The Conveyor Belt Model for Fruit Bearing Vegetables: Application to Sweet Pepper Yield Oscillations

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Keywords: *Capsicum annuum*, crop growth model, yield oscillations, fruit abortion, bifurcation analysis

Abstract

An absolute-sink-strength regulated crop growth model was developed to address the problem of sweet pepper synchronised yield oscillations (flushes). Yield oscillations in sweet pepper production are caused by crop physiology (fruit abortion at times of heavy fruit load per plant) and result in periodic oversupply at the market level, as synchronisation occurs within, but also between glasshouses, due to weather conditions. Smart growers may not only aim to maximise production yields, but also to desynchronise their temporal yield pattern from that of the market, in order to target higher prices during low supply periods. The parameters that growers can change are those concerning pruning, harvesting at a green marketable stage, and climate control, whereas breeders may adjust physiological constants. The model consists of three ordinary differential equations and two partial differential equations, with fruit dry weight as second independent variable. Both the number of fruits per square meter and the average ripeness of fruits with a particular weight are discretised into 40 weight classes. Sinks, from vegetative, fruit growth and maintenance draw on a common assimilate pool, eliminating the need for a relative-sink strength 'top-down' partitioning approach. The vegetative biomass is considered as two parts, for growing and non-growing biomass respectively. The model arrives at plausible output values for known biological variables and simulates assimilate-dependent abortion and thus fruit set explicitly, although not yet fully validated. A bifurcation analysis is conducted to identify the regions in parameter space where either yield oscillations or a stable growth pattern occurs.

INTRODUCTION

A major complication for growers of sweet (bell) pepper (*Capsicum annuum*) is the periodic oversupply, and accompanying low prices, due to synchronous oscillations in crop yield with a period of about 6 to 8 weeks. These 'yield flushes' exist at the plant level as a result of 'abortion' (spontaneous abscission) of young fruits in periods with heavy fruit loads. The resulting 'demographic gaps' in the fruit population are difficult to prevent. To a lesser extent the growth of cucumber is characterised by the same phenomenon. Current simple models that describe crop growth make use of measured anthesis or fruit set data in order to predict harvest as a function of time (Gijzen et al., 1990; Rijsdijk and Houter, 1993; Nederhoff and Vegter, 1994). More detailed models (Gijzen et al., 1998; Marcelis et al., 2006) on the other hand, follow each new fruit with a new set of equations, which makes optimal control approaches very cumbersome.

By means of a modelling approach, of which this is the first report, we aim to identify the most effective as well as practical ways for both the breeder and the growers to control fruit dynamics with the sweet pepper case as a challenging example. We sought for a model that captures fruit demography in only a few continuous equations, treats assimilate-shortage-induced fruit abortion in an endogenous manner, includes fruit quality characteristics such as weight and ripeness, and reflects grower's practices regarding pruning and harvesting. Such a model did not seem to exist. The 'big-leaf big-fruit' model by De Koning (1994) comes close, as it does not use the cohort structure, but does not distinguish between small and large fruit altogether. Conceptually, the lettuce model by van Henten (1994) was taken as a starting point, even though it obviously had no fruit dynamics at all. Because of space limitations, we will not further review other models, for which we refer to Marcelis (1993).

MODEL DESCRIPTION

Below, all assumptions and equations of the crop model are described, for values of the constants used in the equations, see Table 1.

Assimilates Balance, Photosynthesis and Maintenance

The central variable of the model is that for the common pool of 'free assimilates', A_T (g m^{-2}). Assimilates are produced by the photosynthesis process and are used by vegetative growth, fruit growth and maintenance. One common assimilate pool is adopted following Heuvelink (1995) who reported that all sinks have reasonably fast access to all assimilates although a certain transport resistance also plays a limited role. The dynamics of the 'assimilates pool' are described by the following equation:

$$\frac{dA_T(t)}{dt} = P(I,C,T,V_i) - \sum_{i=y,o} m_i V_i - r_v \frac{\sigma_{VA_c}(A_c)}{c} V_y - \frac{\sigma_{FA_c}(A_c)}{c} \int_w g_{Fw}(w) N(w,t) dw \qquad (1)$$

in which the four terms are the input of assimilates from photosynthesis and three assimilate usage terms: for maintenance, vegetative growth and fruit growth respectively. The rest of this chapter will be used to unravel the individual components from this central equation to describe them in more detail.

The production of assimilates as a function of light (I), carbon dioxide (C), temperature (T) and vegetative structural matter (V_i), is described by the following equation:

$$P(I,C,T,V_i) = P_{\max}(I,C,T)\left[1 - e^{-c_{LA}\, s \sum_{i=y,o} f_{Li} V_i(t)}\right] \qquad (2)$$

where $P_{\max}(I,C,T)$ is the maximum gross assimilation rate (g m^{-2} day^{-1}). As we report model behaviour for constant I, C and T, we simply report a fixed value for $P_{\max}$. The second term in square brackets, represents the standard exponential function (Goudriaan and van Laar, 1978) for effective leaf area, with c_{LA} (m^2 m^{-2}) a shading constant, s (m^2 g^{-1}) the specific leaf area, f_{Li} (-) the fraction leaves for each part of vegetative biomass V_i (g m^{-2}). The indexes y and o stand for the young and older parts of the vegetative part of the shoot respectively. In fact, the exact definition is rather in terms of growth, V_y grows and thus acts as a net sink, V_o does not. The idea is that sweet pepper (as well as tomato) grows upwards, and is pruned in such a way that a cylindrical form is obtained of which only the upper part grows. V_y corresponds mostly to this upper, growing part, as well as other locations where leaves still grow. Both V_y and V_o have photosynthetically active leaves and require maintenance, although the maintenance rate m_o may be supposed to be lower than m_y. For simplicity, we have not modelled what happens when the assimilate level is too low to 'pay for' maintenance. Fruit maintenance is neglected, or thought to be compensated by photosynthesis in fruits, which is omitted as well.

Vegetative Growth

The dynamics of both fractions are described by the following equations:

$$\frac{dV_o(t)}{dt} = a_v V_y(t), \qquad \frac{dV_y(t)}{dt} = -a_v V_y + r_v\, \sigma_{VA_c}(A_c)\, V_y(t) \qquad (3)$$

As described above, V_y grows exponentially with a maximum growth rate r_v (day^{-1}) only restricted by assimilate concentration A_c, given by $A_T / v_p (V_y + V_o)$, in which v_p represents the proportionality constant between phloem volume and total vegetative dry weight. Levels of water and nutrients are supposed to be non-limiting. The transition from V_y to V_o, is modelled as a first order process, with a_v (day^{-1}) representing the 'aging rate' that also reflects the speed at which the outgrowth of leaves occurs. The assimilate dependency of vegetative growth $\sigma_{VAc}(A_c)$ is a monotonously increasing function with saturation, approaching unity for large values of A_c. As we will use this type of (dimensionless) function more often, we introduce it in a general form:

$$\sigma_{ij}(x; K_{ij}, H_{ij}) = \frac{(x / K_{ij})^{H_{ij}}}{1 + (x / K_{ij})^{H_{ij}}} \text{, with } ij = VA_c, FA_c, aw, aA_c, hw, hR \tag{4}$$

The index i refers to a process or parameter, j to the variable to which that process is sensitive, where for i, V = vegetative growth, F = fruit growth, a = abortion, h = harvest, and for j, A_c = assimilate concentration, w = weight, and R = ripeness.

In the equation, K_{ij} is the saturation constant (with same dimensions as the saturation variable x), and H_{ij} the 'sigmoidicity' (dimensionless). For H_{ij} equal to unity, a simple hyperbolic relationship is obtained, for $H_{ij}=2$ a sigmoidal function, and for H_{ij} assuming larger values, a sharper threshold-like function follows. In biochemical terms, this equation corresponds to a H^{th}-order Michaelis-Menten reaction. Although the crop model operates on a higher aggregation model, and interpreting on a biochemical level may not be appropriate, one may translate the assimilate dependency of growth processes in terms of the assimilate 'concentration' A_c (-) in the role of the substrate for growth (with H_{VAc} and H_{FAc} here equal to 2). In the model, where assimilate dependency of fruit growth will be modelled in exactly the same manner, the values of K_{VAc} and K_{FAc} determine the relative sink strengths, but *at the micro level*, in contrast to other models, where relative sink strengths are computed at the macro level (counting leaves and fruits), reflecting their non-local ('top-down') *partitioning* of assimilates. Here, the mechanisms are strictly local and *even* with K_{VAc} equal to K_{FAc}, realistic results can be obtained, reflecting that no hierarchical, 'rule of priority' among leaves and fruit is necessary. The conversion factor c (g g^{-1}) for the fraction of dry matter that results from assimilate dry matter c is assumed equal for the vegetative growth and fruit growth.

Fruit Growth and Development

The last term of equation 1 represents the sum, over all weight classes, of assimilate storage into fruits. The function $g_{Fw}(w)$ is described below. Fruit growth and fruit development are modelled by two separate state variables: weight and 'ripeness' (summed temperature-days). The model uses a partial differential equation to describe the rate of change of the number of fruits per square meter, N (fruit m^{-2}), as a function of fruit dry weight and time. For simulation, the fruit dry weight variable w (g fruit^{-1}) is discretised into 40 weight classes with a fixed difference of 0.6 grams dry weight per weight class. The next equation describes the fruit growth dynamics as a function of weight and time:

$$\frac{\partial N(w,t)}{\partial t} = -a(w, A_c)N - h(w, R/N)N - \sigma_{FA_c}(A_c) g_{Fw}(w) \frac{\partial N(w,t)}{\partial w} \tag{5}$$

Flowering, F (fruits day^{-1} m^{-2}) adds fruits to the start of the 'conveyor belt' N as a flux boundary condition, with a value depending dynamically on total vegetative biomass:

$$\left.\frac{\partial N(w,t)}{\partial t}\right|_{w=w_{start}} = F = \max(0,\min(F_{max},[V_y + V_o - c_s]F_{max}/c_r) \quad (5b)$$

Fruit (and flower) abortion in sweet pepper is assumed to be caused by an insufficient supply of assimilates to the fruits. The fruits are only vulnerable when they are small. Since our main variable for fruits is the number of fruits per square meter, a real number, we are not concerned with the fate of individual fruits. Consequently, fruit abortion, as is fruit harvest are not treated as discrete events, but are represented by incremental changes to the number of hanging fruit. The abortion 'rate' $a(w, A_c)$ (day^{-1}) as a function of fruit weight w and assimilate concentration A_c is descriptively modelled as:

$$a(w,A_c) = a_{max}\left[1-\sigma_{aw}(w;K_{aw},H_{aw})\right]\left[1-\sigma_{aA_c}(A_c;K_{aA_c},H_{aA_c})\right] \quad (6)$$

where a_{max} (day^{-1}) is the maximal abortion rate. Both sensitivities of fruit abortion to weight as to assimilate supply area assumed to be quite critical, reflected by high values for H_{aw} and H_{aAc} (both 15). K_{aw} (at 1 g fruit^{-1}) represents the weight above which the fruits become less vulnerable to fruit abortion. When this boundary fruit weight K_{aw} is viewed in a biological context it could in fact be seen as the mathematical representation of fruit set, i.e. the fruit weight limit after which the fruit is out of abortion risk. Likewise, K_{aAc} (-) is the assimilate concentration above which the fruits are barely sensitive to abortion anymore.

Finally, we come to the most important process of fruit growth. We model the growth rate as a function of fruit dry weight w:

$$g_f(w) = k\,w\left[1-w/w_f\right]^n \quad (7)$$

where w_f (g fruit^{-1}) is the maximum dry weight and the exponent n defines the shape of the growth curve (Richards, 1959). While $g_f(w)$ could be proposed as model for individual fruit growth, here it is incorporated as the local speed of the 'conveyor belt' (the last term of equation 5 and 8). At the start of the conveyor belt, the fruit dry weight is around 0.4 gram. Although simple and flexible, it misses a mechanistic interpretation. A study is underway in order to incorporate a biophysical model, such as that proposed by Fishman and Génard (1998), in place of this expression. The parameter k (day^{-1}) is the most salient one: it reflects the fruit sink strength, and the maximum relative speed of the conveyor belt.

Harvest

In addition to not treating harvest as a discontinuous event, we do not assume that fruits can be instantly picked once they have reached a critical weight or ripeness, which is common in other models. Rather, a maximum harvest rate h_{max} (day^{-1}) exists, which reflects the total capacity of the working staff (see this example mentioned at the start of this section). The model allows for fruits to be harvested according to weight, but also according to ripeness. How ripeness (R) is modelled is explained in the next subsection. The harvest rate is given by:

$$h(w,R/N) = h_{max}\left[f_{hw}\sigma_{hw}(w;K_{hw},H_{hw}) + (1-f_{hw})\sigma_{hR}(R/N;K_{hR},H_{hR})\right] \quad (8)$$

where σ_{hw} is the dependency of the harvest rate on fruit dry weight (in practice given in size) and σ_{hr} is the dependency of the harvest rate on fruit ripeness. f_{hw} is a 'soft' switch, taking values between zero and one, according to the harvest practices. K_{hw} is the threshold (preferred) harvest dry weight (g fruit^{-1}) and H_{hw} reflects the selectivity of the staff responsible for harvest to fruit size. High values for H_{hw} indicate that the staff is well trained to recognise fruits with harvestable size and instructed not to pick fruits with lower size. If fruits are picked according to their ripeness (colour, shine), K_{hR} (Cday fruit^{-1}) is the threshold (preferred) value for ripeness and H_{hR} is the ability of the staff to recognising harvestable ripeness of the fruits. Before describing the last term, for fruit growth, we continue to give the definition of the ripeness variable R.

Ripeness Dynamics

The variable behind ripeness, $R(w,t)$ (in Cday m^{-2}) is defined as the temperature sum ('thermal time') received by all fruits in a certain weight class. In order to obtain the 'ripeness per piece of fruit' of a specific weight w, $R(w,t)$ is divided by the number of fruits $N(w,t)$. The mathematical expression that keeps track of R is a co-flow of N, as its first term integrates $N(w,t)$ and represents the actual temperature sum. The other terms track the changes in N, as R shares the same rates for abortion harvest and development.

$$\frac{\partial R(w,t)}{\partial t} = r\left[T - T_b\right]N - a(w, A_c)R - h(w, R/N)R - \sigma_{FA_c}(A_c)g_{Fw}(w)\frac{\partial N}{N\partial w}R \qquad (9)$$

Here, r (Cday °C^{-1} day^{-1} fruit^{-1}) describes the temperature dependent ripening rate, linearly proportional to the temperature T (°C) above a base value T_b (°C). Where we write Cday ('celciusday') as dimension in order to reflect the chosen formulation, the dimension of ripeness could equally represent a colour, if the development of colour can be reasonably modelled with the same expression.

RESULTS: MODEL BEHAVIOUR

The model was implemented as a set of three differential equations in Vensim (www.vensim.com) and two partial differential equations implemented as two series of 40 ordinary differential equations by discretizing the independent fruit weight variable. For lack of space we only present the base run without much explanation: The vegetative growth shows a very short period of exponential growth until the first fruits start growing. This results in a severe assimilate shortage, which slings the system into the first oscillation. The yield oscillations have a period of about 50 days (Fig. 1a), the total vegetative plant size (V_o+V_y) after 300 days arrives at about 800 grams dry weight (Fig. 1b), and the harvestable yield at the end of one season comes to 27 kg/m^2 fresh weight (Fig. 1c) For the calculation of dry weight to fresh weight, reported measurements by Marcelis and Baan Hofman-Eijer (1995) were adopted (see Table 1 for fitted curve). Of interest is that the average size of the harvest, at unchanged harvest practices, decreases 'spontaneously' over the course of the season (Fig. 1c), as the plant is larger.

Extensive analysis of the oscillating pattern (bifurcation analysis) revealed a strong influence of the maximal fruit sink strength k. In Fig. 2 a bifurcation diagram is shown with the minimum and maximum of oscillations in daily harvested fresh weight as a function of k, the maximal fruit sink strength. As k increases more fruits can be harvested, but also with a larger amplitude of oscillations (until k=0.3 day^{-1}). Thus, small changes in k, might have a large effect on the oscillations. This also implies that previous breeding efforts to create fast growing varieties, might actually have enlarged the problem of yield oscillations.

DISCUSSION AND FUTURE RESEARCH

Previous studies (Heuvelink et al., 2004) concluded that "Yield fluctuations in sweet pepper are primarily the result of an irregular fruit set pattern. Fruit set was shown to be positively correlated with plant source:sink ratio."

This paper presents the first reported attempt to model the fruit set and abortion process in sweet pepper explicitly, with dependencies on assimilate level and individual fruit weight. The source:sink ratio, used in most previous modelling efforts, was judged not a local variable to steer the abscission process in a mechanistically interpretable way, but at the empirical level, such a measure reconstructed in the model indeed correlates with fruit set (not shown). But the big gain of this model is the actual emergence of abortion, resulting from an assimilate shortage during fruit growth. The temperature and light dependencies that are sometimes ascribed to the abortion process are already partly reflected in the similar dependencies of the photosynthesis influx in the assimilate pool. From the simulated abortion and the natural delay incorporated, an oscillating pattern appears in the output variables. Thus this model successfully simulates abortion and resulting oscillations without use of external (outside the model boundaries) oscillators.

We wish to state clearly that the model arrives at plausible values for known biological variables, but it is not empirically validated. Key output variables are tested against values found in literature, but more extensive testing against experimental datasets is on the way. Analytical and dimensional analysis is expected to unveil that certain ratios (functions) of parameters are responsible for behaviour rather than the absolute values. Therefore it is possible to reproduce the yield pattern with a different set of parameters (say both a_v and r_v increased), but with different growth form for another variable, say vegetative growth. This 'internal validation' can predict, through elimination, biologically valid regions in 'parameter space', before experiments are carried out.

The effect of the input variables, such as light and temperature, is studied in three ways: as constant, as smooth, pre-defined functions (e.g. sinusoidal light intensity pattern over the season according to latitude), and as measured time series. Using constant or smooth input variables, we can relate certain system behaviours (e.g. endogenous period of oscillations) better to model constants. By eliminating the natural noise from the input variables, by definition present in empirical time series, it becomes easier to trace cause and effect within the system. However, the influence of climatic variables on growth and development is currently subject to thorough testing against empirical time series.

The numerical implementation of the partial differential equations as series of ordinary differential equation requires the discretization of the second independent variable (w). The details around fruit weight at fruit set are currently being translated into a more explicit model version.

The method used to simulate the ripeness dynamics provides a generic way of simulating accumulating components along with the growth dynamics. In future research we wish to use a similar approach to model the accumulation of vitamins, Ca^{2+} or other secondary elements of interest in order to predict healthiness or disease proneness of fruits (e.g. blossom-end-rot), also at a post-harvest stage.

Finally, a recent multi-disciplinary version of the model incorporates harvest strategies, quality-dependent prices formation, and post-harvest storage dynamics, reflected financial optimization practices that growers employ to secure a healthy income. A game-theoretical analysis is conducted in which the breeder can determine an optimal innovation strategy, dependent on synergistic or counterbalancing actions by growers and traders (Schepers et al., 2006).

ACKNOWLEDGEMENTS

For fruitful discussions, we thank Gerard van Willigenburg, Fokke Buwalda, Ep Heuvelink, Pol Tijskens, Leo Marcelis, Eldert van Henten and Gerrit van Straten.

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Tables

Table 1. Parameters (in order of appearance, grouped per process, dimensions, see text).

P_{max}, c_{LA}, s, f_{Lo}, f_{Ly}	19.41	0.5	0.02	0.75	0.75
m_o, m_y, c, a_v, r_v	0.005	0.025	0.8	0.04	0.1
K_{VAc}, H_{VAc}, K_{Fac}, H_{FAc}, v_p	0.2	2	0.2	2	10^{-7}
K_{aw}, H_{aw}, K_{aAc}, H_{aAc}	1.5	15	0.15	15	
K_{hw}, H_{hw}, K_{hR}, H_{hR}	15	15	750	15	
F_{max}, c_s, c_r, w_{start}	2.5	50	60	0.7	
a_{max}, h_{max}, f_{hw}	0.4	0.2	0		
r, T, T_b	1	20	5		
k, w_f, n	0.25	25	2		

Dryweight / Freshweight = $w / 250 + [\, 6 + 3w\,]^{-1}$

Figures

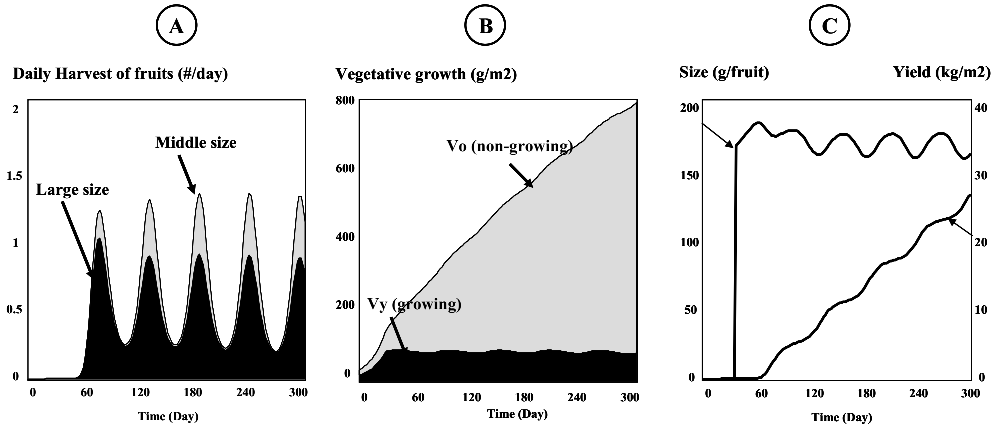

Fig. 1. Base run oscillations for parameters in Table 1. a) the numbers of harvested fruits are displayed for large and middle sized fruits (superimposed). b) the growing and non-growing vegetative parts of the shoot (superimposed). c) the average fruit size and the cumulative marketable fresh weight yield (large and middle sized fruits).

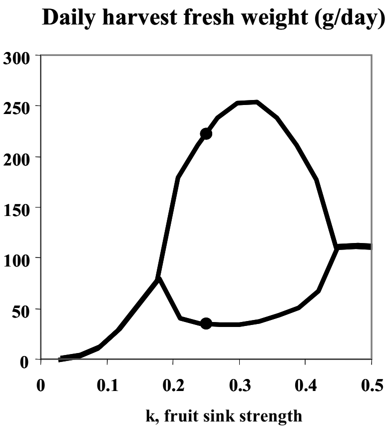

Fig. 2. Bifurcation diagram showing the minimum and maximum of oscillations in daily harvested fresh weight as a function of *k*, the maximal fruit sink strength. The period of oscillations decreases from about 50 to 40 days as *k* increases (not shown).