Tree Physiology 25, 583–597

Modeling effects of weather and source–sink relationships on mango fruit growth

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Received April 2, 2004; accepted October 10, 2004; published online March 1, 2005

Summary We modeled the effects of weather and source–sink factors on mango fruit growth. The peach fruit-growth model "Cashoo" was adapted for mango fruit. The model accounts for the main processes of fruit growth, i.e., leaf photosynthesis, fruit demand, fruit respiration, and storage and mobilization of leaf and stem reserves. Simulations for three successive years and for various leaf-to-fruit ratio treatments showed good agreement with observed fruit growth data. Simulations of fruit growth under different climatic conditions, especially with contrasting temperature and radiation, and for different values of initial fruit dry mass and leaf-to-fruit ratio, showed that variations in fruit growth among years can be partly explained by climatic variations through their effects on leaf photosynthesis, fruit demand and fruit growth rate. However, climatic changes contribute substantially less to observed variability in fruit growth than to initial fruit dry mass and leaf-to-fruit ratio.

Keywords: climatic changes, fruit demand, leaf-to-fruit ratio, Mangifera indica, photosynthesis, reserves, respiration.

Introduction

Fruit dry mass is an important component of fruit quality, because dry matter comprises mainly carbohydrates, 60% of which are sugars and acids, the main compounds contributing to fruit taste (Mukerjee 1959, Fishman and Génard 1998). The amount of carbohydrate supplied to tree fruits depends on the amount produced by leaf photosynthesis, which is related to leaf area and photosynthetic capacity and activity. The latter is influenced by climatic conditions (Rosati et al. 1999, Le Roux et al. 2001) and can be affected by changes in source–sink relationships, as has been reported in many species, including apple (Palmer 1992), grapevine (Naor et al. 1997) and mango (Urban et al. 2003). The amount of carbohydrate supplied to tree fruits also depends on sink demand, which is generally defined as the sum of assimilates required for maintenance and potential growth of the sink organ, the latter being determined under optimal environmental conditions, i.e., non-limiting supplies of carbon (C) and other resources (Warren-Wilson 1972, Ho 1992). The potential growth of fruit is the product of fruit mass (i.e., sink size) and relative fruit growth rate (i.e., sink activity). The balance between sources and sinks is maintained through a pool of reserves within the plant, which in turn is affected by the activities of the sources and sinks.

Some cultural practices, by manipulating either source size or sink size, influence source–sink relationships involved in fruit growth. Thinning, which controls crop load by removing the smallest fruits, usually increases the size of the remaining fruit (Goffinet et al. 1995). Pruning or partial defoliation decreases total leaf area, and thus source size (Layne and Flore 1993). Girdling is known to favor carbohydrate accumulation and fruit size in citrus trees (Cohen 1984), improve the quality of peach and nectarine fruit (Augusti et al. 1998) and reduce shoot growth of peach trees (Cutting and Lyne 1993). The effects of girdling, which interrupts basipetal phloem transport, are largely dependent on species, time of girdling and size of the girdled branch. Decreased net photosynthesis as a result of girdling has been reported (Lu and Chacko 1998, Di Vaio et al. 2001), but in the presence of strong sinks such as developing fruits, branches maintain high rates of gas exchange (Schaper and Chacko 1993). Girdling also affects hormone transport and concentration in peach (Dann et al. 1985, Cutting and Lyne 1993).

Interannual variation in fruit growth is generally believed to be caused by climatic variation (De Silva et al. 1997, Stanley et al. 2000). Light is required for photosynthesis, and it has been suggested that increased irradiance improves fruit size of mango (Mendoza and Wills 1984), pear (Kappel and Neilsen 1994) and apple (Morgan et al. 1984). Fruit growth depends on physiological and biochemical processes that are influenced by the temperature prevailing during fruit development (e.g.,

Tukey 1960, Haun and Coston 1983, Marsh et al. 1999). Many studies have shown that cumulative degree days after full bloom adequately explain the variability in fruit growth between years and local sites (Mosqueda-Vasquez and Ireta-Ojeda 1993, Burondkar et al. 2000).

Mango fruit is an important tropical horticultural crop characterized by heterogeneity in fruit size at harvest (Léchaudel 2004). The objective of this study was to quantify the effects of weather and source–sink factors, i.e., early sink size and leaf-to-fruit ratio, and their interactions on mango fruit growth and size at harvest. Because models of fruit growth based on dry mass increment have successfully identified environmental factors limiting fruit growth (Grossman and Dejong 1994, Génard et al. 1998), we used a modified version of the model "Cashoo" of Lescourret et al. (1998; see also Génard and Lescourret 2004) that was originally designed for peach. The model functions at the branch level, which is the production unit, and accounts for the effect of changing source–sink relationships on fruit growth by simulating the main processes involved, i.e., source activity, mobilization of reserves, respiration and fruit demand. In the first step, these processes were characterized and the capacity of the model to account for differences in fruit dry mass between various leaf-to-fruit ratio treatments applied to girdled branches was tested. We also studied the sensitivity of fruit growth to the model parameters. In a second step, the combined effects of weather and source–sink factors were modeled and the effects of climatic conditions, leaf-to-fruit ratio and initial fruit dry mass on fruit growth and final size were assessed.

Materials and methods

Plant material

The study was conducted during the 2000, 2001 and 2002 growing seasons on 11-year-old (in 2000) mango trees (*Mangifera indica* L.) of cv. 'Lirfa', grafted on 'Maison Rouge', growing on La Réunion island (20°52′48″ S, 55°31′48″ E). The 2000 experimental plot, called Orchard 1, consisted of 10 rows, 7 m apart, with each row containing nine 3-m-tall trees spaced 5 m apart. The trees observed in 2001 were located in an adjacent plot, called Orchard 2, and were spaced 5 × 6 m apart and were about 3-m high. In 2002, experimental data were acquired from both orchards. In 2000, 2001 and 2002 there were two, one and two flowering periods, respectively.

During the experiment, trees were irrigated every 2 days on a 100% replacement of evaporation basis. Six weeks after flowering, 10 to 15 branches per tree were chosen, representing less than 10% of the total branches of the tree canopy. All branches were chosen from the top of the canopies to reduce the variability in light received by the leaves, which could significantly change C assimilation and fruit growth. Branches were girdled by removing a 10–15-mm-wide band of bark. Defruiting and defoliation were performed if needed to divide branches into 10, 25, 50, 100 and 150 leaf-to-fruit ratio (LF) treatments (with 50 leaves for five fruits, 100 leaves for four, two and one fruits, and 150 leaves for one fruit, respectively). However, the number of fruits or leaves removed was small compared with the initial number on the girdled branch. To keep the leaf-to-fruit ratio constant within each treatment, newly emerging leaves were removed. Girdling was performed after fruit drop, when fruit length was about 5 cm.

Model presentation

We adapted the "Cashoo" peach model of C partitioning at the fruit-bearing shoot level (Lescourret et al. 1998) to account for the physiological properties of mango. The model describes the functioning of a system composed of three main components: fruit, leaves and stem. Seasonal dry mass of the fruit was simulated on a daily basis, and photosynthesis was simulated on an hourly basis. The part of the original peach model concerning vegetative growth was changed because, unlike those of peach, mango leaves and stem do not grow during the fruit growing season. Carbohydrate partitioning depends on organ demand and priority rules. The priority rules used for mango were: (1) maintenance of the system; (2) reproductive growth; and (3) accumulation of reserves in the leaves and then in the stem. When the potential fruit demand is higher than carbohydrates supplied by photosynthesis, the fruit may obtain assimilates from leaf and stem reserves. Organ respiration and reserve mobilization are represented as in the model of Lescourret et al. (1998). Mango-specific equations were developed for the regulation of C assimilation and for computing fruit demand. A schematic representation of the model is presented in Appendix 1 and the model parameters are listed in Table 1.

Carbon assimilation by leaves In many plant species, a balance is maintained between source supply and sink demand (Fujii and Kennedy 1985, Ho 1992, Foyer et al. 1995, Quereix et al. 2001). We adapted the simple model proposed by Ben Mimoun et al. (1996), which assumes that light-saturated leaf photosynthesis (P_{max}; μmol CO_2 m^{-2} s^{-1}) is an asymptotic function of fruit demand (D_{fruit}; g C m^{-2} day^{-1}):

$$P_{max} = \frac{p_1 D_{fruit} p_2}{p_1 D_{fruit} + p_2} \text{ if } P_{max} < P^*_{max}$$
$$P_{max} = P^*_{max} \text{ if } P_{max} \geq P^*_{max} \quad (1)$$

where p_1 (μmol CO_2 m^{-2} s^{-1} g^{-1} C) is the initial slope of the response curve of P_{max} to D_{fruit}, p_2 (μmol CO_2 m^{-2} s^{-1}) is a parameter and P^*_{max} (μmol CO_2 m^{-2} s^{-1}) is the potential light-saturated photosynthesis.

To calculate photosynthetic rate per unit leaf area (P_l; μmol CO_2 m^{-2} s^{-1}), we used the formulation in the original model of Lescourret et al. (1998):

$$P_l = (P_{max} + p_3)\left(1 - \exp\left(\frac{-p_4 PPF}{P_{max} + p_3}\right)\right) - p_3 \quad (2)$$

where PPF is photosynthetic photon flux (μmol m^{-2} s^{-1}), and parameters p_3 and p_4 were estimated experimentally. Net photosynthesis of shaded leaves was calculated from the radiation

Table 1. Parameters used in the mango model.

Parameter	Equation	Value (SE)	Significance
Carbon assimilation by leaves			
p_1 (μmol CO_2 m^{-2} s^{-1} g^{-1} C)	1	3.85 (0.57)	Initial slope of the response curve of light-saturated photosynthesis to fruit demand
p_2 (μmol CO_2 m^{-2} s^{-1})	1	33.23 (11.91)	Parameter of the response of light-saturated leaf photosynthesis to fruit demand
P^*_{max} (μmol CO_2 m^{-2} s^{-1})	1	15.0	Potential light-saturated photosynthesis
p_3 (dimensionless)	2	0.483 (0.074)	Parameters of the response of leaf photosynthesis to radiation and light-saturated photosynthesis
p_4 (dimensionless)	2	0.034 (0.007)	
Maintenance respiration			
MRR_{leaves} (g C g^{-1} h^{-1})	4	1.56 10^{-4}	Maintenance respiration rate of leaves, stem and fruit components
MRR_{stem} (g C g^{-1} day^{-1})	4	8.58 10^{-4}	
MRR_{fruit} (g C g^{-1} day^{-1})	4 and 14	1.15 10^{-3} (1.1 10^{-4})	
Q_{10}^{leaves} (dimensionless)	4	2.11	Q_{10} value for leaves, stem and fruit components
Q_{10}^{stem} (dimensionless)	4	1.96	
Q_{10}^{fruit} (dimensionless)	4	1.90	
Fruit growth			
RGR_f^{ini} (dd^{-1})	6	0.0105 (0.0003)	Initial relative growth rate
a (g^{1-b})	7	16.736 (1.637)	Parameters for computing the maximum fruit dry mass from the initial fruit dry mass
b (dimensionless)	7	0.624 (0.036)	
GRC_{fruit} (g C g^{-1})	5,13 and 14	0.04 (0.01)	Growth respiration coefficient of the fruit
c_{fruit} (g C g^{-1})	5 and 13	0.4239 (0.0048)	Carbon content of the fruit
Reserve mobilization			
r_4	8	0.0162	Mobile fraction of reserves in leaves
r_5	9	0.0164	Mobile fraction of reserves in stem

received by those leaves (g(PPF)), obtained by an empirical linear relationship with PPF.

The fraction of sunlit and shaded leaf area was estimated from fish-eye photographs (Lescourret et al. 1998). We photographed 37 branches (6, 7, 8, 9 and 7 from the 10, 25, 50, 100 and 150 LF treatments, respectively). Two photographs were taken above each studied branch. Hourly fractions of sunlit and shaded leaf area were calculated based on gap fractions derived from the digitized hemispherical photographs. There was no difference between gap fraction values within a treatment or between treatments (data not shown). The amount of C fixed by leaf photosynthesis during a day (C_l; g C day^{-1}) was determined as the sum of hourly photosynthesis of the sunlit plus shaded leaf area (cf. Lescourret et al. 1998):

$$C_l = \left(\sum_{h+} P_l^{sunlit} LA_{sunlit} + \sum_{h+} P_l^{shaded} LA_{shaded} \right) k \qquad (3)$$

where LA is total leaf area (m^2) and $k = 0.0432$ (conversion coefficient of leaf photosynthesis from μmol CO_2 s^{-1} to g C h^{-1}).

Maintenance respiration Maintenance respiration (MR; g C day^{-1}) was calculated based on the Q_{10} values (Penning de Vries and Van Laar 1982) for the stem, leaves and fruit:

$$MR_i = MRR_i (Q_{10}^i)^{\frac{\theta - \theta_{ref}}{10}} DM_i \qquad (4)$$

where MRR_i is maintenance respiration rate (g C g^{-1} day^{-1}) of organ i at the reference temperature θ_{ref} (°C), Q_{10}^i is the Q_{10} value for organ i, θ is mean temperature of the day (°C) and DM_i (g) is dry mass of organ i. For leaves, MRR_{leaves} expressed in g C g^{-1} h^{-1} was converted to g C g^{-1} day^{-1} by accounting for the hours of darkness in each day. Daytime respiration was considered in Equation 2.

Fruit demand Daily C demand for fruit growth (D_{fruit}; g C day^{-1}) was calculated as in Lescourret et al. (1998):

$$D_{fruit} = \frac{\Delta DM_f^{pot}}{\Delta dd} \frac{\Delta dd}{\Delta t} (c_{fruit} + GRC_{fruit}) \qquad (5)$$

where $\Delta DM_f^{pot}/\Delta dd$ (g dd^{-1}) is potential fruit growth rate based on degree days (dd) after full bloom, c_{fruit} (g C g^{-1}) is fruit C content and GRC_{fruit} (g C g^{-1}) is the growth respiration coefficient of fruit.

Potential fruit growth or sink strength is generally described as the product of sink size and sink activity. Potential fruit growth rate (ΔDM_f^{pot}), attained when the fruit is grown under optimal environmental conditions, in our case under 100 or 150 LF, was represented by a logistic equation:

$$\frac{\Delta DM_f^{pot}}{\Delta dd} = RGR_f^{ini} DM_f \left(1 - \frac{DM_f}{DM_f^{max}} \right) \qquad (6)$$

where Δdd is daily variation in degree days (dd), RGR_f^{ini} is initial relative fruit growth rate (dd^{-1}), DM_f is fruit dry mass (g), i.e., sink size, and DM_f^{max} is maximal final dry mass (g).

Maximal final fruit mass generally depends on the final number of cells in the fruit, as demonstrated for apple (Goffinet et al. 1995), peach (Scorza et al. 1991), tomato (Bertin et al. 2002), apricot (Jackson and Coombe 1966) and mango fruit (Léchaudel 2004). In commercial mango cultivars, cell division in the flesh occurs until 35 to 45 days after full bloom (Saini et al. 1971). Because the number of cells is often difficult to determine, we used a simple relationship between DM_f^{max} and "initial" fruit dry mass, assumed to be proportional to the number of cells. Initial fruit dry mass was measured at 350 degree days, which corresponds to 60 to 70 days after full bloom when the cell division phase was finished and the number of cells in the flesh was fixed. The relationship was:

$$DM_f^{max} = a(DM_f^{ini})^b \quad (7)$$

where DM_f^{ini} is initial fruit dry mass at 350 degree days, and a and b are parameters.

Mobilization of reserves If the amount of carbohydrates available from current photosynthesis is less than the amount required for maintenance and growth of the system, reserves are taken from the leaves (R_l; g C day^{-1}):

$$R_l = r_4 RM_l \quad (8)$$

If leaf reserves are insufficient to meet demand, reserves are taken from the stem (R_s; g C day^{-1}):

$$R_s = r_5 RM_s \quad (9)$$

where r_4 and r_5 represent the mobile fractions of reserves and RM_l and RM_s are the C mass of reserves in the leaf and stem, respectively.

Model inputs: climatic data and initial conditions

Climatic data, i.e., maximum, minimum and mean daily temperatures (°C) and hourly global radiation (GR), were collected at a meteorological station situated close to the orchard. Photosynthetic photon flux (μmol m^{-2} s^{-1}) was calculated from GR (W m^{-2}) as:

$$PPF = k_1 k_2 GR \quad (10)$$

where $k_1 = 0.5$, the fraction of global radiation that is photosynthetically active (Penning de Vries and Van Laar 1982), and $k_2 = 4.6$ μmol W^{-1} s^{-1}, a conversion factor.

Initial fruit dry mass values required by the model were chosen equal for each year and for each leaf-to-fruit ratio treatment to the mean of first measurements. Initial values for the ratio of reserve mass to dry mass in leaves and stem were obtained from the first measurement or reserve data in 2000. Those values are required for calculating the initial mass of reserves in leaves and stem.

Model parameterization

Leaf gas exchange was measured with an infrared gas analyzer equipped with a leaf chamber system with a red + blue light source (LI 6400, Li-Cor, Lincoln, NE). Calculations were performed according to von Caemmerer and Farquhar (1981). Measurements were made in the tracking mode at ambient carbon dioxide concentration, C_a = 36 Pa on young, well-exposed, fully expanded leaves (n = 6–12) in three leaf-to-fruit ratio treatments (25, 50 and 100 LF). Measurements were performed from 0800 to 1600 h on 7 days between November 15, 2000 and January 4, 2001, on six branches per treatment.

Parameters of the response of net photosynthesis to PPF, p_3 and p_4, were estimated regardless of the leaf-to-fruit ratio, based on the whole set of leaf gas exchange data and nonlinear least-squares regression. The function g(PPF), representing the radiation received by the shaded leaves, was determined from radiation measurements gathered over 3 days with an SP Lite pyranometer (Kipp & Zonen, Delft, Holland). Measurements were made successively above shaded leaves (PPF_{shaded}) and above sunlit leaves (PPF_{sunlit}). The parameters of the g function were estimated by linear least-squares regression.

Light-saturated leaf photosynthesis was derived from gas exchange data measured when PPF was > 1300 μmol m^{-2} s^{-1}. Parameters p_1 and p_2 of Equation 1 were estimated by nonlinear least-squares regression from data of light-saturated photosynthesis obtained on leaves from the 25, 50 and 100 LF treatments during the 2000 growing season. Fruit demand was measured on fruits on the same branch and was calculated from their growth rate, dry mass and C content.

Total leaf area per branch (LA; m^2) was empirically calculated from the number of leaves (n_{leaves}; $R^2 = 0.94$ and $n = 50$):

$$LA = 0.0051(n_{leaves})^{0.937} \quad (11)$$

The growth respiration coefficient was derived from construction cost measurements on peel, flesh and stone of mango fruit made during the 2000 growing season. Total nitrogen (N) and C concentrations (g g_{DM}^{-1}) of each tissue sample were measured on 5 mg of powdered plant material with an automated CN analyzer (Carlo Erba analyzer ANA1500, Thermo Finnigan, Les Ulis, France) according to the ANCA-MS technique. Ash content was determined by combustion of 1-g aliquots for 12 h in a muffle furnace at 420 °C and weighing the residue. The construction cost (CC; g glucose g^{-1}) was calculated as a function of the carbon (C), nitrogen (N) and ash (A) concentrations (g g_{DM}^{-1}) of fruit tissue, and the energetic costs of N assimilation and carbohydrate translocation (Vertregt and Penning de Vries 1987, Wullschleger et al. 1997):

$$CC = (5.39C + 0.80A + 5.64 f_{Nh} N - 1.191)(1 + r_T) \quad (12)$$

where f_{Nh} is the fraction of N used in growth that is assimilated heterotrophically, assumed to be equal to 1 for fruits (Wullschleger et al. 1997), and r_T is the added cost of translocating photosynthates from sources to sinks, assumed to be equal to 5.3% (Vertregt and Penning de Vries 1987). Fruit CC was cal-

culated as the weighted mean of the CCs of the various fruit tissues.

The coefficient GRC_{fruit} (g C g_{DM}^{-1}) is expressed in the model:

$$GRC_{fruit} = CC\alpha - c_{fruit} \quad (13)$$

where $CC\alpha$ is the construction cost in C ($\alpha = 0.4$, the concentration of C in glucose) and c_{fruit} is fruit C content.

In 2002, total fruit respiration was derived from gas exchange measurements on fruits during 4 days in the growing season before the ripening stage (100 to 133 and 100 to 126 days after full bloom for the 10 and 100 LF treatments, respectively). On each measurement day, three fruits from the 10 and 100 LF treatments were harvested, weighed and placed in a closed chamber. Carbon dioxide production was measured over 5 h by gas chromatography (with an Agilent M200 apparatus, Agilent Technologies, Palo Alto, CA). A column (Poropak type B) was used isothermally at 60 °C. The carrier gas was helium. Total respiration rate per fruit (R; g C day^{-1}) was described according to the model of Thornley (1970), which accounts for both maintenance and growth respiration:

$$R = MRR_{fruit}DM + GRC_{fruit}\frac{dDM}{dt} \quad (14)$$

where DM is fruit dry mass (g), dDM/dt is fruit growth rate (g day^{-1}), and MRR_{fruit} and GRC_{fruit} are the coefficients for maintenance (g C g^{-1} day^{-1}) and growth (g C g^{-1}) respiration, respectively. We estimated MRR_{fruit} by linear regression with Equation 14, and the value of GRC_{fruit} was calculated with Equation 13 based on measurements of total fruit respiration. Fruit dry mass was determined from fruit fresh mass by an allometric relationship, and dDM/dt was derived from fruit dry mass.

We used the values of maintenance respiration rates of stem (MRR_{stem}) and leaves (MRR_{leaves}) at 20 °C, and the corresponding Q_{10} values (Grossman and DeJong 1994) for peach. We used the Q_{10} value for peach fruit maintenance respiration proposed by DeJong et al. (1987).

Parameters of potential fruit growth (RGR_f^{ini}, a and b) were estimated from measurements of seasonal variation in fruit growth in the 100 and 150 LF treatments during the 2000 growing season, and in the 100 LF treatment during the 2001 and 2002 growing seasons.

Daily variation in degree days (Δdd) was computed based on the maximum and minimum daily temperatures recorded, and on the lower and upper temperature thresholds (Baskerville and Emin 1969). Growth and development of tropical plants often occur between 10 and 40 °C (Mosqueda-Vasquez and Ireta-Ojeda 1993). We fixed the upper temperature threshold at 40 °C. We estimated the base temperature (T_b) for mango fruit development in La Réunion and the parameters of potential fruit growth by minimizing the following criterion:

$$\sum_k \sum_j \frac{1}{N_{kj}} \sum_i (DM_{kji}^c - DM_{kji})^2 \quad (15)$$

where k is the data set, N_{kj} is number of fruits measured for data set k at date j, and DM_{kji}^c and DM_{kji} are the dry mass of fruit i, calculated by Equations 5 and 6, respectively, and measured at date j for data set k.

Reserve mobilization parameters, r_4 for the mobile fraction of leaf reserves and r_5 for the mobile fraction of stem reserves, were assessed by model calibration. For the calibration procedure, we used the leaf and stem reserve data collected between 0800 to 1600 h from November 15, 2000 to January 4, 2001 (no relationship between time of day and reserve content was found). On each measurement day, leaf areas and fresh masses of the different components (stem and leaves) were measured. A sample of each component was weighed, freeze-dried and its dry mass recorded. The freeze-dried samples were then stored at –20 °C until analyzed for glucose, fructose and sucrose concentrations by high performance liquid chromatography (HPLC) following the method of Gomez et al. (2002). Starch was determined by enzymatic hydrolysis to glucose (Gomez et al. 2003).

The criterion minimized during model calibration takes into account the reserve concentrations of both leaves and stem:

$$\sum_{k=1}^{3} \frac{1}{\sigma^2_{SR_k} N_{SR_k}} \sum_i n_{ki} (SR_{ki}^c - \overline{SR}_{ki})^2 + \frac{1}{\sigma^2_{LR_k} N_{LR_k}} \sum_i n_{ki} (LR_{ki}^c - \overline{LR}_{ki})^2 \quad (16)$$

where k is the leaf-to-fruit ratio treatment (25, 50 and 100 LF), SR and LR are the reserve concentrations (g g_{DM}^{-1}) in stem and leaves, respectively, σ^2 is the variance in observed data, N is the number of measurement dates per treatment, n_{ki} is the number of measurements at date i for treatment k, xR_{ki}^c is the C reserve concentration at date i for treatment k calculated by the model, and $\overline{xR}_{ki}$ is the corresponding mean of n_{ki} measurements, where x = S for stem and x = L for leaves.

Model evaluation: measurements of fruit growth and statistics

Two types of fruit growth measurements were made: continuous diameter measurements during the growing season (nondestructive); and diameters, fresh and dry masses at given dates (destructive). During the first flowering period of the 2000 growing season, six fruits from five leaf-to-fruit ratio (10, 25, 50, 100 and 150 LF) treatments were harvested on 7 days between November 15, 2000 and January 4, 2001. The diameters of eight fruits, all originating from the first flowering period, and the diameters of eight additional fruits, from the second flowering period, were measured on 9 days between October 29 and December 20, 2000, and on 6 days between December 11, 2000 and February 7, 2001, respectively. These measurements were performed for the 10, 25, 50, 100 and 150 LF treatments for the first flowering period, and for the 10, 25, 50, 75 and 100 LF treatments for the second period. In 2001, there was only one flowering flush. Six fruits from the 10 and 100 LF treatments were harvested on 7 days between October 19, 2001 and January 21, 2002. During the 2002 growing season, the diameters of 10 fruits from the 100 LF

treatment were measured on 8 and 7 days for the two flowering periods in Orchard 2, and on 8 days for the first flowering period in Orchard 1. Dry mass (DM) of the fruit was related to fruit diameter (D) by an empirical relationship obtained from the 2001 data ($R^2 = 0.91$, $n = 210$):

$$DM = 0.8736\, e^{0.0527D} \quad (17)$$

The model was tested with all data sets obtained during 2000, 2001 and 2002 growing seasons for each leaf-to-fruit ratio. The climatic conditions of the corresponding year and fruit dry mass of the corresponding branch at the first date of measurement were used as input data to run the model. The initial values of stem dry mass, and reserve concentrations in the stem and in the leaves, were means obtained from measurements on stems ($n = 104$) and leaves ($n = 232$). We compared simulated and measured fruit growth of individually monitored fruits. The standard deviation of simulated values was calculated by running the model for each single initial fruit dry mass value.

The experimental setup is described in Table 2. The root mean squared error (RMSE) method, which describes the mean distance between simulation and measurement data (Kobayashi and Salam 2000), evaluated (1) the goodness of fit of the model for data used for parameter estimation (quality of adjustment) and (2) the predictive quality of the model on independent data. The RMSE design was:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{N} n_i (DM_i^c - \overline{DM}_i)^2}{\sum_{i=1}^{N} n_i}} \quad (18)$$

where DM_i^c is fruit dry mass at date i simulated by the model and $\overline{DM}_i$ is mean dry mass measured at date i for n_i fruits. A relative RMSE (RRMSE) was calculated as the ratio between the RMSE and the mean of all measurements.

Simulations

The model was run from dd = 350 by combining three factors: weather, leaf-to-fruit ratio and initial fruit dry mass. For weather, 14 scenarios were chosen, corresponding to seven growing seasons between 1996 and 2002, and two experimental sites, one in the northwest of the island and the other in the southwest, which correspond to the two extremes of the production zone of mango on La Réunion Island and which differ in daily mean temperature and total radiation. Mean daily temperature over the fruit growth season was 1 °C higher and daily irradiation was 6.5 mol m^{-2} higher in the southwest than in the northwest. Three leaf-to-fruit ratios were tested: 50 and 100, corresponding to realistic field conditions; and 10, corresponding to an extreme condition. Low and high values of initial fruit dry mass, 7 and 21 g, respectively, were considered to cover a realistic range of initial values. Because temperature strongly influences rates of fruit growth and maturation, temperature sum (dd; degree days) is often used as an index of physiological time. We observed that the mean temperature sum to reach harvest was about 1100 degree days after full bloom (data collected over three growing seasons and at three leaf-to-fruit ratios). A dd = 1100 is in agreement with the calculated heat units required to reach maturity for other mango cultivars, such as 'Carabao' (Mendoza and Wills 1984). Therefore, simulations were terminated at dd = 1100.

Table 2. The experimental setup to calibrate and validate the model. Abbreviation: LF = leaf-to-fruit ratio.

Flowering episode	LF	Measurement	Use of data
2000			
First	10	Destructive	Validation
	25	Destructive	Calibration
	50	Destructive	Calibration
	100	Destructive	Calibration
	150	Destructive	Validation
First	10	Nondestructive	Validation
	25	Nondestructive	Validation
	50	Nondestructive	Validation
	100	Nondestructive	Calibration
	150	Nondestructive	Calibration
Second	10	Nondestructive	Validation
	25	Nondestructive	Validation
	50	Nondestructive	Validation
	75	Nondestructive	Validation
	100	Nondestructive	Calibration
2001			
One	10	Destructive	Validation
	100	Destructive	Calibration
2002			
First (Orchard 1)	100	Nondestructive	Calibration
First (Orchard 2)	100	Nondestructive	Calibration
Second (Orchard 2)	100	Nondestructive	Calibration

Photosynthesis, mobilization of leaf and stem reserves, maintenance and growth respiration, demand and growth rate of the fruit were measured daily. The mean values of each variable were subjected to analysis of variance (fixed effects) to identify the main effects and the first-order interactions of the three factors, i.e., weather, leaf-to-fruit ratio and initial fruit dry mass. The contribution of the different factors and interactions to the variance of the studied variables was calculated as the ratio of the corresponding sum of squares to the total sum of squares.

Results

Estimation of model parameters

Construction costs (CC), measured during the 2000 season on fruit tissues from the 25, 50 and 100 LF treatments, were 1.19 ± 0.07 g glucose g^{-1} ($n = 69$) for the peel, 1.06 ± 0.03 g glucose g^{-1} ($n = 69$) for the pulp and 1.23 ± 0.04 g glucose g^{-1} ($n = 69$) for the stone, respectively. The resulting global fruit cost was 1.11 ± 0.03 g glucose g^{-1} ($n = 69$). This value is consistent with data for grapevine fruit (1.1–1.4 g glucose g^{-1}; Vivin et al.

2003) and tomato fruit (1.15–1.24 g glucose g^{-1}; Gary et al. 1998). For the flesh component, CC was close to that estimated for cantaloupe flesh (1.11 g glucose g^{-1}; Valantin et al. 1999), whereas the CC cost estimated for seeds of cantaloupe (1.2–1.8 g glucose g^{-1}) appears higher than for mango stone. The estimated coefficient of growth respiration was GRC_{fruit} = 0.04 ± 0.01 g C g^{-1} (n = 69), which is in the range of values found for tomato (0.112 g C g^{-1}; Penning de Vries et al. 1989), peach (0.0843 g C g^{-1}; Dejong and Goudriaan 1989) and cucumber (0.043 g C g^{-1}; Marcelis and Baan Hofman-Eijer 1995). For maintenance respiration, the coefficient was estimated at $MRR_{fruit} = 1.15 \times 10^{-3} \pm 1.1 \times 10^{-4}$ g C g^{-1} day^{-1} (n = 30), a value close to those estimated for peach (6.7×10^{-4} g C g^{-1} day^{-1}; Dejong and Goudriaan 1989), cucumber (4.1×10^{-3} g C g^{-1} day^{-1}; Marcelis and Baan Hofman-Eijer 1995), tomato (3.3×10^{-3} g C g^{-1} day^{-1}; Walker and Thornley 1977) and lettuce (2.6×10^{-3} g C g^{-1} day^{-1}; Van Iersel 2003).

Mean calculated light-saturated photosynthesis was 10.8, 9.8 and 7.6 µmol CO_2 m^{-2} s^{-1} for leaves from 25, 50 and 100 LF treatments, respectively (Figure 1). The decrease was about 10% in leaves of the 50 LF treatment compared with leaves of the 25 LF treatment, and about 22% in leaves of the 100 LF treatment compared with leaves of the 50 LF treatment. This decrease is in the same range as that observed for net assimilation in mango leaves by Urban et al. (2002). Light-saturated photosynthesis increased as fruit demand increased, regardless of the treatments (Figure 1). Estimated parameter values relating light-saturated photosynthesis and fruit demand in Equation 1 were: p_1 = 3.85 ± 0.57 µmol CO_2 m^{-2} s^{-1} g^{-1} C and p_2 = 33.23 ± 11.91 µmol CO_2 m^{-2} s^{-1} (n = 60). The P^*_{max} value was 15 µmol CO_2 m^{-2} s^{-1}, the maximal value of all measurements of leaf photosynthesis performed during this trial. This value is at the low end of the range of values estimated for several other tree species (13–26 µmol CO_2 m^{-2} s^{-1}; Higgins et al. 1992). The estimated parameters linking net photosynthetic response to PPF were p_3 = 0.483 ± 0.074 (n = 289) and p_4 = 0.034 ± 0.007 (n = 289). For shaded leaves, the g(PPF) function was (R^2 = 0.96, n = 142):

$$PPF_{shaded} = 0.0529\,PPF_{sunlit} \quad (19)$$

We obtained a base temperature of 16.0 °C, which is in the range of base temperatures published for mango fruit, i.e., 0.33–17.9 °C (Oppenheimer 1947 cited in Shinde et al. 2001; Mosqueda-Vasquez and Ireta-Ojeda 1993). The values of parameter estimates of potential fruit growth obtained from seasonal fruit dry mass under conditions of non-limiting growth were RGR_f^{ini} = 0.0105 ± 0.0003 dd^{-1} (n = 384), a = 16.736 ± 1.637 and b = 0.624 ± 0.036. The initial relative growth rate is of the same order of magnitude as that estimated for peach fruit (0.009 dd^{-1}; Lescourret et al. 1998).

Values of the mobilization of reserves parameters r_4 (obile fraction of leaf reserves) and r_5 (mobile fraction of stem reserves) were 0.0162 (n = 232) and 0.0164 (n = 104), respectively. These parameters allowed us to predict seasonal changes in leaf and stem reserve concentrations corresponding to the data sets for model adjustment (25, 50 and 100 LF treatments), and to another independent data set (10 and 150 LF

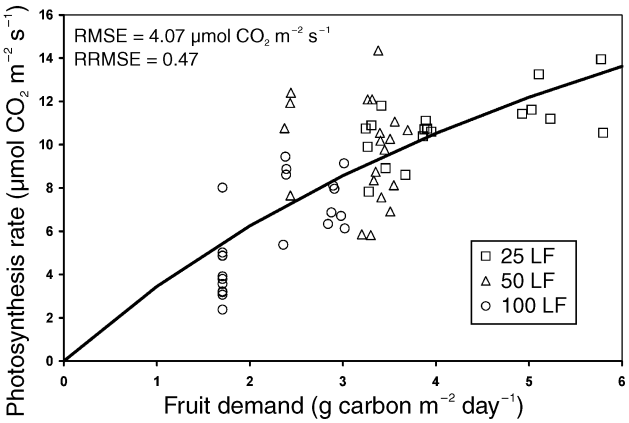

Figure 1. Light-saturated photosynthesis as a function of fruit demand for three leaf-to-fruit ratio treatments (25, 50 and 100 LF). Symbols and the solid line represent measured values and the function fitted to experimental data, respectively. Abbreviations: RMSE = root mean squared error; and RRMSE = relative root mean squared error.

treatments) (Figure 2). Leaf and stem reserve concentrations decreased during fruit growth in all treatments (Figure 2). The model absolute error (RMSE) was about 0.027 and 0.013 g C g^{-1} for observed values varying between 0.04 and 0.20 g C g^{-1}

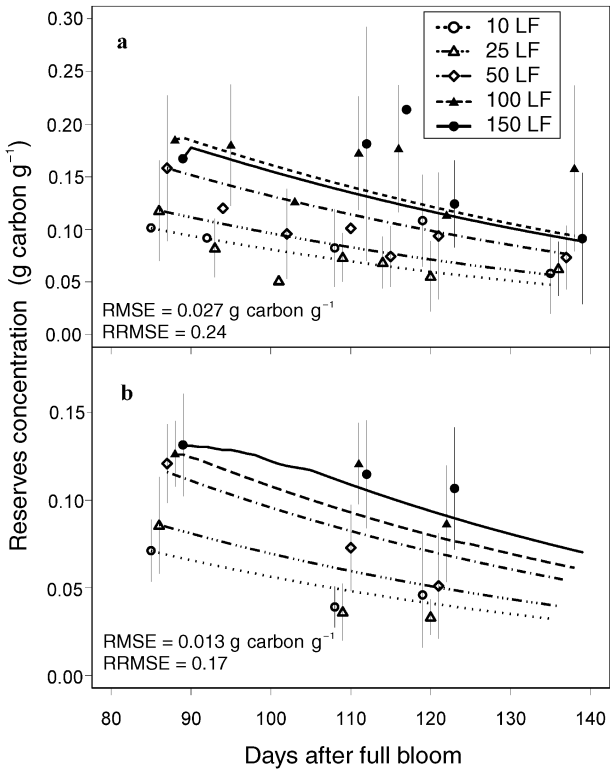

Figure 2. Observed (symbols) and model-predicted (lines) values of reserve concentrations (g carbon g^{-1}) in leaves (a) and stem (b), for five leaf-to-fruit ratio treatments (10, 25, 50, 100 and 150 LF). Vertical bars represent standard deviations of measurements.

and 0.04 to 0.14 g C g^{-1}, respectively, which corresponds to relative errors (RRMSE) of 17 and 24%.

Model testing

The results of the simulations for the different leaf-to-fruit ratios and the different years are presented in Figure 3. The RRMSE values for adjustment quality (Figure 3) and predictive quality (Figure 4) are considered acceptable because they were always less than 21 and 15%, respectively. Variability in fruit growth within each LF treatment, described by the standard deviation for mean fruit dry mass, was large. The model correctly simulated this variability in the high LF treatments. The model also correctly simulated the global decrease in fruit growth from years 2000 to 2001 for non-limiting source conditions (100 LF treatment; Figure 3).

Analysis of model sensitivity to parameters

A sensitivity analysis of final fruit dry mass was performed

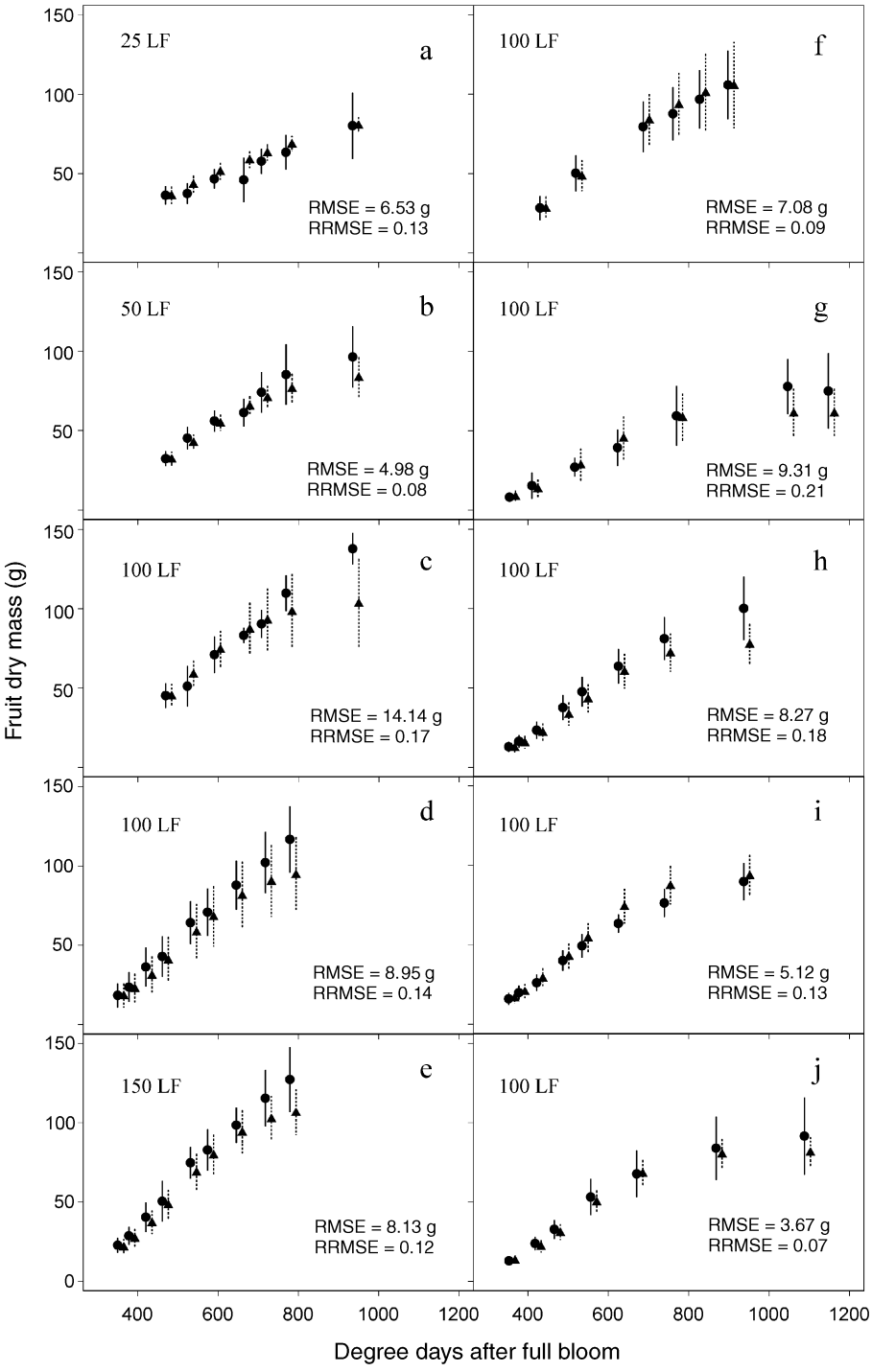

Figure 3. Means and standard deviations of fruit dry mass according to degree days, either observed (● and solid line) or predicted by the model (▲ and dotted line, offset by 15 degree days to ensure readability). Corresponding data sets were used for parameter estimation and include (1) years 2000 (a–f), 2001 (g) and 2002 (h–j); (2) destructive (a–c, g) and nondestructive measurements (d–f, h–j); and (3) first (a–e, g–i) and second flowering (f, j). The leaf-to-fruit ratio (LF), root mean squared error (RMSE) and relative mean squared error (RRMSE) are indicated in each graph.

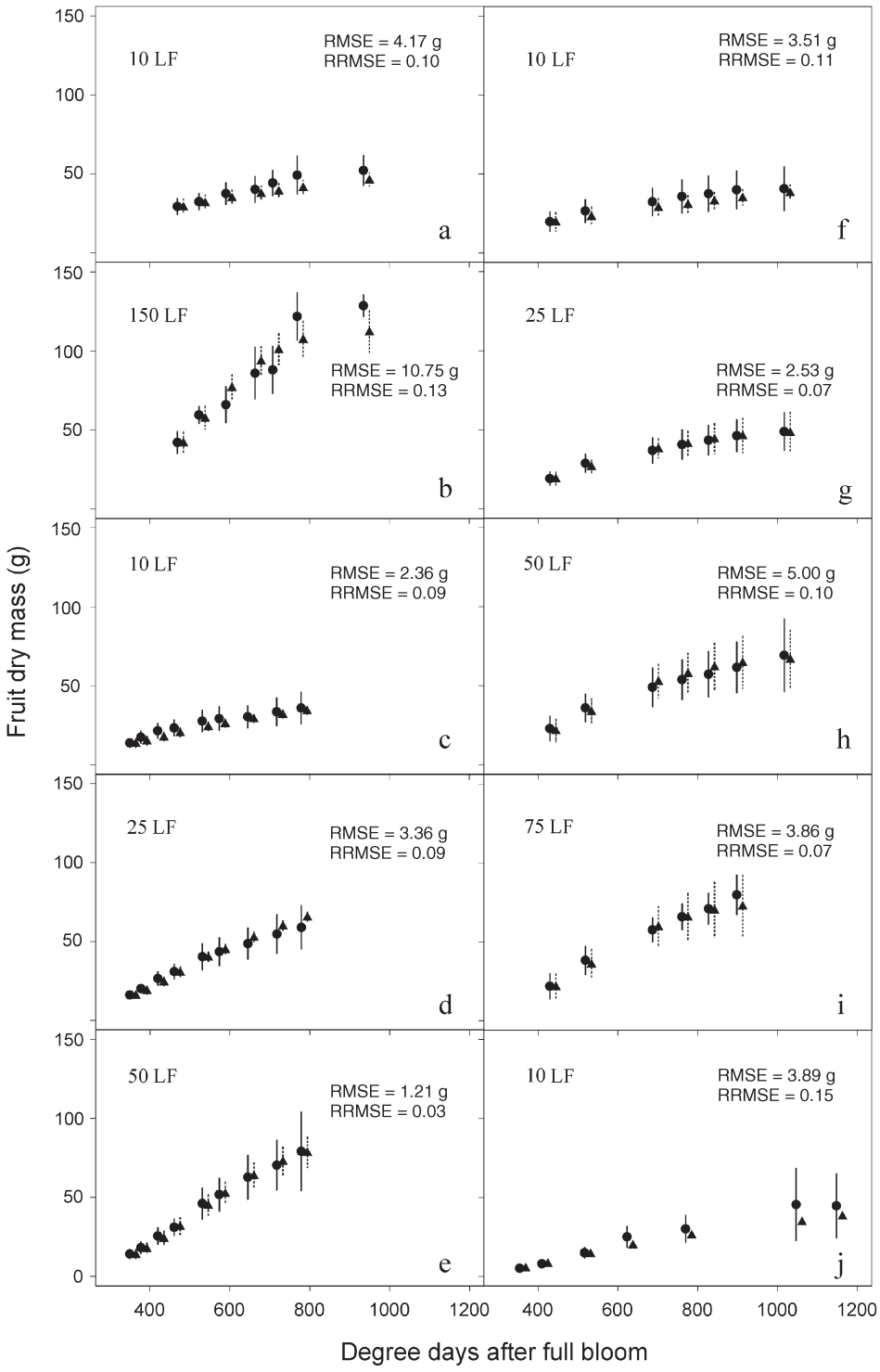

Figure 4. Means and standard deviations of fruit dry mass according to degree days, either observed (● and solid line) or predicted by the model (▲ and dotted line, offset by 15 degree days to ensure readability). Corresponding data sets were used for evaluation of the predictive quality of the model and include (1) year 2000 (a–i) and 2001 (j); (2) destructive (a–b, j) and nondestructive measurements (c–i); and (3) first (a–e, j) and second flowering (f–i). The leaf-to-fruit ratio (LF), root mean squared error (RMSE) and relative mean squared error (RRMSE) are indicated in each graph.

based on the environmental conditions of the growing season in 2000, which extended from Days 67 to 119 after full bloom, for three leaf-to-fruit ratios, corresponding to the 10, 50 and 100 LF treatments. The model appeared to be sensitive to the parameters of potential fruit growth, especially the initial fruit dry mass at 350 degree days (DM_f^{ini}), from which maximum final dry mass was calculated, regardless of treatments (Table 3). Variations in *a* and *b*, parameters required to calculate the potential dry mass at harvest, also had an effect on final fruit dry mass, but only for fruits from the 50 and 100 LF treatments, which correspond to intermediate and sink-limiting conditions, respectively. The model was less sensitive to the parameters of potential fruit growth and fruit demand, RGR_{ini} and GRC_{fruit}, and to the parameters of fruit maintenance respi-

Table 3. Sensitivity of final fruit dry mass to ± 20% variations in model parameters. Values are expressed as a percentage of the reference condition. Simulations for the calculation of final fruit dry mass were performed on fruits from treatments 10, 50 and 100 leaves per fruit (LF) during the 2000 growing season. See Table 1 for definitions of parameter abbreviations; DM_f^{ini} = initial fruit dry mass at 350 degree days.

Parameter	Extent of variation (%)	Treatment		
		10 LF	50 LF	100 LF
Carbon assimilation by leaves				
P^*_{max}	+20	+11	0	0
	–20	–12	0	0
p_1	+20	+2	+4	0
	–20	–3	–9	–3
p_2	+20	+9	+2	0
	–20	–10	–4	–2
p_3	+20	0	0	0
	–20	0	0	0
p_4	+20	+2	+1	0
	–20	–3	–2	–1
Maintenance respiration				
MRR_{stem}	+20	–1	–1	0
	–20	+1	+1	0
MRR_{leaves}	+20	–1	–1	0
	–20	+1	+1	0
MRR_{fruit}	+20	–2	0	0
	–20	+2	0	0
Q_{10}^{leaves}	+20	0	0	0
	–20	+1	0	0
Q_{10}^{stem}	+20	0	0	0
	–20	0	+1	0
Q_{10}^{fruit}	+20	–1	0	0
	–20	+1	0	0
Fruit demand				
RGR_f^{ini}	+20	+2	+5	+3
	–20	–2	–9	–6
DM_f^{ini}	+20	+9	+10	+12
	–20	–9	–14	–13
a	+20	+1	+13	+15
	–20	–1	–17	–19
b	+20	+1	+22	+26
	–20	–1	–24	–29
GRC_{fruit}	+20	–1	0	0
	–20	+1	0	0
c_{fruit}	+20	–7	–2	–1
	–20	+9	+2	0
Reserve mobilization				
r_4	+20	0	0	0
	–20	0	0	0
r_5	+20	0	0	0
	–20	0	0	0

ration. For the parameters of C assimilation by leaves, final fruit dry mass was sensitive to parameters p_2 and P^*_{max}, but only for fruits from the 10 LF treatment (which corresponds to a source-limiting condition) and to parameters p_1 and p_2 for fruits of the 50 LF treatment. Variations in parameters of maintenance respiration and mobilization of leaf and stem reserves did not affect final fruit dry mass, regardless of the treatments.

Contributions of weather changes, initial fruit dry mass and leaf-to-fruit ratio to fruit growth and the underlying physiological processes

The contributions of the different factors and their interactions to the variance of the studied variables are presented in Table 4. Weather, initial fruit dry mass and leaf-to-fruit ratio significantly affected all of the studied variables. Under natural conditions (Table 4), the contribution of initial fruit dry mass was the highest for all sink variables, including fruit respiration (93%), demand (71.5%) and fruit growth rate (89.8%), as well as stem reserve mobilization (67.6%). The contribution of the leaf-to-fruit ratio was large for leaf photosynthesis and leaf reserve mobilization, less important for stem reserve mobilization and fruit demand, and small for fruit respiration and growth rate. Under the contrasting condition (Table 4), the leaf-to-fruit ratio contributed to more than 50% of fruit growth and the underlying physiological processes, except stem maintenance respiration. Under the contrasting condition, the contributions of the other source–sink factors and the weather were minimized; however, the contribution of the initial fruit dry mass to fruit demand was large, about 41%. The seasonal mean of daily photosynthesis was 30% higher in leaves of the 50 LF treatment than in leaves of the 100 LF treatment. Based on the simulations, the mean balance over the season between mobilization of reserves and accumulation of reserves calculated for various source–sink relationships and weather conditions was negative, almost null and positive in leaves from the 10, 50 and 100 LF treatments, respectively. Among the interactions, that between leaf-to-fruit ratio and initial fruit dry mass was the most important, regardless of leaf-to-fruit ratio conditions, through its impact on underlying processes of fruit growth, such as reserve mobilization, fruit respiration and fruit demand. The contribution of weather, i.e., daily temperature and radiation changes, was the least of the three factors examined. The contribution of weather was especially low for fruit respiration, mobilization of leaf and stem reserves, and for almost all studied variables under the contrasting conditions. The weather contributed to fruit demand between about 5 and 3% according to source–sink conditions. Under natural conditions, the largest effects of weather were on photosynthesis (about 6.2%) and fruit growth rate (about 9.3%). The simulated period of fruit growth (between 350 and 1100 degree days) was about 155 ± 23 days. The contribution of the interaction between weather and any other factor was weak.

Discussion

Quality of model predictions

The predictive quality of the model, assessed in the various LF treatments during three successive years, was statistically acceptable (RRMSE values always < 21%). The model predicted the main processes involved in fruit growth, provided that the leaf-to-fruit ratio of the studied branch was known. The model successfully predicted, regardless of the treatment, the dynamics of the pool of carbohydrates stored in leaves and stems,

Table 4. Simulated contributions of different sources of variation, weather (7 years and two sites), leaf-to-fruit ratio (50 and 100 leaves per fruit for the natural condition and 10 and 100 leaves per fruit for the contrasting condition), initial fruit dry mass (DM_f^{ini}; 7 and 21 g) and first-order interactions, to photosynthesis, rate of leaves (RM_{leaves}) and stem (RM_{stem}) reserves mobilization, seasonal mean daily fruit respiration rate (RR_{fruit}), fruit demand (D_{fruit}) and fruit growth rate. Contributions are calculated as the percent of the corresponding sum of squares of each variable to the total sum of squares. Asterisks indicate significance: ns = nonsignificant; * = $P < 0.05$; ** = $P < 0.01$; and *** = $P < 0.001$.

Variable	Photosynthesis (%)	RM_{leaves} (%)	RM_{stem} (%)	RR_{fruit} (%)	D_{fruit} (%)	Fruit growth rate (%)
Natural condition						
Weather (C)	6.2 ***	1.3 ***	3.3 ***	1.4 ***	4.6 ***	9.3 ***
Leaf-to-fruit ratio	67.8 ***	71.0 ***	15.6 ***	3.3 ***	14.0 ***	0.2 ***
DM_f^{ini}	25.5 ***	23.5 ***	67.6 ***	93.0 ***	71.5 ***	89.8 ***
C:LF	0.1 ***	0.6 ***	1.5 *	0.0 ns	0.3 *	0.0 ns
$C:DM_f^{ini}$	0.1 ***	0.2 ns	0.6 ns	0.1 ***	0.7 ***	0.4 ***
$LF:DM_f^{ini}$	0.3 ***	3.4 ***	10.9 ***	2.1 ***	8.8 ***	0.2 ***
Residuals	0.0	0.1	0.5	0.0	0.1	0.0
Contrasting condition						
Weather (C)	0.7 ***	0.8 ***	3.0 **	0.5 ***	3.0 ***	1.7 ***
Leaf-to-fruit ratio	96.7 ***	77.4 ***	0.2 ns	58.2 ***	50.8 ***	76.9 ***
DM_f^{ini}	1.4 ***	10.4 ***	46.4 ***	33.3 ***	40.9 ***	10.2 ***
C:LF	0.3 ***	0.8 ***	2.7 **	0.1 ***	0.3 ***	0.6 ***
$C:DM_f^{ini}$	0.0 ns	0.1 ns	0.7 ns	0.0 **	0.3 ***	0.1 ns
$LF:DM_f^{ini}$	0.9 ***	10.4 ***	46.4 ***	7.8 ***	4.7 ***	10.6 ***
Residuals	0.0	0.1	0.7	0.0	0.0	0.1

which reflects the source–sink balance of the system (Layne and Flore 1993, Iglesias et al. 2002).

Effect of initial fruit dry mass on source–sink relationships

Differences in fruit size are mainly a result of differences in cell count, with cell size having only a minor effect (Bradley 1959). Fruit size is therefore generally regarded as a function of cell division during the early stages of fruit growth (Westwood 1967). Early fruit size assessed after completion of the cell division phase appears to be a good indicator of cell number in fruit flesh. In apple, Stanley et al. (2000) found that, under conditions of non-limiting growth after the cell division phase, fruit mass at harvest was well correlated with fruit mass 50 days after pollination, which is comparable to the date at which we determined the initial fruit dry mass. In kiwifruit, measurements made 50 days after anthesis explain nearly 75% of the variation in fruit growth (Hall et al. 1996). By relating potential fruit mass to early fruit size (i.e., for mango, DM_f^{ini} at 350 degree days), our model highlights the influence of cell number on fruit growth. Sensitivity analysis showed that the model is highly sensitive to DM_f^{ini}, and our virtual experiment showed that DM_f^{ini} contributes more to fruit growth rate than weather and other source–sink factors such as leaf-to-fruit ratio. Use of DM_f^{ini} to calculate DM_f^{max} allowed us to model variability from one year to another, especially between 2000 and 2001, two years characterized by profoundly different rates of fruit growth. Limited fruit growth was observed in 2001, regardless of the treatments, as was lower DM_f^{ini}. Small fruit size during the early stages of development could be a result of resource limitation during cell division.

Effect of leaf-to-fruit ratio on source–sink relationships

Variations in simulated reserves in the 10 and 25 LF treatments are consistent with data for cherry and citrus showing that foliar carbohydrate concentrations are low and decrease in source-limiting conditions (Layne and Flore 1993, Iglesias et al. 2002). Similarly, it has been reported that storage carbohydrate concentrations are high in leaves as a result of a light crop load in apple (Wünsche et al. 2000) and pecan (Marquard 1987) trees, as in mango leaves in the 100 LF treatment. The high foliar carbohydrate concentration suggests that not all assimilates produced by leaf photosynthesis are used to support fruit growth (Warren-Wilson 1972). Increasing the leaf-to-fruit ratio from 50 to 100 LF increased source size and thus the production of assimilates of the branch, but there was no substantial increase in fruit size. Our findings at the source and sink levels confirm that, in the case of non-limiting C supply, i.e., high leaf-to-fruit ratio, fruit growth rate is limited by sink size, as reported previously (Wareing and Patrick 1975). The sink limitation was balanced by the buffer role played by reserves, as previously observed in sour cherry trees (Layne and Flore 1993) and alfalfa (Baysdorfer and Bassham 1985). Carbohydrates produced in excess of fruit demand were mainly stored in the leaves in the 100 LF treatment, as indicated by both the simulated and measured reserve concentrations.

Changes in source–sink balances in response to leaf-to-fruit ratio or crop load are generally associated with alterations in source activity (Wünsche et al. 2000) that result in a significant decrease in leaf photosynthesis, as we observed in mango with increasing leaf-to-fruit ratio. Similar findings have been reported for peach (Ben Mimoun et al. 1996, Quilot et al. 2004), grapevine (Naor et al. 1997) and apple (Palmer 1992). This relationship is well represented by the empirical relationship between fruit demand and light-saturated photosynthesis

used in our model. Several studies have shown that end-products of C fixation play a role in the feedback inhibition of photosynthesis (Goldschmidt and Huber 1992, Iglesias et al. 2002). Lescourret et al. (1998) chose to use a direct relationship between the amount of leaf reserves and light-saturated photosynthesis in their model of fruit growth. However, Quereix et al. (2001) suggested that a phloem-based feedback signal related to source–sink balance may also play a major role in photosynthesis regulation.

Leaf N content is an important determinant of photosynthetic capacity (Harmens et al. 2000). Photosynthetic capacity of leaves and the amount of leaf N per unit leaf area increase in the presence of fruits (Urban et al. 2003). It may be possible to use biochemical models of photosynthesis that take account of the effects of changes in source–sink relationships on photosynthetic capacity to improve fruit growth models.

Effects of weather on source–sink relationships

Simulations have shown that weather influences processes involved in fruit growth at the source level (photosynthesis) as well as at the sink level (fruit demand and growth rate). The effects of weather on photosynthesis include: (1) the direct effect of light on the rate of electron flow, which depends on the PPF (Farquhar et al. 1980); and (2) the indirect effect of light on the leaf mass-to-area ratio and on leaf N content per leaf area (Urban et al. 2003). In our model, only the direct effect was considered; however, a strong effect of light on the mass-to-area ratio has been observed in mango leaves (Urban et al. 2003). Direct and indirect effects of light on photosynthesis need to be represented in a more detailed way in future versions of our model.

The contribution of weather to fruit demand could be associated with the daily variation in degree days used to compute fruit demand. The sum of growing degree days from full bloom varied among seasons, confirming that seasonal temperature profiles differ between seasons and among sites (cf. Stanley et al. 2000). In our study, the response of fruit growth to changes in temperature between seasons was in accordance with our simulation results. An analysis of variance indicated that fruit growth differed significantly but weakly among sites and among seasons.

The small contribution of weather to fruit growth can be explained by the interannual variation in duration of fruit growth as indicated by the simulations. This variation of about 23 days was of the same order as the variation in mean harvest date (Bérnard Augais, Établissement Public Local d'Enseignement et de Formation Professionnelle Agricole de St-Paul, France, personal communication). A similar variation in the time from pollination to harvest between years has been noted previously; for apples, it varies from 132 to 157 days after full bloom (Stanley et al. 2000). The influence of temperature during the early stages of fruit development has been identified in many species, including satsuma mandarin (Marsh et al. 1999) and apples (Austin et al. 1999). It has been suggested that temperature may affect the rate of cell division, which was not considered in our model, whereas it may have less impact on the cell expansion phase.

The contribution of weather to fruit growth was less than the contribution of source–sink factors. Several studies are consistent with this finding. Robinson et al. (1991) reported no significant variation in fruit size assessed over 10 years in two apple cultivars. Temperature after cell division explained a minor part of the total variation in kiwifruit growth rate (Hall et al. 1996). These experimental results and simulations indicate that, although temperature may affect fruit growth, other factors, particularly those influencing source–sink balance, are much more important.

We studied the roles of source activity, sink demand, fruit respiration and leaf and stem reserves in mango fruit growth with field trials and simulations. Our model accurately accounted for variations in these factors and their interactions, and predicted with good accuracy variations in fruit dry mass on girdled branches. Because all branches were girdled in the same manner, regardless of the leaf-to-fruit ratio, treatments could be compared and conclusions about the effect of leaf-to-fruit ratio on factors playing a role in fruit growth can be considered as valid; however, additional field studies are needed to extrapolate results obtained on girdled branches to non-girdled branches. The model was sensitive to C assimilation parameters and to potential fruit growth parameters, especially the initial fruit dry mass, regardless of treatments. An accurate estimate of initial fruit dry mass is crucial for running the model. The model was less sensitive to parameters required for maintenance respiration and reserve mobilization in leaves and stem. Simulations of fruit growth made under various weather conditions and at different source–sink levels (initial fruit dry mass and leaf-to-fruit ratio) demonstrate that if weather contributes to the variations in leaf photosynthesis, fruit demand and fruit growth rate, the contribution to fruit growth and fruit size is globally lower than that of the initial fruit dry mass and the leaf-to-fruit ratio. Further studies are needed to determine if the effects of climatic factors become more important at particular periods of fruit growth, especially during the initial phase.

Acknowledgments

The authors gratefully acknowledge J. Joas and Y. Caro (CIRAD-Réunion, Pôle Agroalimentaire) for assistance with total fruit respiration measurements, and D. Bancel and E. Rubio (INRA-Avignon, Unité PSH) for assistance with biochemical analysis. This work was partly funded by the Action Thématique Programmée CIRAD-INRA "Modélisation de la croissance des fruits dans une architecture ligneuse pour une meilleure maîtrise de la production et de sa qualité."

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Appendix 1

Figure A1. Schematic representation of the model. Model parameters: p_1 = initial slope of response curve of light-saturated photosynthesis to fruit demand; p_2 = parameter of the response of light-saturated photosynthesis to fruit demand; P^*_{max} = potential light-saturated photosynthesis; p_3 and p_4 = parameters of the response of leaf photosynthesis to radiation and light-saturated photosynthesis; r_4 and r_5 = mobile fraction of reserves in leaves and stem, respectively; temperature; MRR_{fruit}, MRR_{leaves} and MRR_{stem} = maintenance respiration rate of fruit, leaves and stem, respectively; Q_{10}^{fruit}, Q_{10}^{leaves} and $Q_{10}^{stem} = Q_{10}$ value for fruit, leaves and stem, respectively; GRC_{fruit} = growth respiration coefficient of the fruit; a and b = parameters for computing maximum fruit dry mass from initial fruit dry mass; DM_f^{ini} = initial fruit dry mass; RGR_f^{ini} = initial relative growth rate; and c_{fruit} = carbon content of fruit.