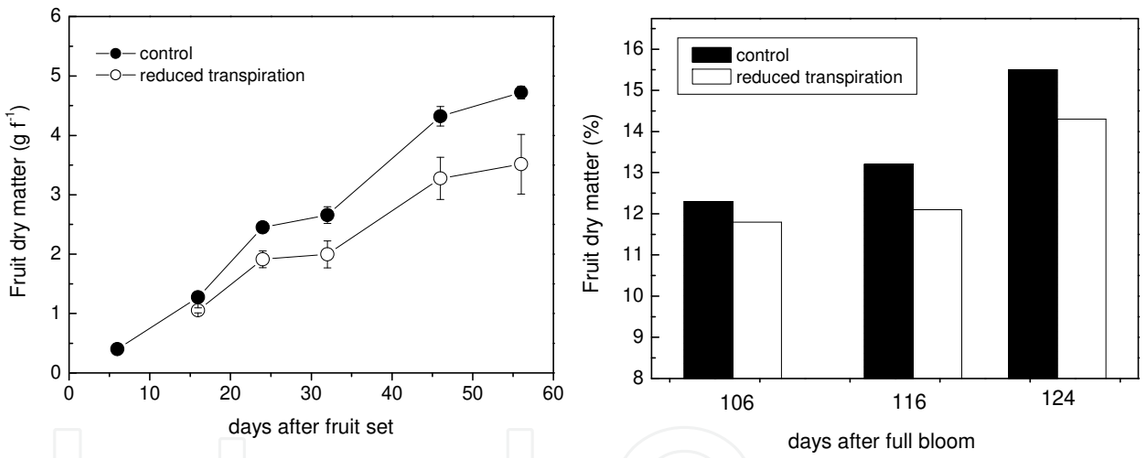


Fig. 10. Dry matter accumulation in fruit of apricot (left) and peach (right) measured in transpiring fruit (control) and under reduced transpiration. (Redrawn from Montanaro et al., 2010 and Morandi et al., 2010b).

Plant water status and transpiration play a key role in supplying the various plant tissue with Ca, particularly those with a low transpiration rate such as fruit (Bangerth, 1979). Mechanisms by which Ca is accumulated into fruit have been searched in a number of fleshy and stone fruit (e.g. apple, tomato, kiwifruit, apricot) (Ferguson and Watkins, 1989; Montanaro et al., 2006 and 2010; Liebisch et al., 2009) with fewer attempts to separate transpirational mechanisms apart from others (e.g. hormonal, metabolic). Recently, a study was undertaken to (i) investigate the relationship between accumulation of Ca and transpiration in developing apricot fruit, and (ii) determine the prominence of transpirational flux upon the whole transpiration-independent transportation processes on Ca nutrition (Montanaro et al., 2010). The hypothesis behind this work was that if the fruit

transpiration is the determining factor of the accumulation of Ca (phloem-immobile element) then the import of Ca would be suppressed by restriction of fruit water loss, while the import of phloem-mobile nutrients (i.e. K and Mg) would not be. To test this hypothesis, the seasonal changes of fruit transpiration and Ca, K and Mg concentrations and accumulation were assessed in fruits left to naturally transpire (control) or under restricted transpiration. Restriction of transpiration was obtained through bag application (Photo 3).

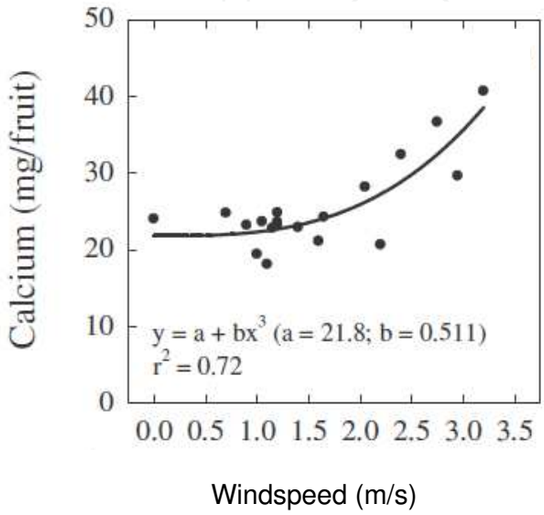


Fig. 11. Whole fruit mineral content for calcium as a function of the mean windspeed to which individual fruit were exposed throughout the growing season. Each point represents a single fruit. (Redrawn from Dichio et al., 2007).

Photo 3. A view of zip-lock bags just mounted on fruit within the canopy of apricot trees (left). After a couple of hours in the microenvironment surrounding the fruit the water vapour condensed (right), hence the relative humidity assumed at saturation point.

Bagging treatments have been widely used to search for fruit response to certain growth condition in terms of skin colour, mineral composition, size, maturity, etc. (Hofman et al., 1997; Amarante et al., 2002). In this study, bags were installed to keep the relative humidity of the air surrounding fruit close to saturation point in order to test whether the limitation of water loss by fruit suppresses the import of some nutrients.

In non-transpiring fruits Ca concentration was significantly affected by restriction of transpiration (it was approximately 30% of that of control fruit), while phloem-mobile elements (K, Mg) were not (Fig. 12).

The evidence that restriction of transpiration did not exert any significant effect on K and Mg concentrations, suggests that the lowest amount of Mg and K accumulated in non-transpiring (bagged) fruit is attributable to the 25% reduction of DM import rather than to the reduced concentration (Fig. 12). At fruit scale, preservation of saturating air humidity significantly lowered the import of Ca due to reduced concentration and reduced DM import according to findings in apple (Tromp and Van Vuure, 1993).

In this study, although plants grew on a Ca-rich soil, the non-transpiring fruits were Ca-deficient compare to control fruits (Fig. 12) and showed the typical visual symptoms of chlorosis. Development of punctual signs of Ca-related disorders have for a long time been associated with mechanisms involved in the movement of Ca within plant parts (Simon, 1977) can conceivably to be explained by differences in transpiration.

The evidence that even though transpiration was negligible, some calcium entered the fruit supports the idea that transpiration is not the only factor governing the movement of Ca through its strong function as driving force of the xylem stream (Bangerth, 1979). Partitioning of Ca amidst plant organs is imputable also to metabolic demand and chemical aspects of the conductive tissues (e.g. adsorption and desorption processes occurring at exchange sites along the walls of the xylem pathway) (McLaughlin and Wimmer, 1999). Calcium delivery to fruit has also been associated to hormonal activities. For example, a mutual relationship between polar basipetal auxin transport and acropetal Ca transport has been reported for tomato, apple and avocado (Stahly and Benson, 1970; Bangerth, 1976; Banuelos et al. 1987; Cutting and Bower, 1989). However, there is still limited information to discriminate (and quantify) the effect of these transpiration-independent stimuli in Ca nutrition. Interpretation of the ratio between concentrations detected in non-transpiring and control fruit would be valuable for assessing of the prominence of transpiration on Ca nutrition.

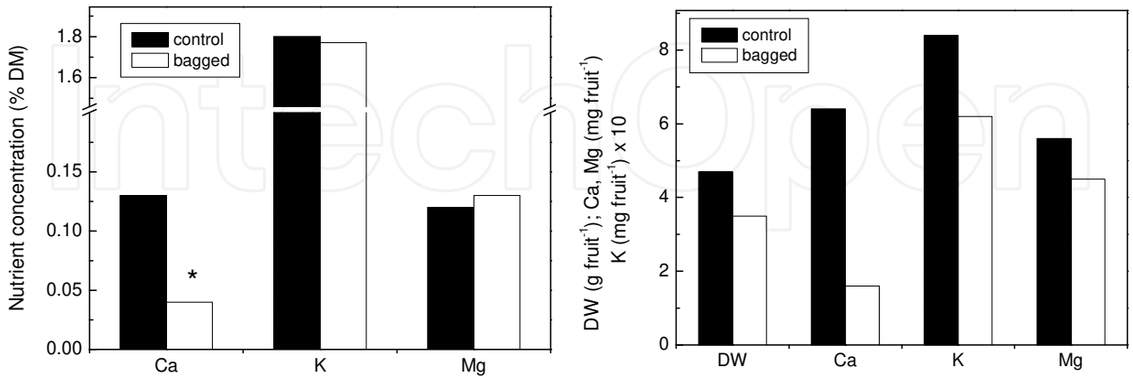


Fig. 12. Concentrations of calcium (Ca), potassium (K) and magnesium (Mg) (left) and amounts per fruit of dry matter (DW), Ca, K and Mg measured at harvest in naturally transpiring apricot fruit (control) and non-transpiring (bagged) fruit. (Redrawn from Montanaro et al., 2010). (For the left figure, * indicates a significant difference at $p < 0.05$, Student's *t*-test between treatments).

In the case of Ca, that ratio was 0.45 about 50 days after bags were positioned on a whole-bagged period basis. Hence, the fruit transpiration accounted for 55% of the Ca concentration gained by fruit. By contrast, that ratio for K and Mg was not severely affected by the restriction of transpiration, so that the ratio was on average 0.97 and 0.91 for K and Mg respectively, indicating a weak effect of restricted transpiration. For K and Mg the transpiration-independent factors operated as well, however their high phloem mobility does not allow for their unmasking.

Calcium movement in plants has been extensively studied in relation to factors such as transpiration flux, hormonal activities, nutrient demand and chemical properties of the conductive system (Bangerth, 1979; Banuelos et al., 1987; Cutting and Bower, 1989; McLaughlin and Wimmer, 1999), however information is still limited to discriminate the relative prominence of each individual factor. Our data were insufficient to indicate the transpiration-independent mechanism(s) by which 45% of the Ca concentration accrued under high humidity condition, but the hormones were possibly involved. For example, in the case of tomato fruit, the polar basipetal auxin transport has been indicted to promote about 15% of Ca concentration in fruit kept at saturating RH (Banuelos et al., 1987). In addition, in kiwifruit a correlation between Ca accumulation and auxin has been reported (Fig. 13).

Calcium accumulation in fruit could be affected also by other factors such as the position of fruiting sites within the canopy. For example, apple fruit in the upper parts of the canopy tend to have lower Ca concentrations than those in the lower parts, the age (and others features) of leaves of fruiting branches may also affect Ca accumulation in fruit (Volz et al., 1996). It as been observed in apple fruit that reducing the leaf:fruit ratios at specific fruiting sites resulted in lower Ca concentrations, with the activity (presumably transpiration) of spur leaves being especially important (Volz et al., 1996; Lang and Volz, 1998).

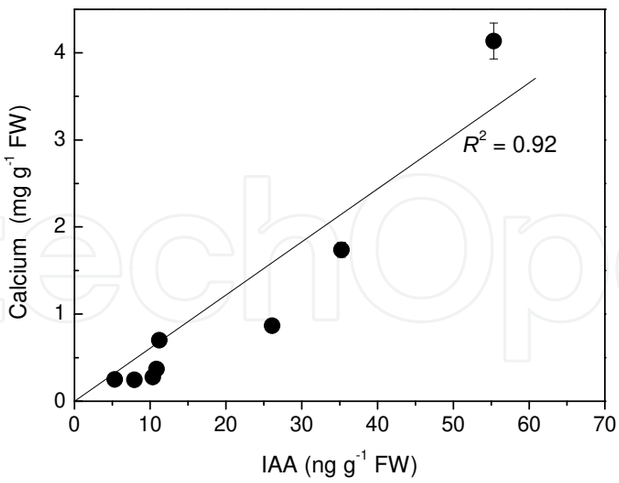


Fig. 13. Correlation between calcium and auxin (IAA) detected in approx. 8-week-old kiwifruit berry (Redrawn from Sorce et al., 2011).

In kiwifruit, relationships exist between fruiting position, leaf:fruit ratios and fruit mineral concentrations. Thorp et al. (2003) demonstrated that a relatively small shift in leaf:fruit ratio was sufficient to affect fruit Ca concentrations, but only in regions of the vine with relatively

low fruit mineral levels and low leaf areas. In the same study, it has been highlighted the role of cane size on that relationship. Large diameter canes have axillary shoots with relatively high leaf areas compared with shoots on small diameter canes, especially at basal positions on the cane (Thorp et al., 2003).

Mechanisms behind the effect of leaves on Ca accumulation in fruit need to be clarify. It should be hypothesised that Ca accumulation in a plant organ is proportional to the sap flow unloaded by the organ and to the relative Ca concentration in sap:

$$Ca = [Ca] \times SAP_{Flow}$$

Hence, transpiration of leaves may helps to drive more sap which carries nutrients. To explain the effect of fruit position and shoot type on Ca accumulation, it could be evoked that the relative rate of Ca use along the transport pathway may affect [Ca]. Hence, fruits located at the tip of a shoot tend to receive a Ca-poor sap compare to fruits at the base.

## 5. Acknowledgments

This work was funded by Ministero dell'Istruzione, dell'Università e della Ricerca - Prin2009 grant.

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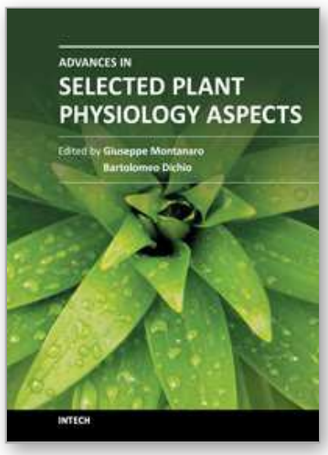


**Advances in Selected Plant Physiology Aspects**

Edited by Dr. Giuseppe Montanaro

ISBN 978-953-51-0557-2
Hard cover, 388 pages
**Publisher** InTech
**Published online** 25, April, 2012
**Published in print edition** April, 2012

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