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A biophysical model of fruit growth: simulation of seasonal and diurnal dynamics of mass

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ABSTRACT

A model of fruit growth was developed, based on a biophysical representation of water and dry material transport, which is coupled with cell wall extension stimulated by turgor pressure. The fluxes of materials connect the growing fruit with the parent plant (by phloem and xylem transport) and with the ambient atmosphere (by respiration and transpiration). The sugars are transported from the phloem to the fruit mesocarp by mass flow, passive diffusion and an active (and/or facilitated) mechanism. The stages after cell division has ceased and when fruit growth is due mainly to cell enlargement were modelled. This enabled us to consider the fruit as a cell community with a constant number of cells and to apply directly the equation describing the effect of hydrostatic pressure on the irreversible cell wall expansion elaborated originally for a single cell. The model was applied to the peach [*Prunus persica* (L.) Batsch] fruit. Seasonal and diurnal fruit growth, expressed in terms of dry and fresh mass changes, was calculated for conditions of water stress with various crop loads. Simulation of the diurnal patterns of fruit fresh mass variation revealed, in agreement with observations, intensive growth by night and midday fruit shrinkage, which depend on plant water status and on crop load.

Key–words: active transport; fruit shrinkage; hydrostatic osmotic pressure; mass flow; sugar; water.

INTRODUCTION

The main processes involved in fruit growth are interrelated by feedback loops which provide a kind of internal control in the system. Fruit enlargement requires the accumulation of water and hydrocarbons. The rate of material accumulation depends on the balance of incoming and outgoing fluxes. The fluxes, in turn, are defined by thermodynamic potentials which are functions of the material concentrations. There is also feedback between the fluxes and the hydrostatic pressure: the pressure controls the fluxes and is influenced by them. All these interrelations are coupled with other physicochemical processes, such as cell wall extension, transformations of the carbohydrates, and their active transport and/or facilitated diffusion, mediated by a carrier, etc. Environmental conditions and agrotechnical treatments play important roles in the control of water and solute movement and accumulation in the fruit. These roles can be better understood and agrotechnical practice improved through the use of a model which describes the biophysical mechanisms of the processes involved in fruit growth and analyses their relationship to the external conditions.

These mechanisms have been discussed in the literature and have been used by several authors as tools to analyse physiological processes in plant cells and organs. The flux of solution into the grape berry, as governed by differences in water potentials in the stem and the berry, was considered and the hydrostatic and osmotic components of the potentials were estimated by treating the fruit as one compartment (Lang, Thorpe & Edwards 1986). The difference between the water potentials in the stem and in the fruit was considered as the driving force in a model of the water import rate into tomato fruit which also takes into consideration the role of the tomato anatomy (Bussières 1994). One-compartment fruit representation has been applied to fruit growth calculation by means of numerical integration of the equation for water balance, using empirically determined water influx and transpiration as input values (Lee 1990) or by means of phenomenological equations with statistically fitted parameters for water influx and transpiration (Génard & Huguet 1996). Movement of water in plant tissue through two distinct pathways, the symplasmic and the apoplasmic, was analysed by Molz & Ferrier (1982), who included the case of tissue composed of several cells in series. The possibility of sucrose import to sink regions via symplastic and apoplasmic paths operating in parallel or in series was reviewed by Patrick (1997). A model of solution transport to the root was elaborated and analysed by Steudle and coworkers (reviewed by Steudle 1993): the root was treated as one compartment separated from the outside medium by a composite membrane, which was considered to be built from ‘membrane-like elements arranged both in series and in parallel’. In fact, the root xylem is separated from the medium by several layers of cells, which can be crossed in different ways, so that each layer could be regarded as a different compartment. This, however, would result in a multicompartmental

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model with possible multiple pathways between the compartments. The transport characteristics for such a model cannot be estimated, and the composite membrane forms a convenient approximation to this complicated transport system. Uptake of solutes includes passive permeation of solute through the membrane, 'solvent drag' by the mass flow of the water, and active transport. The active and/or facilitated transport makes an important contribution to the uptake of dry materials by fruits, as studied in tomato (Milner, Ho & Hall 1995), in peach (Vizzotto *et al*. 1996) and in tobacco callus (Hunt & Loomis 1976). Influx of water and solutes into the cells leads to irreversible changes in the volume if it is accompanied by cell wall extension. Equations which relate the relative cell elongation to the turgor pressure exerted on the wall, linearly or by a threshold relationship, were suggested by Lockhart (1965), whose approach has been experimentally corroborated by a number of workers. A study of the joint action of auxin and pressure on a single rye coleoptile (Green & Cummins 1974) revealed a threshold turgor pressure below which no extension occurs, and showed a hysteresis in the relationship between growth rate and turgor. Threshold and hysteresis are phenomena usually connected with phase transitions in membrane structures (Blumenthal, Changeux & Lefever 1970; Nagle & Scott 1978). Possibly, some kind of co-operative transformations occur in the cell walls under the action of hydrostatic pressure. Biochemical changes in cell wall structures which may be connected with wall extension have been examined (Fry 1989; Cosgrove 1993; Passioura, Condon & Richards 1993), but a mathematical formalism for these structural changes has not yet been elaborated, and the Lockhart's (1965) equation has been used as a convenient approximation in a number of recent studies: for example, it was adopted by Nonami & Boyer (1990) to describe stem growth and by Arkebauer, Norman & Sullivan (1995) for simulation of leaf expansion.

The aim of the present work was to develop a model of fruit growth, based on biophysical representation of water and dry material transport coupled with the process of extension stimulated by turgor pressure. This representation may relate fruit growth and several important quality characteristics of the fruit, such as water content and sugar concentration, on the one hand, to environmental conditions and basic agrotechnical treatments, on the other hand. The model was applied to the simulation of seasonal and daily growth of fruit under various conditions of crop load and water status in the tree. The results of simulations were compared with observations performed in our laboratory (INRA, Avignon Centre) or reported by other authors.

MATERIALS AND METHODS

Plant material

The model was parametrized, calibrated and validated for the late-maturing peach [*Prunus persica* (L.) Batsch] cv. 'Suncrest'/GF 677. The measurements were performed on peach trees planted in 1981 in the orchard of the INRA Avignon Centre. Trees were gobled trained and received routine horticultural care suitable for commercial orchards. This care included winter pruning, summer pruning, weekly irrigation from June to harvest, hand thinning in April, and pest control. Fungicides and insecticides were applied every 2 weeks from February to July. Weeds were destroyed by weed-killer.

Crop load measurements

At the beginning of June 1993, three treatments with leaf-to-fruit ratios set to 6, 18 and 30 [referred to below as heavy (HC), moderate (MC) and light (LC) crop load, respectively] were applied to fruit-bearing shoots isolated from the tree by girdling. Shoots with 6 or 18 leaves per fruit were thinned to four fruits and shoots with 30 leaves per fruit to three fruits. Fruits from five replicates (one or two fruit-bearing shoots, according to fruit size) were harvested each week from 7 June to the beginning of fruit maturation. During the 10–15 d of the maturation period, 7–16 replicates were harvested, according to treatment. At each harvest, the fresh and dry masses of fruit flesh and stone were recorded. The proportion of imported sugars converted to insoluble structural compounds was measured during the 'crop load' experiment, as described in greater detail by Génard & Souty (1996). Fifty-three measurements collected during the period 1993–96 were used for the allometric study of the correlation between fruit mass and skin area.

Mass loss observations

The rate of water loss from hanging detached apples has been found to provide a good estimate of evaporation from attached fruits (Jones & Higgs 1982; Lang 1990). These observations support the method used in the present study for estimation of the permeation coefficient of water vapour through the peach fruit surface. Freshly harvested peaches were placed in a room with controlled temperature and humidity and weighed 10 times at intervals of 45 min. At the end of the experiment, the surface area of each fruit was measured. The mass loss observations, together with the known relative humidity of the ambient atmosphere and the known surface area of the fruit, enabled us to estimate the permeation coefficient of the fruit surface to water vapour according to Ben-Yehoshua, Burg & Young (1985).

Theoretical methods and modelling technique

The fluxes of solutions were described by means of equations of non-equilibrium thermodynamics (Katchalsky & Curran 1965). Our treatment of the fruit as one compartment with composite transport of incoming materials was adapted from the membrane-equivalent model of the root (Steudle, Murrmann & Peterson 1993). The theory of pressure-dependent cell enlargement (Lockhart 1965) was applied.

Development of the model included: (i) analysis of the system from the biophysical point of view; (ii) definition of governing equations which describe the processes involved in fruit growth; (iii) incorporation of external conditions which influence fruit growth and represent input variables; (iv) search for parameters needed for numerical calculations (experimental results, obtained independently of the observations of the main state variables, were used, including our own measurements and observations, both *in vivo* and *in vitro*, reported by other workers), and (v) calibration of the model to estimate the parameters which were not determined in independent experiments. Following these steps, sensitivity analysis and validation of the model against a set of observations of the dynamics of the state variables were performed.

In simulating both diurnal and seasonal processes, the natural unit is the hour, which was also used as the time step in the numerical integration. For the numerical calculations two versions of computer program were employed, based on FORTRAN language and on ACSL (Advanced Continuous Simulation Language). ACSL Optimize (MGA Software 1996) was used for the model calibration with the aim of estimating parameters which cannot be determined in independent experiments.

MODEL DEVELOPMENT

General analysis of the system

The model simulates fruit growth during the period when there is no cell division (for a peach, this is the last 2–3 months of fruit development). This enables us to consider the fruit as a cell community with a constant number of growing cells. Growth of the stone during the last stage of fruit growth may be neglected and its mass is assumed to be constant. The fruit flesh is treated as a single compartment, separated from the exterior by composite membranes. The ambient atmosphere and the parent plant are treated as the external compartments. Gas and water vapour exchange take place through the fruit surface (respiration and transpiration processes). The temperature of the fruit is assumed to be equal to that of the ambient atmosphere. The parent plant supplies the fruit with water and with dry materials which are brought through xylem vessels and phloem sieve tubes. Dry materials reach the fruit mostly as soluble carbohydrates. Uptake of one representative compound (called 'sugar' in the following analysis) is taken into consideration. The contribution of amino acids and small ions to the osmotic pressure (which is proportional to the sum of their concentrations in the fruit flesh) is approximated as constant with time. The proportion of imported sugar converted to insoluble structural compounds is also assumed to be constant, which is in accordance with our observations. The main state variables of the system are the amounts of water (w) and of dry matter (s) in the fruit pulp. The hourly information coming from the external compartments includes: temperature and relative humidity of the ambient atmosphere, water potential in xylem vessels, and sugar concentration in phloem sap. This information forms the model input. Use of the input together with theoretical analysis quantified by the governing equations enables us to compute the fruit osmotic and hydrostatic pressures, the water and sugar uptake rates, the transpiration losses of water, and other auxiliary variables needed to obtain the main state variables. A list of the model variables is presented in Appendix 1.

Governing equations

The rate of change in the amount of water in the fruit with time ($\mathrm{d}w/\mathrm{d}t$) is the algebraic sum of the water inflow from xylem (U_x) and phloem (U_p) and the water outflow due to fruit transpiration (T_f)

$$\mathrm{d}w/\mathrm{d}t = U_x + U_p - T_f. \quad (1)$$

The rate of change in the amount of dry matter ($\mathrm{d}s/\mathrm{d}t$) is the difference between the uptake from phloem (U_s) and loss through fruit respiration (R_f):

$$\mathrm{d}s/\mathrm{d}t = U_s - R_f. \quad (2)$$

Previous studies on peaches (Pavel & DeJong 1993a) showed that, under field conditions, peach fruits can satisfy part of their total growth carbohydrate requirements by fruit photosynthesis. Depending on the exposure of the fruit to light, this contribution amounts to 5–9%. As a first approximation, this contribution is neglected in Eqn 2, in comparison with that from the parent plant.

Fruit transpiration leading to mass loss is assumed to be proportional to the fruit surface area (A_f) and to be driven by the difference in relative humidity between the air-filled space within the fruit (H_f) and the ambient atmosphere (H_a):

$$T_f = A_f \alpha \rho (H_f - H_a), \quad (3)$$

where ρ is the permeation coefficient of the fruit surface to water vapour and $\alpha = M_W P^*/RT$, with M_W = 18 g mol^{-1} being the molecular mass of water, P^* the saturation vapour pressure, R = 83·0 cm^3 bar mol^{-1} K^{-1} the gas constant and T temperature on the absolute scale (K). The dependence of P^* on temperature has been tabulated (Nobel 1974), but for the purpose of simulation we treated the dependence as an exponential function: P^* = 0·008048 exp[0·0547 (T – 273·15)] bar, which gives a satisfactory approximation over the temperature range of 283–323 K. The fruit surface area is related to the fruit total mass (W_T) by the empirical equation

$$A_f = \gamma (W_T)^{\eta}. \quad (4)$$

The fruit total mass is equal to $W_T = s + w + W_S$, where W_S is the fresh mass of the stone. The parameters γ and η depend on the fruit geometry and on the density of the fruit material. They can be estimated empirically from an allometric study. For peach, they were estimated empirically as described in 'Materials and methods'.

The flow density (J) through a membrane is described by

the equation drawn from non-equilibrium thermodynamics (Katchalsky & Curran 1965):

$$J = L[P_1 - P_2 - \sigma(\pi_1 - \pi_2)], \quad (5)$$

where the subscripts 1 and 2 indicate the compartments separated by the membrane; L is the hydraulic conductivity coefficient; $P_{1,2}$ are the hydrostatic pressures in the respective compartments; $\pi_{1,2}$ are the respective osmotic pressures, and σ is the reflection coefficient, which is a measure of the impermeability of the membrane to the solute, ranging from 1 (fully impermeable membrane) to 0 (when the membrane does not discriminate between the solute and water). The osmotic pressure is given by the equation $\pi = RT \Sigma_j C_j^{(m)}$ in which, according to Nobel (1974), $C_j^{(m)} = n_j/(V_w^* n_w)$, where n_j is the number of moles of osmotically active solute, n_w is the number of moles of water, and V_w^* is the partial molal volume of water ($V_w^* \cong 18$ cm^3 mol^{-1}). The hydrostatic and osmotic pressures are the components of the water potential (Ψ), which is expressed as their difference (Nobel 1974):

$$\Psi = P - \pi.$$

The total flow(U) through a membrane of area A is

$$U = AJ. \quad (6)$$

This equation is used to describe the influx of solutions from xylem and phloem into the fruit compartment. The fluxes are calculated as mass flow, in g h^{-1}, but in the case of dilute solutions with density ≈ 1 g cm^{-3}, they are numerically equal to the volume fluxes measured in cm^3 h^{-1}. Using subscripts x, p and f for xylem, phloem and fruit variables, respectively, and combining Eqns 5 and 6, we get

$$U_x = A_x L_x[P_x - P_f - \sigma_x(\pi_x - \pi_f)] \quad (7)$$

and

$$U_P = A_p L_p[P_p - P_f - \sigma_p(\pi_p - \pi_f)]. \quad (8)$$

This description of fluxes implies that different composite membranes separate the fruit compartment from phloem and from xylem, i.e. different kinetic parameters and different pathways may be involved. It is known that $\pi_x << \pi_f$, so, in the following calculations, the approximations $\pi_x = 0$ and $\sigma_x = 1$ are used, assuming that water entering from the xylem must cross the plasma membrane, which appears to have a reflection coefficient close to unity (Nobel 1974; Murphy & Smith 1994). The vascular network enters the fruit and enlarges as the fruit grows, with A_x and A_p increasing in parallel with fruit growth. It is convenient to relate this time dependence to a characteristic of the growing fruit having the dimension of area. Therefore, A_x and A_p are assumed to be proportional to the fruit surface area A_f (calculated with Eqn 4), with constant non-dimensional coefficients of proportionality: $A_x(t) = a_x A_f(t)$ and $A_p(t) = a_p A_f(t)$.

If $\sigma_p < 1$, part of the sugar can be transported from the phloem to the fruit by mass flow (U_p). The contribution of sugar to the mass flow is $(1 - \sigma_p)C_s U_p$, where $C_s \cong (C_p + C_f)/2$ is the mean concentration of the solute in the membrane, with C_p and C_f being the sugar concentrations in phloem and fruit, respectively, in accordance with non-equilibrium thermodynamics (Katchalsky & Curran 1965). In the following discussion, dimensionless (g g^{-1}) values are used for these concentrations. This sugar contribution has to be subtracted from U_p when the water inflow is calculated with Eqn 1, but the mass of water in the mass flow is much greater than that of the solute and so the water inflow may be approximated by U_p. However, the transport of sugar by mass flow, $(1 - \sigma_p)C_s U_p$, must be taken into account when the sugar uptake is calculated. The saturating kinetics of the carbohydrate uptake observed *in vitro* for various fruits, as cited in the Introduction, points to the important role of active or facilitated transport (denoted by U_a). In addition, passive diffusion, driven by the difference in concentrations across the membrane, may take place. The total uptake of carbohydrates comprises these three constituents

$$U_s = U_a + (1 - \sigma_p)C_s U_p + A_p p_s(C_p - C_f), \quad (9)$$

where p_s is the solute permeability coefficient. The saturating uptake rate, U_a, is assumed to be dependent on the phloem concentration according to the Michaelis-Menten equation. As observed by Johnson, Hall & Ho (1988), the uptake of sugars by fruit slices declines with increasing fruit age. The phenomenon of a reduction in the ability of the cells of senescing leaves to accumulate sugars was discussed by Milthorpe & Moorby (1969). This reduction may be of the same nature as that in fruit cells. To describe this phenomenon, a generalized form of the Michaelis-Menten equation has been applied. Generalization of the Michaelis-Menten theory, including the activity of a fully non-competitive inhibitor, leads to a speed reduction by a factor of $1 + C_I/K_I$ (Thornley & Johnson 1990), where C_I is the inhibitor concentration and K_I is the equilibrium constant for the formation of an inhibitor-carrier complex. The generalized Michaelis-Menten equation for fully non-competitive inhibition has the form

$$U_a = sv_m C_p/[(K_M + C_p)(1 + C_I/K_I)], \quad (10)$$

where v_m is the maximum uptake rate per unit of dry mass and K_M is the Michaelis constant. The rate U_a will decline with fruit age if the inhibitor accumulates in the growing fruit. We assumed that this accumulation proceeds exponentially, i.e. $C_I = C_I^* \exp(t/\tau)$, with C_I^* being the value of C_I at the initial point $t = 0$. (If the time zero point is placed, for instance, at bloom termination, C_I^* must be recalculated accordingly.) It is more convenient to introduce another parameter: $t^* = -\tau \ln(C_I^*/K_I)$, which has the dimension of time. Thus, Eqn 10 may be written as

$$U_a = sv_m C_p/\{(K_M + C_p)[1 + \exp((t - t^*)/\tau)]\}. \quad (11)$$

The generalized equation contains two additional parameters as compared with the basic Michaelis-Menten equation: t* and τ, describing the activity of an inhibitor. The exponential accumulation of the inhibitor is hypothesized for the model; we do not know what compound fulfils this role. The exponential accumulation characterizes an auto-

catalytic reaction. The concentration of ethylene has been observed to increase exponentially in the ripening peach fruit (Tonutti, Bonghi & Ramina 1996; Souty *et al*. 1997). A regulatory factor which inhibits sugar accumulation could be one of the co-products of ethylene biosynthesis.

The dry material loss through fruit respiration (R_f) comprises two components: that due to growth respiration, which is proportional to the rate of dry material intake, and that due to maintenance respiration, which is proportional to the dry mass (Thornley & Johnson 1990):

$$R_f = q_g(\mathrm{d}s/\mathrm{d}t) + q_m(T)s, \quad (12)$$

where q_g and $q_m(T)$ are the coefficients for growth and maintenance respiration, respectively. The effect of temperature (T) on maintenance respiration is addressed by the Q_{10} concept (Penning de Vries & van Laar 1982; Pavel & DeJong 1993b): $q_m(T) = q_m(293)\, Q_{10}^{(T-293)/10}$.

Now all fluxes which contribute to the water and sugar balances are represented by equations containing the parameters and input functions, as well as osmotic and hydrostatic pressures in the fruit. The osmotic pressure can be calculated from the concentrations as described above. To calculate the hydrostatic pressure, the following procedure is performed. The relative rate of irreversible volume (V) growth of the fruit compartment is presented in the form of Lockhart's equation (Lockhart 1965), yielding

$$\mathrm{d}V/\mathrm{d}t = V\phi(P_f - Y) \quad (\text{if } P_f \geq Y), \quad (13)$$

where ϕ is the coefficient which describes extensibility of the cell walls and Y is the threshold value of the hydrostatic pressure in the fruit, above which irreversible expansion occurs. The change in fruit mass is calculated as the sum of Eqns 1 and 2. If each equation is divided by the appropriate density (D_w for water density and D_s for that of sugar), the rate of volume change may be obtained from

$$\mathrm{d}V/\mathrm{d}t = (U_x + U_p - T_f)/D_w + (U_a - R_f)/D_s. \quad (14)$$

The second term in Eqn 14 is small compared with the first and may be neglected. Under the condition of steady irreversible growth, the right-hand sides of Eqns 13 and 14 must be equal, which means that one of the variables on the right-hand sides of these equations is dependent and may be represented as a combination of other variables. This dependent variable is the hydrostatic pressure in the fruit. Setting Eqns 13 and 14 equal, inserting fluxes from Eqns 7 and 8, and solving the resulting equation for P_f, one obtains

$$P_f = [A_xL_x(P_x + \pi_f) + A_pL_p(P_p - \sigma_p\Delta\pi) - T_f + D_wV\phi Y]/(A_xL_x + A_pL_p + D_wV\phi) \quad (\text{if } P_f \geq Y), \quad (15)$$

where $\Delta\pi = \pi_p - \pi_f$ and, as mentioned above, $\sigma_x = 1$ and $\pi_x = 0$. Equation 15 is valid under the condition $P_f \geq Y$. The hydrostatic pressure P_f has the same physical meaning as the cell turgor discussed by Ray, Green & Cleland (1972) and represents 'the value of turgor pressure that must prevail, during steady growth, to satisfy the requirement for simultaneous volume increase by water uptake and yield of the cell wall'. Equation 15 shows that P_f diminishes when the hydrostatic pressure in xylem and phloem decreases and when the transpiration rate rises. When $P_f < Y$, Eqns 13 and 15 are no longer valid. Because the cell walls are quite rigid, the volume will not change appreciably in response to the pressure changes, and the right-hand side of Eqn 14 becomes 0, which gives another equation for P_f:

$$P_f = [A_xL_x(P_x + \pi_f) + A_pL_p(P_p - \sigma_p\Delta\pi) - T_f]/(A_xL_x + A_pL_p) \quad (\text{if } 0 \leq P_f < Y) \quad (16)$$

If the environmental conditions lead to very low P_f values, the cell wall stresses are relieved and P_f is assumed to stay close to zero.

The water potentials in xylem and phloem, needed for calculation of P_f, are assumed to be equal to the measured water potential in the stem, Ψ_w. This gives $P_x = \Psi_w$ and $P_p = \Psi_w + \pi_p$. Inserting Eqns 15 and 16 into Eqns 7 and 8 enables us to calculate the fluxes. After the fluxes have been calculated, integration of Eqns 1 and 2 over time yields the main state variables of the system:

$$w(t) = w_o + \int (U_x + U_p - T_f)\,\mathrm{d}t \quad (17)$$

and

$$s(t) = s_o + \int (U_s - R_f)\,\mathrm{d}t, \quad (18)$$

where w_o and s_o are initial masses of water and dry matter in the fruit flesh, respectively. After Eqns 17 and 18 have been solved, the fruit total mass and volume, sugar concentration, water content and other auxiliary variables which are important characteristics of the fruit may be calculated using the state variables $w(t)$ and $s(t)$. For osmotic pressure calculations, it is assumed that a fraction Z of the accumulated sugar remains in soluble form, and the rest is converted into structural material.

Input of external signals

The numerical calculations require two environmental inputs as functions of time: temperature and relative humidity of the ambient atmosphere (Eqn 3). These may be inputted in a tabulated form based on meteorological observations. As default inputs, sinusoidal functions for both of the signals are installed in the model, with a maximum for the temperature and a minimum for the humidity at midday. The maximum and minimum temperatures were 25 and 15 °C, respectively, and maximum and minimum relative humidities were 0·95 and 0·40, respectively. To compare the model predictions with the measured dry and fresh pulp masses of fruit during the 1993 growing season, the relative humidity and temperature measured hourly during that season were applied. The data were collected by the INRA, Avignon, meteorological station situated close to the orchard. These meteorological data were also used for all subsequent simulations.

As mentioned above, the parent tree forms a part of the fruit surroundings, and signals are transmitted from it to the fruit by the xylem and phloem fluxes. The hydrostatic pressure in the xylem and the phloem and the osmotic pressure of the phloem sap are among the characteristics needed for the model calculations. They depend, in turn, on

environmental and managerial conditions, but this dependence is not addressed in the fruit model, where xylem and phloem are represented as external compartments, on which information can be obtained from experimental data. Diurnal variations in xylem pressure have been reported for several plant species (Andersen, Brodbeck & Mizell 1995). It is at a minimum between 1200 and 1600 h and reaches values of –12 to –27 bar (–1.2 to –2.7 MPa), depending on species and irrigation conditions. The xylem pressure is maximal before dawn, when it ranges from –2 to –6 bar (–0·2 to –0·6 MPa). These figures are in agreement with the measured values of the stem water potentials in peach trees reported previously (Garnier & Berger 1986): the minimal potential of a normally watered tree was approximately –10 bar (–1 MPa) at midday; the potential then rose to a maximal value of approximately –2 bar (–0·2 MPa) in the evening and maintained this value during the night. These data were used as the default values for Ψ_w in the present study, with a function falling sinusoidally to –10 bar (–1 MPa) at midday, rising to –2 bar (–0·2 MPa) in the evening and remaining constant at –2 bar (–0·2 MPa) during the night, in accordance with measurements on peach trees (Simonneau & Habib 1991, 1994). To simulate fruit growth under conditions of water stress, the default curve for water potential was lowered in accordance with reported measurements (Berman & DeJong 1996).

According to measurements by Berman & DeJong (1996), the stem water potentials under stress conditions are different for different thinning treatments, ranging from –12 to –16 bar (–1·2 to –1·6 MPa) around midday. This range of potentials was chosen for the water stress simulation. Three treatments of crop load (light, moderate and heavy, denoted as LC, MC and HC, respectively), each under two conditions of water status in the tree (control and water stress, denoted as CT and WS, respectively), were simulated by the model. In addition, severe water stress (SS) was simulated under MC. Table 1 summarizes the values of signals used for the simulation of the combined effect of water stress and crop load on the fresh and dry mass of fruit.

A sugar concentration of 0·17 in the phloem has been reported for various plant materials (Ruan & Patrick 1995; van Bel 1993), and a value of 0·14 has been measured in peach seedlings 3 h before the end of the day (Escobar-Gutierrez 1995). Diurnal fluctuations of the sugar concentration have been observed in the phloem of *Salix* sp. (Peel & Weatherley 1962), in leaves of a legume, *Lupinus albus* (Sharkey & Pate 1976), and in stem exudate from tree tobacco, *Nicotiana glauca* Grah. (Hocking 1980). The fluctuations are correlated with the cessation of photosynthesis during darkness. We took 0·17 (≅ 0·5 M), which is given in the literature as the representative sugar concentration in the phloem (Ruan & Patrick 1995; van Bel 1993), to be the midday concentration in the MC treatment. The highest published value of the concentration (Nobel 1974) is 0·24 (≅ 0·7 M); we therefore used the value of 0·22 in our LC simulation. Assuming, as a first approximation, a linear correlation between the sugar supply and the leaf:fruit ratio, the extrapolation for the HC gave 0·12 as the midday concentration. Because of the lack of information on diurnal variations in the phloem sugar of peach trees, we used the reported difference between daylight and darkness concentrations in the phloem of *Salix* sp. (Peel & Weatherley 1962), 0·08, in the model calculations. The complete set of phloem concentrations used as the model input is presented in Table 1. The osmotic pressure induced by other osmotically active compounds was considered to be constant, as a first approximation.

Parameterization

Some of the parameters of the model were estimated from independent measurements on peach fruit cv. 'Suncrest' as described in 'Materials and methods'. The other parameters were taken from the literature and are converted here to the units used in the model. The values of the parameters are summarized in Appendix 2.

The mass loss observations enabled us to estimate the permeation coefficient of the fruit surface to water vapour, $\rho = 432 \pm 65$ cm h^{-1} (mean ± SE, $n = 9$), which is close to the value found for peach cv. Golden Queen (Nobel 1975). Parameters $\gamma = 6{\cdot}049 \pm 0{\cdot}53$ ($n = 53$) and $\eta = 0{\cdot}601 \pm 0{\cdot}018$ ($n = 53$) in Eqn 4, relating the fruit surface area (in cm^2) to the fruit mass (in g), were determined in the allometric study. The proportion of soluble sugars in the total content of accumulated carbohydrates was estimated as $Z = 0{\cdot}61 \pm 0{\cdot}000723$ ($n = 119$). The fresh mass of the stone was found to be equal to $W_S = 7{\cdot}4 \pm 0{\cdot}00721$ g ($n = 175$).

	LC		MC			HC	
	CT	WS	CT	WS	SS	CT	WS
$(P_x)_{max}$	–2	–4	–2	–5	–6	–2	–6
$(P_x)_{min}$	–10	–12	–10	–14	–24	–10	–16
$(C_p)_{max}$	0·22	0·22	0·17	0·17	0·17	0·12	0·12
$(C_p)_{min}$	0·14	0·14	0·09	0·09	0·09	0·04	0·04

Table1. Values of signals used for simulations of water stress and crop load effects. P_x (bar) and C_p (dimensionless) are inputted as sinusoidal curves with maximum and minimum values given below. The thinning treatments are denoted as LC (light crop load, 30 leaves per fruit), MC (moderate crop load, 18 leaves per fruit) and HC (heavy crop load, 6 leaves per fruit). The notations CT, WS and SS are used for control treatment, water stress and severe stress conditions, respectively

For the parameters which describe the respiration process in peaches (Eqn 12), we adopted the values $q_g = 0{\cdot}21$ (dimensionless) and $q_m(293) = 0{\cdot}000131$ h^{-1} (DeJong & Goudriaan 1989; DeJong & Walton 1989). The figure for $q_m(293)$ agrees well with our estimate of the respiration coefficient based on the gas exchange measurements on the fresh detached cv. 'Suncrest' peach at the end of the growing season (unpublished results). The value of the temperature coefficient, Q_{10}, of the respiration of peach fruit, 2·03, was taken from Pavel & DeJong (1993b). The *in vivo* glucose accumulation rate of pericarp tissue of tomato fruit has been reported (Ruan & Patrick 1995) to be ≈ 0·001 g (g dry mass)$^{-1}$ h^{-1}, and the transfer rate of sucrose in the seed of *Phaseolus* to be ≈ 0·005 g (g dry mass)$^{-1}$ h^{-1} (Patrick 1994). The maximal rate of sucrose transfer through the phloem membrane of peach leaves has been estimated (Moing, Escobar-Gutierrez & Gaudillere 1994) as ≈ 0·003 g (g dry mass)$^{-1}$ h^{-1}. Based on these data, v_m = 0·003 g (g dry mass)$^{-1}$ h^{-1} was adopted for the peach fruit model. The value of K_m for sucrose transport at the tomato tonoplast has been estimated as 0·08 (Milner *et al*. 1995) and this value was used in the model. The extensibility parameter, ϕ, for the growing pea (*Pisum sativus* L.) stem tissue has been reported by Cosgrove (1985) to be 0·008–0·024 h^{-1} bar^{-1} (depending of the pre-treatment and the method of measurement), and comparable values were obtained by Nonami & Boyer (1990) for stems of soybean (*Glycine max* [L.] Merr.) The value ϕ = 0·01 h^{-1} bar^{-1} was used in the model. The wall yielding threshold pressure, Y, has been estimated and cited by Green *et al*. (1971, 1974) as ranging from 3 to 8 bar (0·3 to 0·8 MPa) for various cells. For the peach fruit model, we chose Y = 5 bar (0·5 MPa). For the water uptake parameters, we used for both L_x and L_p the value 0·00972 g cm^{-2} h^{-1} bar^{-1} found for radial hydraulic conductivity of maize roots (Steudle *et al*. 1993), which is of a comparable order of magnitude to the value of 0·02664 g cm^{-2} h^{-1} bar^{-1} calculated for a possible hydraulic conductivity coefficient in plant membranes (Nobel 1974). The sucrose permeability coefficient of the tomato pericarp phloem membrane has been estimated to be $p_s = 3{\cdot}6 \times 10^{-5}$ g cm^{-2} h^{-1} (Ruan & Patrick 1995).

The reflection coefficient of plant cell membranes for sucrose, σ, is usually equal to 1 (Nobel 1974). In the case of composite transport, in which symplasmic unloading could be one of the parallel pathways (which allows uptake of sugar by mass flow), the effective value of σ may be lower (Steudle *et al*. 1993). The experimental data presently available are not sufficient to discriminate between two mechanisms for sugar accumulation (mass flow and active transport), and cannot reveal a possible developmental transition between them. Additional independent experiments are needed to obtain this information. Therefore, the effective value of $\sigma = 0{\cdot}9$ was chosen for the simulation, which means that the sucrose permeability of the composite membrane was considered low but not completely negligible.

Calibration

The parameters which had not been determined in independent experiments were estimated through the model calibration, by fitting the theoretical curves for changes in the main variables to the seasonal observation (see 'Materials and methods'). Seasonal changes of dry and fresh mass of the fruit pulp measured under conditions of moderate loading with sufficient water supply (MC/CT in Table 1) were used for the model calibration.

The following three parameters were estimated by fitting two simulated curves, $s(t)$ and $s(t) + w(t)$, to experimental values of the dry and fresh masses of the pulp, respectively (Fig. 1, MC). Parameters a_x and a_p were assumed to be equal, as a first approximation, and were found to be $a_x = a_p = 0{\cdot}0273 \pm 0{\cdot}0012$. Parameters t^* and τ for the time function in Eqn 11 were estimated to be $t^* = 1138{\cdot}8 \pm 50{\cdot}65$ h and $\tau = 216{\cdot}95 \pm 85{\cdot}8$ h. The overall percentage variation explained by the optimized curve fitting was 97·44%.

RESULTS OF SIMULATIONS

Sensitivity analysis

The hydraulic conductivity, $L = L_x = L_p$, is an important physical parameter in the description of the fruit water supply. It was estimated for the systems in which the membrane area available for the transport of solutions could be estimated independently. In the present model, it occurs (Eqns 7 and 8) as a product with the factor $A = A_x = A_p = a_x A_f = a_p A_f = aA_f$, i.e. it is fully correlated with the parameter $a = a_x = a_p$. In effect, the product La is the parameter in the model. The value of a = 0·0273 (dimensionless) was found by means of the model calibration, subject to $L = 0{\cdot}00972$ g cm^{-2} bar^{-1} h^{-1}; thus, if L is changed by a factor X, one has to change a by factor X^{-1} to obtain the same results of curve fitting.

The sucrose permeability coefficient was adapted from the data obtained by Ruan & Patrick (1995) on the tomato pericarp phloem membrane, $p_s = 3{\cdot}6 \times 10^{-5}$ g cm^{-2} h^{-1}. For a complicated pathway in a composite membrane, the permeability may increase. When we changed the value by two orders of magnitude, to $p_s = 0{\cdot}0027$ g cm^{-2} h^{-1}, we found an increase of only 0·05% in the calculated dry and fresh masses, showing that the transport of sucrose by passive diffusion is much less than that by mass flow or by a facilitated mechanism; therefore, the last term in Eqn 9 may be neglected.

The first two terms of Eqn 9 describe the contributions of active transport and mass flow to sugar accumulation in the fruit. Their relative importance, as estimated by the model computations, changes as the fruit develops. During most of the simulation period, the ratio of active transport of sugar to its import by the mass flow is about 5·5. But about 2 weeks before the end of the season, when the active uptake diminishes strongly because of the inhibitor action, the contributions of the two mechanisms become equal; and during the last few days of the simulation, when

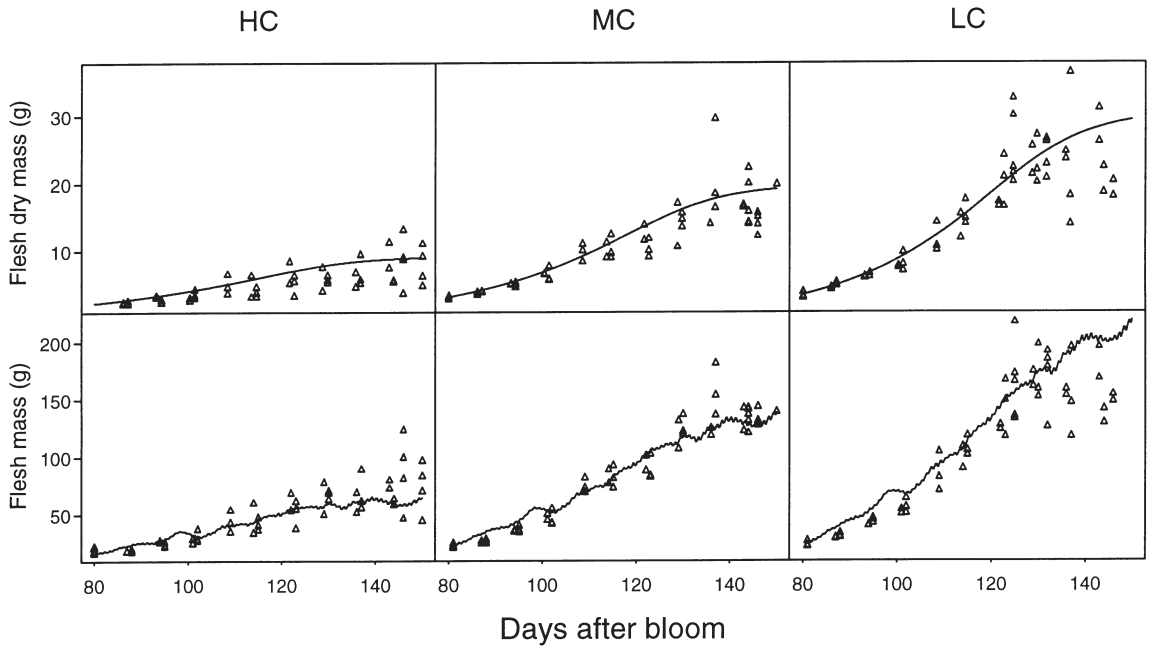

Figure 1. Comparison of simulated (curve) and measured (points) growth of dry and fresh mass of fruit flesh for different thinning treatments, with a leaf-to-fruit ratio of 30 (LC), 18 (MC) and 6 (HC).

growth ceases, the small remaining uptake of sugar is mainly due to the mass flow (the ratio of the sugar active transport to its import by the mass flow becomes 0·1). The relative importance of these two processes in fruit growth is influenced by the parameters v_m and σ_p. To analyse the sensitivity of the growth dynamics to these parameters, the default temperature and humidity data for the ambient atmosphere were inputted into the model, as described above, and MC/CT conditions were taken from Table 1. The fruit fresh mass accumulation was calculated for various values of the parameter v_m with $\sigma_p = 0{\cdot}9$ (Fig. 2). One can see that increases in v_m lead to faster mass accumulation, characterized by a family of sigmoidal curves. Similar calculations of the effect of changing the parameter σ_p used the value $v_m = 0{\cdot}003$ g sucrose (g DW)$^{-1}$ h^{-1} (Fig. 3). Diminishing the reflection coefficient, i.e. increasing the role of the 'solvent drag' term, increased the fresh mass accumulation rate. This increase was accompanied by a change of the form of the growth curve: when σ_p was less than 0·7, the growth curve had an exponential rather than a sigmoidal form. With $\sigma_p = 0{\cdot}9$ the mass flow mechanism of sugar transport has an auxiliary role. If independent experiments were to show that 'solvent drag' has a dominant role in sugar uptake, an inhibition of this mechanism with increasing fruit age would have to be included in the theoretical framework, to describe the fruit growth correctly. The rate decrease, in such a case, could result from plasmodesmata closure at a certain stage of fruit development,

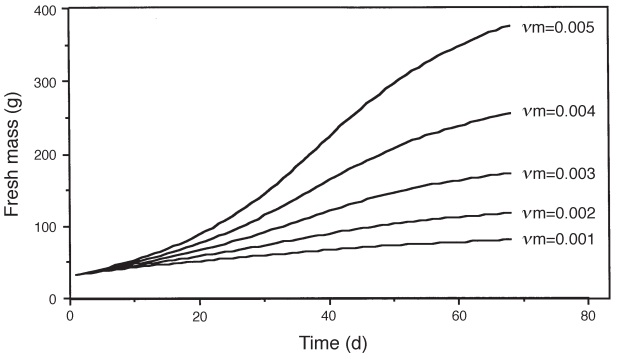

Figure 2. Seasonal dynamics of fruit fresh mass calculated at default temperature and humidity, with values of v_m (maximal rate of active transport) ranging from 0·001 to 0·005 g sucrose (g DW)$^{-1}$ h^{-1}, and other parameters as listed in Appendix 2.

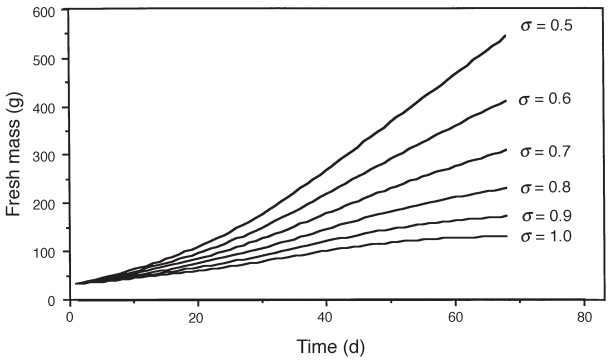

Figure 3. Seasonal dynamics of fruit fresh mass calculated at default temperature and humidity, with values of σ_p (reflection coefficient) ranging from 0·5 to 1·0, and other parameters as listed in Appendix 2.

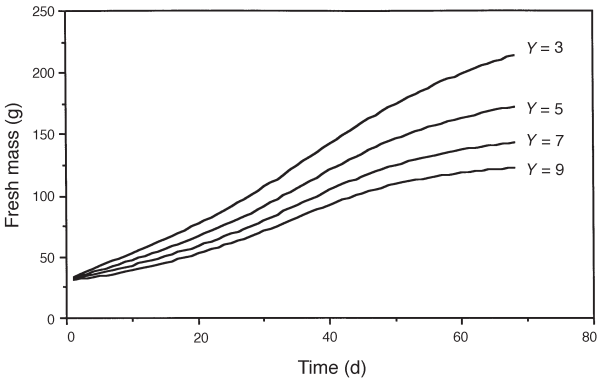

Figure 4. Seasonal dynamics of fruit fresh mass calculated at default temperature and humidity, with values of *Y* (threshold value of hydrostatic pressure) ranging from 3 to 9, and other parameters as listed in Appendix 2.

similar to that described by van Bel (1993) for the phloem transport.

Another important parameter, which could change as our knowledge develops, is *Y*, the threshold value of hydrostatic pressure needed for growth. The growth curves for various values of *Y* are presented in Fig. 4. Changing *Y* does not affect the basic shape of the curves. The influence of this threshold value on growth springs from the development of turgor pressure, which drives cell expansion. The diurnal variation in turgor pressure in fruit, P_f, calculated from the theoretical Eqns 15 and 16, shows a strong decline during the morning and a rise in the evening, in qualitative agreement with reported results for peach fruit (McFadyen, Hutton & Barlow 1996). Figure 5 presents diurnal P_f values for various values of *Y*.

Seasonal fresh and dry mass changes with three different crop load treatments

Comparison of the seasonal changes of dry and fresh mass measured under conditions of low and heavy crop loading (LC/CT and HC/CT in Table 1) with the time course of mass predicted by the model validated the model (Fig. 1, HC & LC). In the simulations of HC and LC, the same parameters were used as for curve fitting with MC data. The observed changes in fruit fresh and dry masses for peach cv. 'Suncrest' during the season were smaller when the crop loading was greater. The simulations of dry and fresh mass dynamics for three different crop loads fitted the observations well (Fig. 1), supporting the model assumption that the effect of crop load on fruit growth can be simulated by changing the sugar supply to the phloem. According to the model, the increase in crop loading leads to restriction in carbohydrate supply. The sugar concentration in the phloem directly influences the rate of sugar uptake by the fruit and results in diminished sugar concentration and osmotic pressure in fruits growing under conditions of high crop load. Under such conditions, the water uptake and therefore the fresh mass accumulation decrease also.

Combined effect of water stress and crop load on seasonal fresh and dry mass changes

A set of model computations was performed to simulate the combined effect of water stress and crop load. The conditions for the simulations are summarized in Table 1. The seasonal changes in dry and fresh mass were calculated for the three crop load treatments (LC, MC and HC) under control conditions during the first 3 weeks. Afterwards, two levels of irrigation (CT and WS) were applied to each of the loading treatments until the end of the season. The calculated growth dynamics for MC fruit are presented (Fig. 6) for two watering conditions. One can see that water stress has a strong effect on the fresh mass accumulation whereas the dry mass dynamics changed only slightly. The end-of-season values of the dry mass of pulp and the fresh mass of fruit growing under various conditions are compared in Fig. 7. The most representative experimental data concerning the combined effect of water stress and crop load on the fresh and dry mass of peach fruit were obtained by Berman & DeJong (1996), who used a different method from ours for crop loading experiments: they denoted trees bearing 163, 265 and 561 fruits as low, moderate and high crop load, respectively. Nevertheless, the resulting patterns are qualitatively similar. Water stress caused significant decreases in fruit fresh mass in both the experiment (Berman & DeJong 1996) and the simulations. The differences in fruit dry mass are negligible. In the treatments with restricted carbohydrate supply, the ability of the fruit to accumulate water decreased. When water stress was applied, the fresh mass reductions for LC, MC and HC treatments, as calculated by the model, were 17, 24 and 28%, respectively, whereas the experiments of Berman & DeJong (1996) showed fresh mass reductions of 23, 26 and 37%, respectively. According to the model, reduction of the xylem water potential (water stress) reduces the water influx, and restriction of the carbohydrate supply leads to lower osmotic pressure in the phloem and, consequently, a lower turgor pressure, which also reduces the water influx.

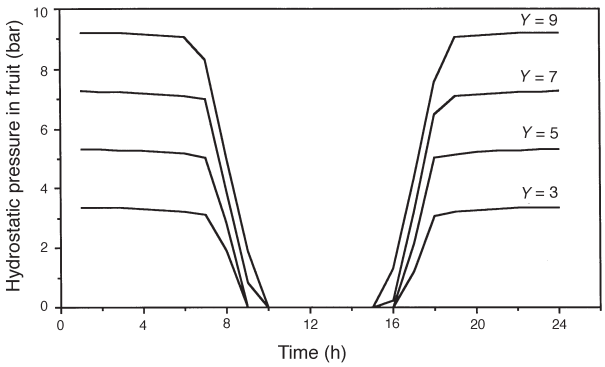

Figure 5. Diurnal changes of hydrostatic pressure in fruit (P_f) calculated at default temperature and humidity, with values of *Y* (threshold value of hydrostatic pressure) ranging from 3 to 9, and other parameters as listed in Appendix 2.

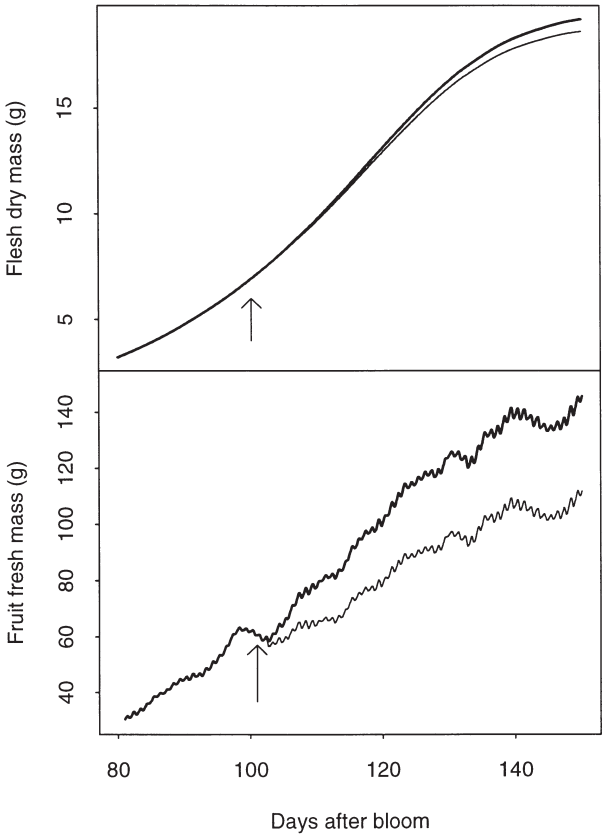

Figure 6. Simulated seasonal growth of flesh dry mass and fruit fresh mass under various watering conditions. The upper curve of each pair was obtained under simulated control conditions, the lower one with water stress applied at the time indicated by the arrow and continuing until the end of the season.

Diurnal changes in fruit mass

The diurnal patterns of fruit growth reveal additional features of the growth process. The changes in flesh dry mass, fruit total mass and transpiration flow during a 4-day period (106–109 days after bloom) were calculated under conditions denoted in Table 1 as MC/CT (Fig. 8). The model predicts that diurnal patterns of fruit dry and fresh mass are not directly correlated. One can see that during the daytime, when transpiration reaches its maximum value, the fresh mass does not increase or even diminishes, whereas the dry matter accumulates during this time. The most intensive accumulation of fruit fresh mass takes place during the night. This behaviour follows from the mechanisms described theoretically and from the various signals governing the processes of water and sugar accumulation. The humidity in the ambient atmosphere (external signal) is minimal near midday, and the transpiration varies in response to the fluctuations in humidity (Eqn 3). When transpiration increases, the hydrostatic pressure in the fruit diminishes (Eqns 15 and 16), which causes the growth to slow down and, eventually, to cease (Eqn 13). The low plant water potential (external signal) during the daytime reduces the water influx to the fruit (Eqns 7 and 8) so that it cannot compensate for the high rate of fruit transpiration; therefore, the water balance becomes zero or negative during the daytime. The uptake of dry matter depends on the sugar concentration in the phloem (Eqns 9 and 10), which is maximal during daylight (external signal), resulting in more intensive sugar accumulation via an active transport mechanism, which may compensate for the possible reduction in its uptake via mass flow.

The effect of crop load on diurnal patterns of peach fruit growth, as related to the water status in the fruit, was investigated experimentally by McFadyen *et al*. (1996), who observed cessation of fruit growth or even shrinkage during the day, whereas in the late afternoon the growth rate increased. Crop load had a significant effect: the slowdown in growth and the shrinkage of fruit during the afternoon were stronger in the case of heavy crop loading. These phe-

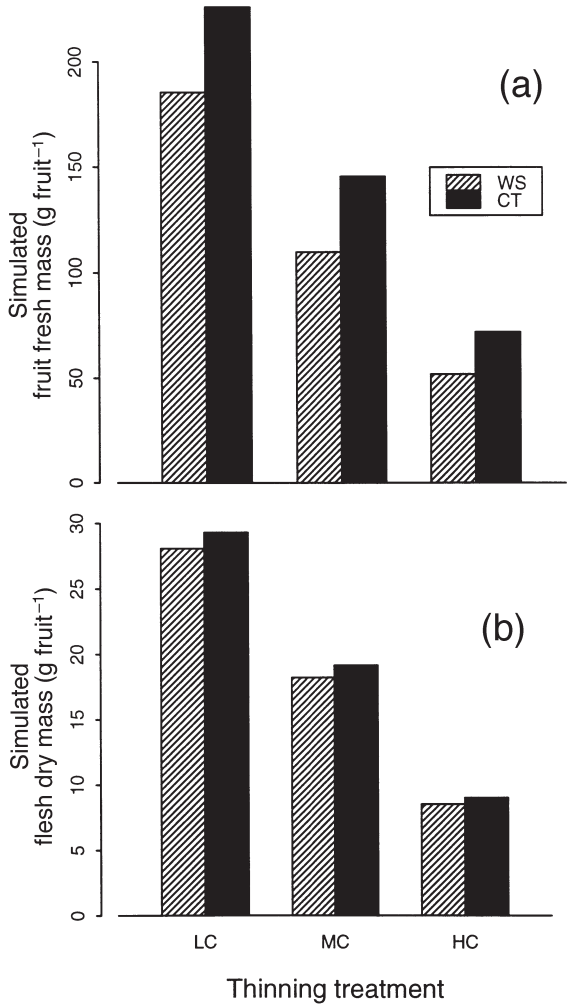

Figure 7. Combined effects of water stress and crop load on the fruit flesh dry mass and on fruit fresh mass at the end of the season. The calculated data are presented in a similar form to the experimental data of Berman & DeJong (1996; Fig. 4) in order to demonstrate the similarity between simulated and measured results.

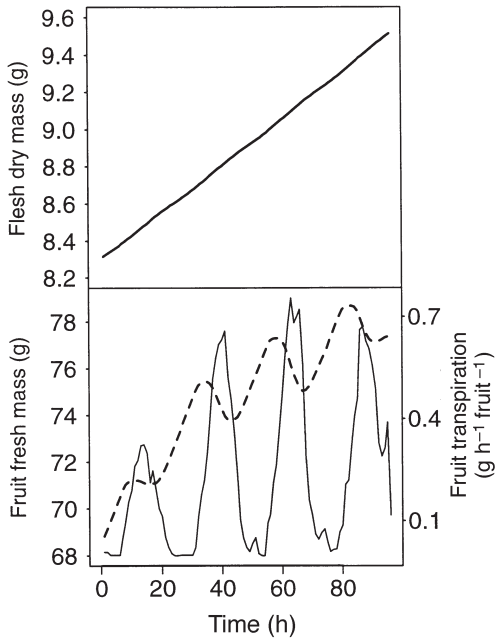

Figure 8. Patterns of 4 d (106–109th days after bloom) simulations obtained for normal irrigation (CT) and moderate crop load (MC) conditions. The upper graph represents the growth of flesh dry mass. The lower graph shows the calculated changes in fruit fresh mass (dashed curve) as compared with the calculated fruit transpiration (smooth curve). The coincidence of fruit shrinkage with the peak of transpiration is demonstrated.

nomena may also be simulated by the model. Curves of relative fruit mass changes during one day (107th day after bloom) were calculated (Fig. 9) for the cases of low, moderate and high crop loading, all with normal irrigation. One can see that the shrinkage becomes stronger with increased crop loading. The model calculations also qualitatively match the measurements of the fruit potentials performed in parallel with their growth observations by McFadyen *et al*. (1996). For instance, the fruit osmotic pressure is calculated to be lower in the HC treatment than in the LC, although the calculated difference is less than the measured one.

The influence of water stress on the diurnal changes in fruit diameter was studied experimentally by Huguet & Génard (1995) for *Prunus persica* (L.) Batsch cv. 'Dixired'. They reported a slowdown in growth near midday under conditions of continuous watering of the trees, which were grown in pots. When the watering was stopped for 3d (severe stress), strong shrinkage of the fruit was observed. After irrigation was resumed, fruit growth resumed in parallel with that of the control fruits. The model simulation of this phenomenon is presented in Fig. 10 for moderate crop load. Curve CT was calculated under the control conditions; curve WS corresponds to the water stress conditions applied for 4 d, as shown in the figure; and curve SS was obtained under conditions of 4 d of severe stress. The fruit growth simulated under the mild water stress conditions reveals greater shrinkage than that under control conditions, with a return to the normal growth rate after removal of the stress. The fruit shrinkage caused by the severe stress was much stronger, but in this case also the fruit returned to normal growth, in agreement with the observations of Huguet & Génard (1995).

CONCLUSIONS

The theoretical framework developed here enables us to build a model of fruit growth. The model takes into consideration only fundamental biophysical processes and their response to external signals; it describes the stages of fruit development subsequent to the completion of cell division, when the fruit can be approximated by a community of

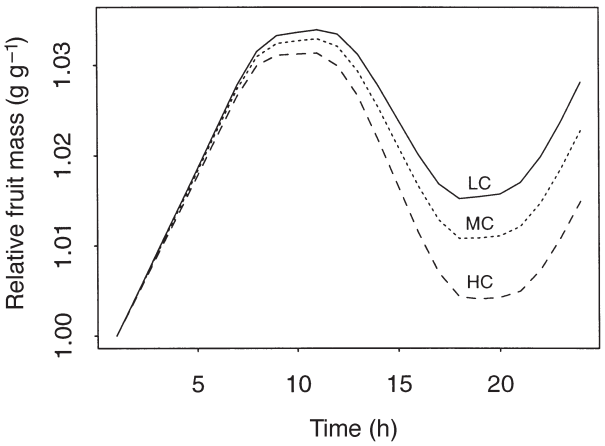

Figure 9. Influence of thinning treatment on the midday shrinkage of fruit. The relative changes in fruit fresh mass during one day (107th day after bloom) were computed under normal irrigation (CT) and various thinning treatments (LC, MC and HC).

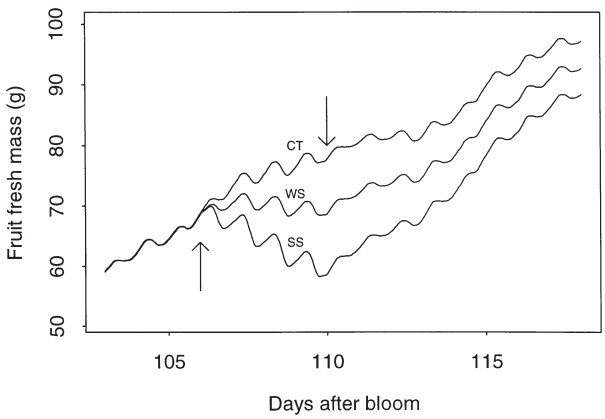

Figure 10. Influence of the watering conditions on the midday shrinkage of fruit. The simulated changes of fruit fresh mass over 15 d are shown, with water stress being applied in the middle of the period. The arrows indicate the time of water stress onset (arrow pointing up) and cessation (arrow pointing down). The indexes CT, WS and SS denote the curves obtained under conditions of normal irrigation, water stress and severe water stress, respectively.

growing cells. This restriction enables us to simplify the theoretical analysis and to clarify the relationship of the basic mechanisms to an internal system of feedback control. The sugar transport mechanism remains outside the feedback control; its time-dependent inhibition, which is yet to be studied, may be governed by a hormonal or any other developmental signal coming from the parent tree or produced in the fruit. Among other theoretical limitations, it must be mentioned that the model does not consider sugar transformations, nor the uptake of osmotically active compounds other than sugar. More detailed compartmentation might reveal additional possible specific mechanisms involved in the fruit growth process, but we do not have enough data for such a more detailed model. The input of the sugar concentrations in the phloem, representing in this model an external compartment, was based on experiments with plant materials other than peach. Measurements of diurnal changes of sugar concentrations in the phloem of peach stems under different crop loadings are needed to provide more exact input to the model. It is encouraging that acceptable predictions were obtained for the LC and HC data using the optimized parameter estimates obtained from the MC data.

An extension of the fruit growth model, taking into account leaf photosynthesis and leaf-stem-fruit sugar transport, is now under development. It will compute the sugar concentration in the phloem for various crop loadings as an output variable, replacing the experimental values used in the present fruit model.

Using the theoretical approximations, the basic effects connected with fruit growth were calculated, analysed and compared with our experimental data as well as with recent observations of other workers (Berman & DeJong 1996; McFadyen *et al*. 1996). Seasonal and diurnal dynamics of fruit fresh and dry mass simulated by the model demonstrate its ability to explain and predict the fruit growth under various environmental conditions.

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APPENDIX 1: LIST OF VARIABLES FOR THE MODEL OF FRUIT GROWTH

A_f (cm^2)	fruit area
C_f (dimensionless, g/g)	concentration of sugar in fruit pulp
C_p (dimensionless, g/g)	concentration of sugar in phloem
H_a (dimensionless)	relative humidity in ambient atmosphere
J ($g\ cm^{-2}\ h^{-1}$)	flow density
P_f (bar)	hydrostatic pressure in fruit
P_p (bar)	hydrostatic pressure in phloem
P_x (bar)	hydrostatic pressure in xylem
R_f ($g\ h^{-1}$)	fruit respiration rate
s (g)	dry material in the pulp per fruit
T_f ($g\ h^{-1}$)	fruit transpiration rate
U_a ($g\ h^{-1}$)	active uptake of sugar
U_p ($g\ h^{-1}$)	mass flow from phloem to fruit
U_x ($g\ h^{-1}$)	mass flow from xylem to fruit
U_s ($g\ h^{-1}$)	total rate of sugar uptake
w (g)	amount of water in the pulp per fruit
W_T(g)	total fresh mass of fruit
π_f (bar)	osmotic pressure in fruit
π_p (bar)	osmotic pressure in phloem
π_x (bar)	osmotic pressure in xylem
Ψ (bar)	water potential in stem

APPENDIX 2: LIST OF PARAMETERS AND CONSTANTS FOR THE MODEL OF FRUIT GROWTH

$a_p = a_x = 0{\cdot}0273$ (dimensionless)	ratio of area of the composite membrane to the fruit area
$D_w = 1$ ($g\ cm^{-3}$)	water density
$H_f = 0{\cdot}996$ (dimensionless)	relative humidity of air space in fruit
$K_m = 0{\cdot}08$ (dimensionless)	Michaelis constant for the equation of active transport
$L_x = 0{\cdot}00972$ ($g\ cm^{-2}\ bar^{-1}\ h^{-1}$)	conductivity of the composite membrane for water transport
$p_s = 0{\cdot}0027$ ($g\ cm^{-2}\ h^{-1}$)	permeability of the composite membrane for sugar transport
$Q_{10} = 2{\cdot}03$ (dimensionless)	temperature ratio of maintenance respiration
$q_g = 0{\cdot}21$ (dimensionless)	growth respiration coefficient
q_m (293) $= 0{\cdot}000131$ (h^{-1})	maintenance respiration coefficient
$R = 83$ ($cm^3\ bar\ mol^{-1}\ K^{-1}$)	gas constant
$t^* = 1138{\cdot}8$ (h)	kinetic parameter in Eqn 11
$v_m = 0{\cdot}0031$ [g sucrose $(g\ DW)^{-1}\ h^{-1}$]	maximal rate of active transport per unit of dry mass
$V_w^* = 18$ ($cm^3\ mol^{-1}$)	partial molal volume of water
$W_s = 7{\cdot}4$ (g)	fresh mass of the stone
$Y = 5{\cdot}0$ (bar)	threshold value of hydrostatic pressure needed for growth
$Z = 0{\cdot}61$(dimensionless)	ratio of soluble sugars in the total carbohydrate pool
$\phi = 0{\cdot}01$ ($bar^{-1}\ h^{-1}$)	cell wall extensibility coefficient in Lockhart's equation
$\rho = 432{\cdot}0$ ($cm\ h^{-1}$)	permeation coefficient of fruit surface to water vapour
$\sigma_p = 0{\cdot}9$ (dimensionless)	reflection coefficient of the composite membrane for sugar
$\tau = 216{\cdot}95$ (h)	characteristic time for inhibitor accumulation
$\gamma = 6{\cdot}049$ and $\eta = 0{\cdot}601$	empirical parameters relating fruit area (cm^2) to fruit mass (g)