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## **Ecophysiological models of fruit quality: a challenge for peach and tomato**

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### **Abstract**

**Fruit quality at harvest is a complex trait, including size, overall flavour (taste and texture) and visual attractiveness (colour, shape), which depend on both genotype and environment. The improvement of fresh product quality is slowed down by this complexity. It is expected that the development of process-based models and their integration in ecophysiological models should facilitate quality management, provided that integration properly accounts for interactions among biological processes. Here we describe some process-based models developed on peach and tomato fruits, which predict final fruit size and composition in primary compounds. Perspectives of integration of such models are discussed.**

### **INTRODUCTION**

Quality became a generic term, which is alternately used to design diverse types of quality: commercial, organoleptic, nutritional and sanitary, which concern in turn producers, distributors and consumers (Shewfelt, 1999). In the past decades, the improvement of both genetic material and technical crop management in horticulture, favoured the producers and distributors, by derivation towards resistant and productive cultivars and long life products, whereas consumer preferences were mostly ignored. Recently, the social demand for improving the taste of fresh product gave rise to new research, especially for fruits. However this improvement, while preserving the previous selected traits, is slowed down by the complexity of quality traits.

In horticulture, most crop or plant models are driven by processes of carbon assimilation and predict allocation among sinks according to specific rules of priority (Marcelis, 1993; Heuvelink and Bertin, 1994). Models dedicated or contributing to the prediction of water balance at plant or fruit level (Lee, 1990; Bussièrès, 1994; Génard and Huguet, 1997; Leonardi *et al.*, 2000; Bussièrès, 2002; Gibert *et al.*, 2005) initiated a move towards quality model, as water accumulation is involved in many criteria of quality, in particular organ size and dilution of accumulated compounds. Table 1 gives a non-exhaustive overview of some of the recent models directly or indirectly dedicated to the prediction of product quality in horticulture. They mainly concern fruit size and dry matter content and the occurrence of blossom end rot (BER) in relation to xylem fluxes. Other quality traits have been seldom subject to modelling, because they are complex traits involving many interacting biological processes during the successive phases of fruit development.

Considering the huge domain of food quality, and the large application area of modelling, this paper focuses on the elaboration of few criteria of quality, *i.e.* fruit size,

water and dry matter contents, composition in sugars and acids, based on our experience on peach and tomato fruit. Final quality is determined through the successive phases of fruit development: a first period of intensive cell division, a second period of cell expansion and rapid growth, and a third period of maturation. Only mechanistic models relative to the first two periods will be presented, according to the organizational level at which they operate. The third period has been hardly described at fruit level, though a model of ethylene emission in fruit has been recently proposed (Génard and Gouble, 2005) which may feed future models, as ethylene is a driving factor of most processes during maturation. Post-harvest evolution of quality will not be considered, though quite determinant for the final perception of quality by consumers.

## **MODELLING PROCESSES INVOLVED IN THE VARIATIONS OF FRUIT SIZE AND DESCRIBED AT THE CELL LEVEL**

Increase in fruit volume largely results from the development of pericarp tissue (Ho and Hewitt, 1986), achieved through two important processes: the production of new cells and cell expansion. During the cell expansion period, DNA endoreduplication occurs in many plant organs and species and may be involved in the control of fruit growth and sugar accumulation (Bergervoet *et al.*, 1996; Traas *et al.*, 1998). Indeed positive relationships between endoreduplication and cell size have been reported in a number of species and organs (Melaragno *et al.*, 1993; Cheniclet *et al.*, 2005). Thus models describing these basic processes should be essential to predict fruit quality.

### **Models of cell division**

A discrete model of cell multiplication has been developed to describe the dynamic of cells during the early division period of tomato fruit (Bertin *et al.*, 2003). It considers two phases: in the first one all cells are dividing and the total cell number increases exponentially; in the second phase, which starts before anthesis, the proliferation activity progressively declines, giving rise to non-dividing or growing cells. The time at which the proliferative activity diminishes, its rate of decrease and the length of the cell cycle are the three model parameters. It was hypothesized that the time at which proliferative activity diminishes is fruit position dependent. Genetic and environmental controls should be integrated in this model to provide realistic prediction of cell population dynamics in fruit. This model is compatible with other continuous phenomenological models proposed in the literature for other organs (e.g. Thornley, 1981). Other complex mathematical models describing the molecular basis for mitotic control have been developed (e.g. Ciliberto and Tyson, 2000), but the high number of parameters (up to 30) would make difficult the application at fruit level.

### **Models of cell expansion**

After cell division ceased, fruit growth results from cell growth and expansion, which rely on the import of dry material and water. Variations in fruit volumes occur at diverse time scales: long term (days) irreversible or plastic variations are determinant for cell expansion (Green *et al.*, 1971), whereas short-term (hours) reversible or elastic variations (Ortega, 1990) reflect short-term responses of phloem and xylem fluxes to fruit environment. Many works intending to model the plastic growth of cell or tissue used the Lockart (1965) equation, which links the volume variation rate of cell or tissue to the

irreversible cell wall extensibility ( $\phi$ ;  $\text{MPa}^{-1} \text{ h}^{-1}$ ) and turgor pressure ( $P$ ; MPa) above a given yield threshold ( $Y$ ; MPa) that must be exceeded for irreversible wall extension:

$$\frac{1}{V} \times \frac{dV}{dt} = \phi \times (P - Y) \quad [1]$$

This model allows analyzing cell growth in response to water relations and cell rheological properties, which prevail in the response of cell growth to environmental stress (Jones and Tardieu, 1998). To account for both plastic and elastic variations of fruit size, equation [1] may be completed as follows (Ortega, 1990):

$$\frac{1}{V} \times \frac{dV}{dt} = \phi \times (P - Y) + \frac{1}{\varepsilon} \times \frac{dP}{dt} \quad [2]$$

where  $\varepsilon$  is the volumetric elastic modulus (MPa).

Other hypotheses have been proposed. Mingo *et al.* (2003) demonstrated that fruit growth is affected by water stress without changes in fruit cellular turgor, and proposed a regulation of cell expansion by sub-epidermal pH for plants growing in drying soil. Thus turgor-based models may not be sufficient for the prediction of cell and fruit growth, especially under stress growth conditions.

### Models of DNA endoreduplication

Endoreduplication is an incomplete cell cycle that leads to the increase of nuclear DNA content (D'Amato, 1964), up to  $256C$  ( $C$  is the haploid nuclei DNA content) in tomatoes (Bergervoet *et al.*, 1996). Very few models predict endoreduplication in plant tissue, and its role in the regulation of cell size and sink function. A mathematical model of DNA endoreduplication has been proposed (Schweitzer *et al.*, 1995; Lee *et al.*, 2004) and applied to tissue slightly endoreduplicated. Recently, a mechanistic model coupling cell multiplication and DNA endoreduplication, has been developed (Bertin *et al.*, in preparation) and applied to tomato pericarp cells. It takes into consideration the progressive decrease of the cell proliferating capacity after each mitotic cycle, and the durations of complete and incomplete cycles. Non-proliferating cells either fully stop the reduplication, or irreversibly switch to repeated synthesis of DNA. The model describes the evolution of cell cohorts at diverse biological states in the tissue. It is assumed that the proportion of cells that switch from proliferative to non proliferative state increases during the pericarp development, whereas the fluxes between two successive classes of DNA content are constant and dependent of the time needed to perform an incomplete cycle.

### MODELLING PROCESSES INVOLVED IN WATER AND CARBON BALANCE AND DESCRIBED AT FRUIT LEVEL

A number of processes affecting fruit quality are described at the fruit level. Those driving the carbon and water balance are of particular importance, because they are directly involved in the growth of fleshy fruits, mainly constituted of water (95% in mature tomato), and in the accumulation and dilution of carbon compounds. Modelling the actual influx and efflux of carbon and water into and from fruit is complex, including transport through the pedicel and epidermis, phloem unloading and regulation of internal osmotic and hydrostatic pressures. Most current models linked the water influx to fruit to the water potential difference between stem and fruits, and to the hydraulic resistance in the pathway (Lee 1989; Johnson *et al.* 1992; Bussi eres 1994). Models presented below present integrative approaches.

### Models of water and dry matter import in fruit

Bussières (2002) linked a sub-model of water import in tomato fruit and a sub-model of water flow in the fruit pedicel. The sub-model of water import ascribes the water transfer pathways into fruit to cylindrical filters, the ends of which are distributed into the fruit (Bussières, 1994). The water import rate through the transfer pathway is inversely proportional to the pathway length and proportional to the difference between the water potential  $\Phi_D$  at the junction of the pedicel with the fruit and the water potential in the fruit. The last depends on the osmotic fruit potential  $\Phi_{osm}$  and on the tissue resistance, which increases with the distance between the end of the pathway and the fruit surface. After integration of all transfer pathways at the entire fruit level, the water import rate per unit surface area of fruit is a decreasing linear function of the fruit radius. The sub-model of flow in the fruit pedicel (Fig. 1) considers that water, transferred mainly through the phloem, is the sum of calyx transpiration and water import in the fruit. This model gives adequate predictions of fruit fresh weight and dry matter content (Fig. 2).

Fishman and Génard (1998) proposed a biophysical model of water and dry matter import in peach fruit. It combines the xylem and phloem fluxes of water and carbon to fruit (Fig. 3A) and the cell expansion rate governed by the Lockart equation (eqn.1). Water and carbon balances are calculated, considering that: (i) transpiration depends on fruit surface, permeation coefficient of the cuticle, temperature and difference of humidity between air and fruit. (ii) respiration is the sum of maintenance and growth respiration. The fruit is considered as one big compartment separated from exterior (xylem or phloem tissue) by a composite membrane and flows across this membrane are described by thermodynamic equations, involving hydraulic conductivity of the membrane, differences in hydraulic and osmotic pressures on both sides of it, and impermeability of membrane to solutes. The total uptake of carbon from phloem is the sum of contributions from mass flow, passive diffusion, and active transport. This model has been successfully applied to predict the seasonal growth of dry and fresh masses of peach fruit for different leaf:fruit ratios (Fig. 3B).

### Model of sugar metabolism

Once imported into fruits, carbon assimilates are partially used for growth and maintenance, and the rest is stored under different forms. The nature of imported and stored carbon compounds is species-dependent and genetically determined. Models of sugar metabolism in fruit are rare, and the SUGAR model (Génard and Souty, 1996) has laid the foundations for many developments. It simulates the partitioning of a given amount of carbon unloaded from the phloem into sucrose, sorbitol, glucose, fructose, other compounds, and  $\text{CO}_2$  produced by respiration (Fig. 4). The fruit is assimilated to one single compartment, and the flux of carbon between two compounds is assumed to be proportional to the amount of carbon in the source one. The SUGAR model has been used to predict environmental effect on peach sugar concentration (Génard and Huguet, 1997; Génard *et al.*, 1999) and to analyze the seasonal variations in individual sugars (Génard *et al.*, 2003).

### Model of acid content

Malic and citric acids are dominant acids in most fruits (Tucker, 1993). A model of citrate metabolism at cellular level has been developed to predict whole fruit concentration during the period of rapid fruit growth (Lobit *et al.*, 2003). As most organic

acids, citrate is stored in the vacuoles of mesocarp cells and permanently exchanged between vacuole and cytosol, where it is synthesized involving a set of mitochondrial enzymes. The model relies on a simplified representation of the mitochondrial citrate cycle, considering only three intermediates, citrate, malate and pyruvate (Fig. 5A). Fluxes between two compounds are assumed to depend on enzyme activity, temperature, origin and target compound concentrations and a general regulation factor accounting for complex metabolic regulations in the successive steps of the citrate cycle. CO<sub>2</sub> produced by these reactions is assimilated to respiration (Re). Transports between cytosol and mitochondria are driven by concentration gradients between the two compartments and depend on temperature and transport activity. Number and activity of mitochondria are considered as constant during the modelled period. Furthermore, all enzymatic and transport activities were assumed to be proportional to the mesocarp dry weight after the end of the cell division period (one month after bloom). Mathematical development led to a single equation giving the net production rate of citrate ( $\phi$  mol day<sup>-1</sup>):

$$\phi = a \times DW_1 \times (1 + b \times (T - T_0)) \times (1 + c \times (T - T_0)) + d \times \frac{Re}{DW_1} \quad [3]$$

where  $a$  (mol g<sup>-1</sup> d<sup>-1</sup>),  $d$  (g mol<sup>-1</sup> d<sup>-1</sup>),  $b$  and  $c$  (°K<sup>-1</sup>) are coefficients, Re is respiration (mol CO<sub>2</sub> fruit<sup>-1</sup> d<sup>-1</sup>) and DW<sub>1</sub> is mesocarp dry weight (g).

Providing daily input of respiration and fresh and dry weight increase, this model predicts well the seasonal variations of citrate concentrations in peach fruit (Fig. 5B).

On the contrary to citric acid, the accumulation of malic acid is species-dependent and can rapidly fluctuate independently from its metabolism enzyme activity. Lobit et al. (2006) recently proposed a model of malic acid accumulation in vacuoles of mesocarp cells, which describes the transport of malate between cytosol and vacuole as a function of temperature, potassium and organic acid concentrations in the vacuole. Despite the complex regulation of malate accumulation, this model succeeded to integrate physiological knowledge in a manner compatible with fruit quality models, as the driving variables can be easily measured at fruit or tissue level.

## COUPLING PROCESSES ACROSS ORGANIZATIONAL LEVELS

The development of process-based models is an initial phase, selecting and describing important processes in the control of fruit quality. Next step for progressing in this field will be the integration of several processes with the description of complex interactions and feedback mechanisms across the various organizational levels. Up to now, most models of fruit quality have simplified the complex fruit system either by considering one single big cell supplied by the plant with carbon and water, or by assuming average cells in homogeneous tissue. Actually fruits are made of different tissues, which are usually composed of heterogeneous cell populations, and cells include several compartments with specific functions. Compromises are unavoidable to give realistic predictions of fruit quality traits with low number of parameters, which in turn should be easily measured or estimated.

Beside the plant level not considered in this presentation, the upper level described by quality model is the whole fruit (organ level), with processes mainly involved in the balance of carbon and water. It is thus assumed that all tissues underwent similar limitations and/or that one tissue predominantly controls the whole fruit behaviour. At a lower scale, models hardly consider the development of differentiated tissue (epidermis, pericarp, jelly or stone), though they should certainly consider this level in the future. For

instance in tomato, the literature has outlined the role of rheological properties of the cuticle and epidermal cells, in the control of fruit growth (Thompson et al 1998; Andrew *et al.*, 2002; Bargel and Neinhuis, 2005). To our knowledge, no current model describes the limitation of growth by epidermis properties, even though cuticle thickness is involved in taste perception. On the other hand, allometric proportions of tissues of different composition likely affect the overall flavour (e.g. more citric acid in jelly tissue than in pericarp of tomato) and the fruit firmness (Davies and Hobson, 1981). Though these two levels may be sufficient to model a large number of fruit quality traits, the cell level may be profitable, because cell number and size control the final fruit size (Mizukami, 2001), and above all because it may be expected that for a given fruit size, low number of large cells would have different impact on fruit composition or texture than large number of small cells. This hypothesis has to be explored.

A first step towards integration and simulation of multiple traits of quality has been passed in the virtual peach fruit model developed by Lescourret and Génard (2005). This model predicts size, dry matter content and sugar composition of peach fruit in response to environmental fluctuations by coupling 3 sub-models: (i) a carbon sub-model which calculates daily carbon availability (assimilation and remobilisation from reserves) and allocates carbon among vegetative and reproductive organs, thus determining the daily carbon flux to any average fruit of the stem. (ii) the SUGAR model (Génard and Souty, 1996; Génard *et al.*, 2003) used this daily influx carbon as input to simulates the metabolic transformations among individual sugars. (iii) a water sub-model developed from Fishman and Génard (1998) in which fruit osmotic pressure is calculated from sugar content simulated by the SUGAR sub-model.

A difficulty of integration is the determination of driving factors or variables and the consideration of interactions and feedback mechanisms. In case of the peach virtual fruit, a theoretical demand for carbon, based on potential fruit growth at high leaf:fruit ratio, determines the carbon entrance in the fruit, which affects the fruit osmotic potential, which in turn affects the entrance of water allowing volume increase. Actually water and carbon simultaneously enter the fruit. Thus permanent adjustments occur to maintain cell turgor, integrating cell expansion and growth, dilution of carbon by water, and sugar accumulation and compartmentation. Similarly, enzymatic activity controlling sugar metabolism and compartmentation exerts a feedback control on the rate of carbon import in fruit (Ho, 2003). However, simplifications are necessary among the numerous steps of regulation, especially at the cell level, because a number of parameters can not be easily measured, and dynamic models including too many parameters may be incompatible with current methods of estimation.

## CONCLUSIONS - APPLICATIONS OF ECOPHYSIOLOGICAL MODELS FOR THE CONTROL OF FRUIT QUALITY

Ecophysiological models should have the potential to mimic complex systems, such as fruit in interaction with its environment, by integrating processes at diverse organizational levels. In this, they represent a powerful tool to understand plant or crop behavior by pointing out key-processes and/or key developmental stages involved in the control of complex traits (Struik *et al.*, 2005). In particular, an issue of ecophysiological models has been the design of virtual plants or virtual fruits, used to perform theoretical experiments and to point out emergent properties of the system (Lescourret and Génard, 2005), to design new ideotypes adapted to specific environments (Kropff *et al.*, 1995) or

to analyze genotype x environment interactions (Reymond *et al.*, 2003; Tardieu, 2003). The potential use of ecophysiological models to analyse Quantitative Trait Loci (QTL), has recently emerged (Yin *et al.*, 1999; Quilot *et al.*, 2005), and let assume new opportunities to improve breeding strategies (Yin *et al.*, 2004). Indeed QTL-based models may first inform on the functional role of QTL associated with potential candidate genes, and secondly predict fruit growth and composition of any virtual genotype defined by its alleles at the different identified QTLs. For this issue, models should be validated under a wide range of environmental conditions and QTL information has to be incorporated. This implies extensive experimentation to define genetic coefficients (parameters genotype-specific and environment-independent), and to provide each genotype with one set of parameters.

Yet more research is still necessary because modeling fruit quality implies the integration of a great number of mechanisms and levels, for which knowledge is still incomplete. Therefore modeling activity and research on the implicated processes have to progress simultaneously, which will be a challenge for the future.

### Literature Cited

- Andrews, J., Adams, S.R., Burton, K.S. and Evered, C.E. 2002. Subcellular localization of peroxidase in tomato fruit skin and the possible implications for the regulation of fruit growth. *J. Exp. Bot.* 53:2185-2191.
- Austin, P.T., Hall, A.J., Gandar, P.W., Warrington, I.J., Fulton, T.A. and Halligan, E.A. 1999. A Compartment Model of the Effect of Early-season Temperatures on Potential Size and Growth of 'Delicious' Apple Fruits. *Ann. Bot.* 83:129-143.
- Bargel, H. and Neinhuis, C. 2005. Tomato (*Lycopersicon esculentum* Mill.) fruit growth and ripening as related to the biochemical properties of fruit skin and isolated cuticle. *J. Exp. Bot.* 56:1049-1060.
- Bar-Tal, A., Fishman, S., Aloni, B. and Génard, M. 1999. Simulation of environmental effects on Ca content in pepper fruit. *Acta Hort.* 507:253-262.
- Bergervoet, J.H.W., Verhoeven, H.A., Gilissen, L.J.W. and Bino, R.J. 1996. High amounts of nuclear DNA in tomato (*Lycopersicon esculentum* Mill.) pericarp. *Plant Sc.* 116:141-145.
- Bertin, N., Fishman, S. and Génard, M. 2003. A model for early stage of tomato fruit development: cell multiplication and cessation of the cell proliferative activity. *Ann. Bot.* 92:65-72.
- Bussièrès, P. 1994. Water import rate in tomato fruit: a resistance model. *Ann. Bot.* 73:75-82.
- Bussièrès, P. 2002. Water import in the young tomato fruit limited by pedicel resistance and calyx transpiration. *Funct. Plant Biol.* 29:631-641.
- Cheniclet, C., Rong, W.Y., Causse, M., Frangne, N., Bolling, L., Carde, J.P. and Renaudin, J.P. 2005. Cell expansion and endoreduplication show a large genetic variability in pericarp and contribute strongly to tomato fruit growth. *Plant Physiol.* 139 (in press).
- Ciliberto, A. and Tyson, J.J. 2000. Mathematical model for early development of the sea urchin embryo. *Bulletin of Mathematical Biology* 62:37-59.
- D'Amato, F. 1964. Endopolyploidy as a factor in plant tissue development. *Caryologia* 17:41-52.
- Davies, J.N. and Hobson, G.E. 1981. The constituents of tomato fruit – the influence of environment, nutrition and genotype. *Crit. Rev. Food Sci. Nutr.* 15: 205–280.

- Dayan, E., Presnov, E., Fuchs, M. and Ben Asher, J. 2002. Rose growth: a model to describe green house rose growth. *Acta Hort.* 593:63-70.
- Fishman, S. and Génard, M. 1998. A biophysical model of fruit growth: simulation of seasonal and diurnal dynamics of mass. *Plant Cell Env.* 21:739-752.
- Génard, M. and Gouble, B. 2005. ETHY. A theory of fruit climacteric ethylene emission. *Plant Physiol.* 139:531-545.
- Génard, M. and Huguet, J.G. 1997. Modelling the effect of irrigation on peach fruit quality. *Acta Hort.* 449:161-168.
- Génard, M., Lescourret, F., Gomez, L. and Habib, R. 2003. Changes in fruit sugar concentrations in response to assimilate supply, metabolism and dilution: a modelling approach applied to peach fruit (*Prunus persica*). *Tree Physiol.* 23:373-385.
- Génard, M., Reich, M., Lobit, P. and Besset, J. 1999. Correlations between sugar and acid content and peach growth. *J. Hort. Sci. Biotech.* 74:772-776.
- Génard, M. and Souty, M. 1996. Modeling the peach sugar contents in relation to fruit growth. *J. Am. Soc. Hort. Sci.* 121:1122-1131.
- Gibert, C., Lescourret, F., Génard, M., Vercambre, G. and Perez Pastor, A. 2005. Modelling the effect of fruit growth on surface conductance to water vapour diffusion. *Ann. Bot.* 95:673-683.
- Green, P.B., Erickson, R.O. and Buggy, J. 1971. Metabolic and physical control of cell elongation rate. *Plant Physiol.* 47:423-430.
- Gutierrez Colomer, R.P., Gonzalez-Real, M.M. and Baille, A. 2006. Dry matter production and partitioning in rose (*Rosa hybrida*) flower shoots. *Scientia Horticulturae Amsterdam* 107:284-291.
- Hamer, P.J.C. 2002. Analysis of strategies for reducing calcium deficiencies in glasshouse grown tomatoes: model functions and simulations. *Agr. Sys.* 76:181-205.
- Heuvelink, E. and Bertin, N. 1994. Dry matter partitioning in a tomato crop: comparison of two simulation models. *J. Hort. Sci.* 69:885-903.
- Heuvelink, E.P., Lee, J.H. and Carvalho, S.M.P. 2001. Modelling visual product quality in cut chrysanthemum. *Acta Hort.* 566:77-84.
- Ho, L.C. 2003. Genetic and cultivation manipulation for improving tomato fruit quality. *Acta Hort.* 613:21-31.
- Ho, L.C. and Hewitt, J.D. 1986. Fruit development. P. 201-240. In: J.G. Atherton and J. Rudich (eds). *The Tomato Crop*. Chapman and Hall, London.
- Ho, L.C., Grange, R.I. and Picken, A.J. 1987. An analysis of the accumulation of water and dry matter in tomato fruit. *Plant Cell Environ.* 10:157-162.
- Johnson, R.W., Dixon, M.A. and Lee, D.R. 1992. Water relations of tomato during fruit growth. *Plant Cell Environ.* 15:947-953.
- Jones, H.G. and Tardieu, F. 1998. Modelling water relations of horticultural crops: a review. *Scientia Horticulturae Amsterdam* 74:21-46.
- Kläring, H.P., Schonhof, I. and Krumbein, A. 2001. Modelling yield and product quality of Broccoli as affected by temperature and irradiance. *Acta Hort.* 566:85-90.
- Kropff, M.J., Haverkort, A.J., Aggarwal, P.K. and Kooman, P.L. 1995. Using systems approaches to design and evaluate ideotypes for specific environments. In: J. Bouma, B.A.M. Bouman, J.C. Luyten and H.G. Zandstra (eds.). *Eco-regional approaches for sustainable land use and food production*. Dordrecht, Netherlands: Kluwer Academic Publ. 417-435.

- Lechaudel, M., Génard, M., Lescourret, F., Urban, L. and Jannoyer, M. 2005. Modelling effects of weather and source-sink relationships on mango fruit growth. *Tree Physiol.* 25:583-597.
- Lee, D.R. 1989. Vasculature of the abscission zone of tomato fruit: implications for transport. *Can. J. Bot.* 67:1898-1902.
- Lee, D.R. 1990. A unidirectional water flux model of fruit growth. *Can. J. Bot.* 68:1286-1290.
- Lee, H-C., Chiou, D-W., Chen, W-H., Markhart, A.H., Chen, Y-H. and Lin, T-Y. 2004. Dynamic of cell growth and endoreduplication during orchid flower development. *Plant Sc.* 166:659-667.
- Leonardi, C., Baille, A. and Guichard, S. 2000. Predicting transpiration of shaded and non shaded tomato fruits under greenhouse environments. *Scientia Hortic-Amsterdam* 84:297-307.
- Lescourret, F. and Génard, M. 2005. A virtual peach fruit model simulating changes in fruit quality during the final stage of fruit growth. *Tree Physiol* 25:1-13.
- Lobit, P., Génard, M., Wu, B.H., Soing, P. and Habib R. 2003. Modelling citrate metabolism in fruits: response to growth and temperature. *J Exp. Bot.* 54:2489-2501.
- Lobit, P., Génard, M., Soing, P. and Habib R. 2006. Modelling malic acid accumulation in fruits: relationships with organic acids, potassium, and temperature. *J Exp. Bot.* 57:1471-1483.
- Lockart, J.A. 1965. An analysis of irreversible plant cell elongation. *J. Theor. Biol.* 8:264-275.
- Marcelis, L.F.M. 1993. Simulation of biomass allocation in greenhouse crops – a review. *Acta Hort.* 328:49-67.
- Marcelis, L.F.M. and Gijzen, H. 1998. Evaluation under commercial conditions of a model of prediction of the yield and quality of cucumber fruits. *Scientia Hortic. Amsterdam* 76:171-181.
- Melaragno, J.E., Mehrotra, B. and Coleman, A.W. 1993. Relationship between endopolyploidy and cell size in epidermal tissue of Arabidopsis. *The Plant Cell* 5:1661-68.
- Mingo, D.M., Bacon, M.A. and Davies, W.J. 2003. Non-hydraulic regulation of fruit growth in tomato plants (*Lycopersicon esculentum* cv. Solairo) growing in drying soil. *J. Exp. Bot.* 54:1205-1212.
- Mizukami, Y. 2001. A matter of size: developmental control of organ size in plants. *Curr. Opin. Plant Biol.* 4:533-539.
- Ortega, J.K.E. 1990. Governing equations for plant cell growth. *Physiol. Plantarum* 79:116-121.
- Quilot, B., Kervella, J., Génard, M. and Lescourret F. 2005. Analysing the genetic control of peach fruit quality through an ecophysiological model combined with a QTL approach. *J. Exp. Bot.* 56:3083–3092.
- Reymond, M., Muller, B., Leonardi, A., Charcosset, A. and Tardieu, F. 2003. Combining quantitative trait loci analysis and an ecophysiological model to analyze the genetic variability of the reponses of maize leaf growth to temperature and water deficit. *Plant Physiol.* 131:664-675.
- Schwarz, D., Kläring, H.P., Ingram, K.T. and Hung, Y.C. 2001. Models-based control of nutrient solution concentration influences tomato growth and fruit quality. *J. Am. Soc. Hortic. Sci.* 126:778-784.

- Schweizer, L., Yerk-Davis, G.L., Phillips, R.L., Srienc, F. and Jones, R.J. 1995. Dynamic of maize endosperm development and DNA endoreduplication. *Proc. Natl. Acad. Sci.* 92:7070-7074.
- Seginer, I., Bleyaert, P. and Breugelmans, M. 2004. Modelling ontogenic changes of nitrogen and water content in lettuce. *Ann. Bot.* 94:393-404.
- Shewfelt, R. 1999. What is quality? *Postharvest Biol. Tec.* 15:197-200.
- Struik, P.C., Yin, X. and de Visser, P. 2005. Complex quality traits: now time to model. *Trends Plant Sci.* 10:513-516.
- Tardieu, F. 2003. Virtual plants: modeling as a tool for the genomics of tolerance to water deficit. *Trends Plant Sci.* 8:9-14
- Thompson, D.S., Davies, W.J. and Ho, L.C. 1998. Regulation of tomato fruit growth by epidermal cell walls enzymes. *Plant Cell Environ.* 21:589-599.
- Thornley, J.H.M. 1981. Organogenesis. In: Rose DA. and Charles-Edwards DA. (eds). *Mathematics and Plant Physiology*. Academic Press, London. 49-65.
- Traas, J., Hülskamp, M., Gendreau, E. and Höfte, H. 1998. Endoreduplication and development: rule without dividing. *Curr. Opin. Plant Biol.* 1:498-503.
- Tucker, G.A. 1993. Introduction. In: GB. Seymour, JE. Taylor and GA. Tucker (eds.), *Biochemistry of fruit ripening*. Chapman and Hall, London. 1-51.
- Yin, X., Stam, P., Dourleijn, C.J. and Kropff, M.J. 1999. AFLP mapping of quantitative trait loci for yield-determining physiological characters in spring barley. *Theoretical and Applied Genetics* 99:244-253.
- Yin, X., Struik, P.C. and Kropff, M.J. 2004. Role of crop physiology in predicting gene-to-phenotype relationships. *Trends Plant Sci.* 9:426-432.

Table 1. Some examples of research focussed on modelling product quality of some horticultural species from the recent literature.

Species	Quality traits	Organs	Modeled levels	Mechanisms considered	Crop conditions	References
<b>Apple</b>	size	Fruit	fruit, fruit compartments	cell number, cell expansion, transfer, assimilate allocation, size-dependence	controlled cabinets	Austin et al. 1999
<b>Broccoli</b>	dry matter content, glucoraphanin	plant	canopy, plant	photosynthesis, assimilate partitioning, growth	greenhouse	Kläring, et al. 2001
<b>Chrysanthemum</b>	global visual quality	plant, flower	plant, flower	photosynthesis, assimilate partitioning, growth	greenhouse	Heuvelink et al. 2001
<b>Cucumber</b>	size, harvest stage	fruit classes	canopy, plant, fruit	light transmission, photosynthesis, assimilate partitioning, fruit growth and dry matter content	greenhouse	Marcelis et al. 1998
<b>Lettuce</b>	nitrate concentration	plant	plant, tissue compartments	photosynthesis, assimilate partitioning, respiration, growth, N, C and water fluxes to the compartments	greenhouse, hydroponics soil	Seginer et al. 2004.
<b>Mango</b>	dry matter mass	mean fruit of age classes	branch, fruit	photosynthesis, respiration, assimilate reserve partitioning, growth, water, N, C fluxes	field, pots	Léchaudel et al. 2005
<b>Peach</b>	ratio flesh weight to total, size, sugars	mean fruit	stem, fruit stone and flesh	carbon, sugar and water sub-models, assimilate and reserve allocations	field, soil	Lescourret et al. 2005
_____	citrate concentration	mean fruit	mesocarp, fruit	citrate cycle, transport and enzyme activities, fruit respiration	field, soil	Lobit et al. 2003
_____	Ratio flesh weight /total, size, sugars	mean fruit	plant, fruit	carbon, sugar and water sub-models, QTL	field, soil	Quilot et al. 2005
<b>Pepper</b>	BER, fruit cracking	mean fruit	canopy, plant, fruit	carbon, calcium and water fluxes in xylem and phloem, transpiration	greenhouse	Bar-Tal et al. 1999
<b>Tomato</b>	Size	fruit, ovary	fruit, cell	cell multiplication	hydroponics	Bertin et al. 2003
_____	size, dry matter content	mean fruit	fruit, pedicel	water potentials, resistances, fluxes in the pedicel, calyx and fruit, water and carbon relationship	greenhouse, hydroponics	Bussières, 2002
_____	dry matter content, BERT	fruit	canopy, plant, cluster, fruit	dry matter accumulation and partitioning, leaves growth, transpiration, calcium flux	greenhouse	Hamer, 2002
_____	dry matter content, BER, firmness	mean fruit	canopy, plant, flower	nutrient uptake and EC calculated from climate and models of photosynthesis and transpiration	greenhouse, hydroponics	Schwarz et al. 2001
<b>Rose</b>	stem length	stem	canopy	assimilate partitioning, morphogenesis	greenhouse	Dayan et al. 2002
_____	shoot, leaves, bud	plant	canopy	dry matter partitioning	greenhouse	Gutierrez Colomer et al. 2006

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Bertin, N. (Auteur de correspondance), Bussières, P., Génard, M. (2006). Ecophysiological models of quality: a challenge for peach and tomato . Acta Horticulturae (718), 633-641.

## Figures

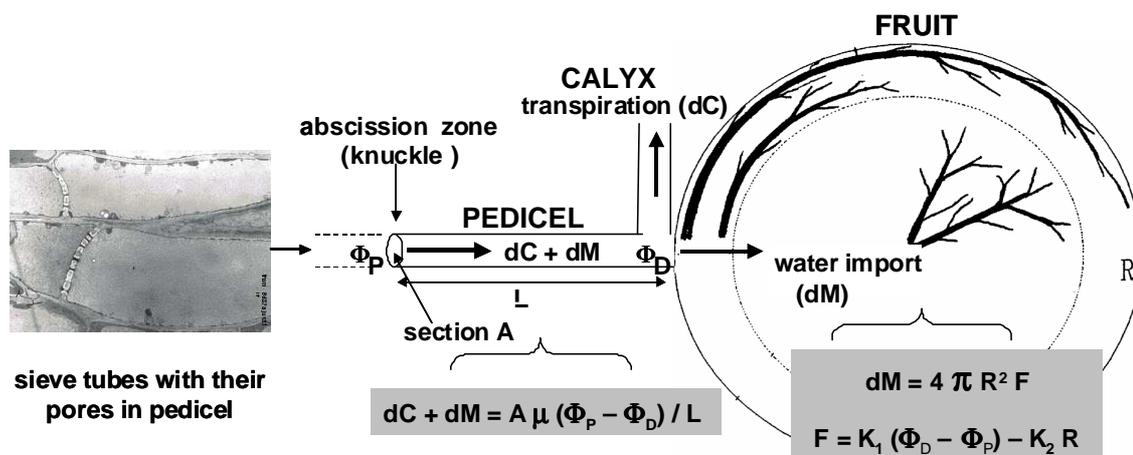


Fig. 1. Model of water import in tomato fruit (Bussi eres, 2002). The transfer rate ( $dC + dM$ ) in a fruit of radius  $R$ , is proportional to the sectional area  $A$  of the pedicel, to the difference of water potentials ( $\Phi_P - \Phi_D$ ) between pedicel endings, and to the pedicel phloem conductivity  $\mu$  divided by the pedicel length  $L$ . Parameters  $K_1$  and  $K_2$  are relative to the transfer pathway permeability into fruit and to the deformation tissue resistance.

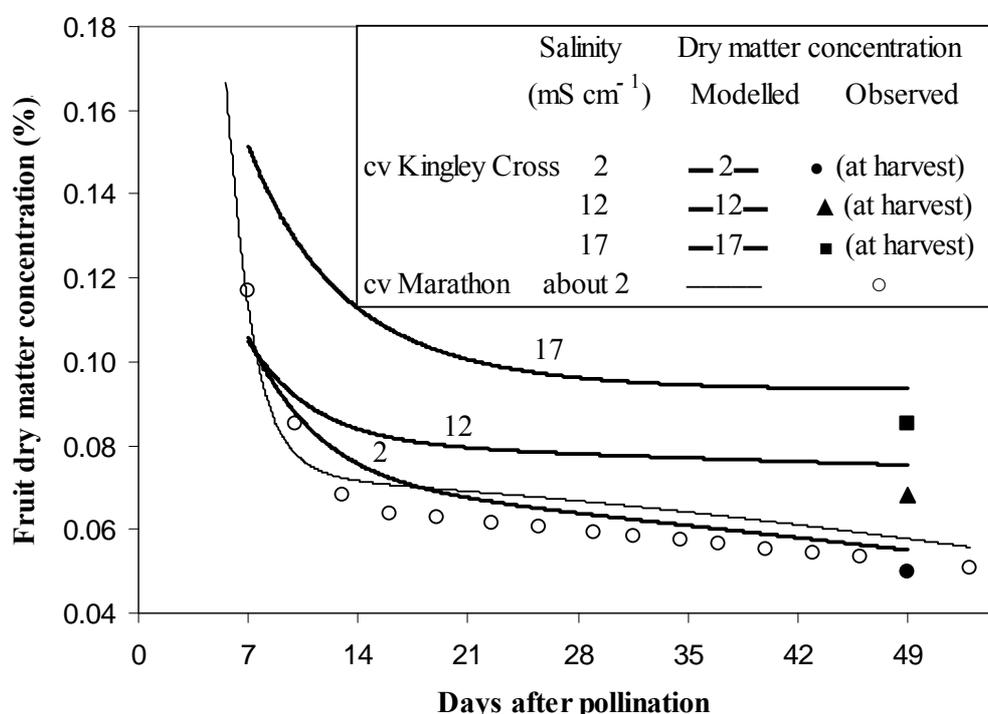


Fig. 2. Dry matter concentration of tomato fruits grown at different salinities (symbols) in the trials of Ho *et al.* (1987) predicted (lines) by the model of water import from Bussi eres (2002).

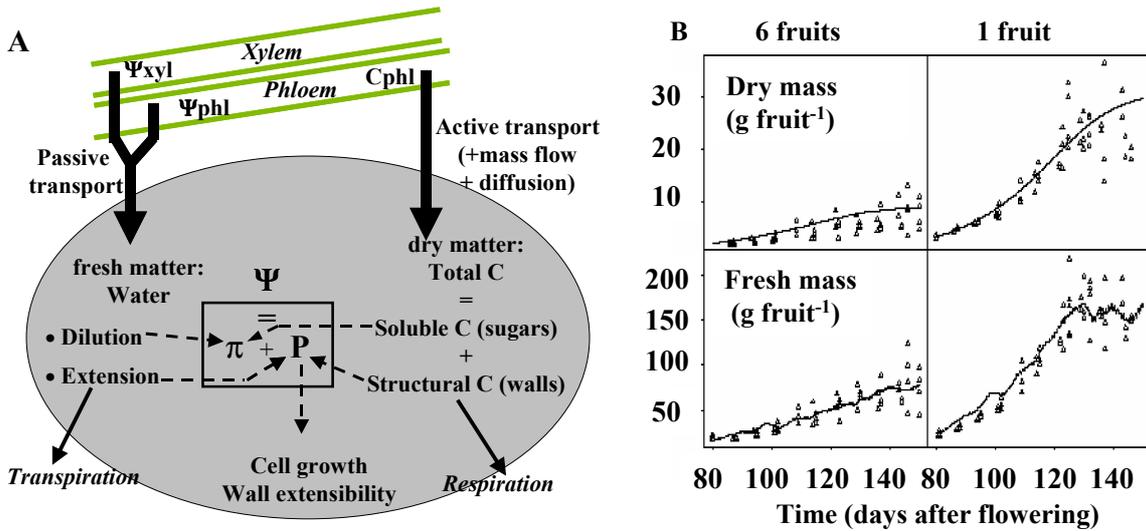


Fig. 3. A- Representation of the Fishman and Génard (1998) model. Cell growth is driven by turgor pressure ( $P$ ), accumulation of carbon ( $C$ ) and phloem ( $phl$ ) and xylem ( $xyl$ ) water influx (full lines).  $\Psi$  is water potential and  $\pi$  is fruit osmotic pressure. Broken lines indicate information flows. B- Seasonal growth of dry and fresh masses of peach fruits for different leaf:fruit ratios measured in the field (symbols) and predicted by the model (lines) (Source: Fishman and Génard, 1998).

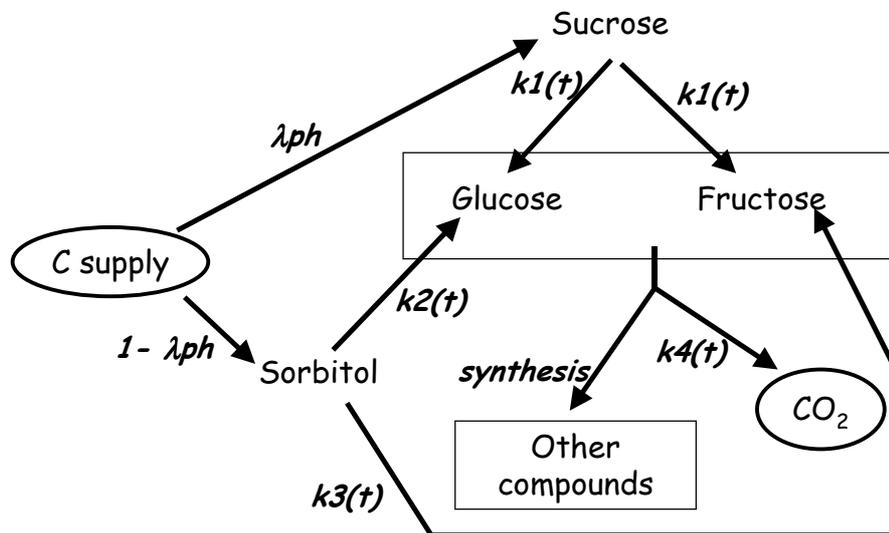


Fig. 4. Representation of the SUGAR model, in which  $\lambda_{ph}$  is the proportion of sucrose in the phloem sap,  $k_1(t)$ ,  $k_2(t)$ ,  $k_3(t)$  and  $k_4(t)$  are the relative rates of sugar transformation among the different pools in peach fruit. Fitting on experimental data determined:  $k_1(t) = k_{1,3} \exp(-k_{1,1} \cdot (t - k_{1,2}))$ ,  $k_2$  and  $k_3$  constant and  $k_4(t) = k_4 \cdot (1/W_{dry}) \cdot dW_{dry}/dt$ , where  $W_{dry}$  is mesocarp dry mass. (Source: Génard *et al.*, 2003).

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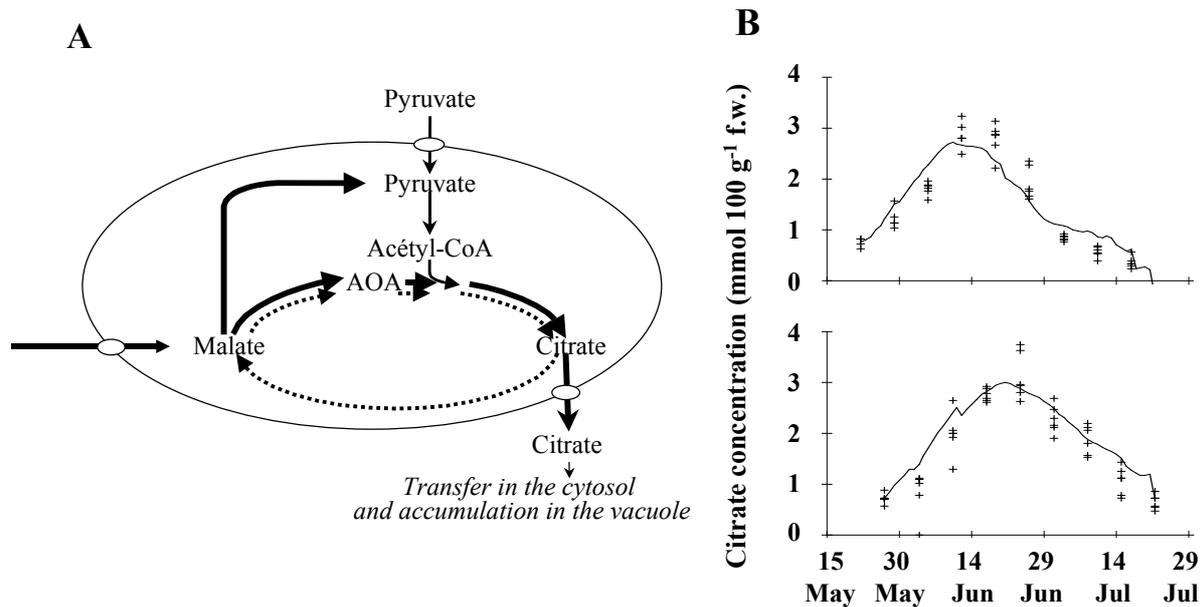


Fig. 5. A- Schematic representation of the citric acid model (Lobit *et al.*, 2003). Dotted and full lines indicate the Krebs cycle and the model ed fluxes, respectively. B- Seasonal variations of citrate concentration in peach fruit measured (symbols) on two different years from the end of May to the end of July (upper and lower graphs) and predicted by the model (lines).