Modelling the effects of photosynthesis on source sink relationships and yield of vegetable crops

Problem presented by

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Contents

1 Introduction

In commercial crops of pepper, cucumber and tomato, fruit production occurs continuously throughout the season. This results in the plant having to support flowers and fruit at different stages of development, and allocate its energy accordingly. If light and temperature were constant this would result in fairly consistent yield. In reality, growers are at the mercy of the climate and variable light and temperature results in fluctuating yield over the season. From experience, we know that variations in light and temperature cause peaks or 'flushes' of yield followed by a lag period. This causes problems because when this happens across a region, it results in wide fluctuations in prices meaning that often when the grower has the most fruit, the prices are low, limiting their profitability. Even though glasshouse technology allows for considerable control over the growth environment, variable production is still a headache for many growers.

The difficulty of this issue from the standpoint of a plant breeder is that yield stability is impossible to assess without doing costly, long trials which may be useless if it happens to be a year with fairly consistent light and temperature. In addition to this, regulation of flowering and yield development is extremely complex leaving researchers with a myriad of variables that could be measured, but frequently there is little to guide a decision into which variables have the greatest influence and should be measured.

Growth models have been developed for many vegetable crops and include modules for light interception by the crop, photosynthesis (how much CO2 does the plant take up), source/sink partitioning (where the plant puts its carbon), dry matter production (net amount of carbon the plant keeps), fruit growth and several others. While we cannot address aspects of all of these modules during the study group, we would like to focus on photosynthesis and source-sink relations.

At the heart of this issue is the fact that vegetable crops with recurrent flowering have to allocate the carbon they take up from mature leaves ('source' tissues) between young leaves, new stem tissue, flowers, roots and developing fruit (collectively termed 'sink' tissues). This distribution of resource to sinks is obviously affected by how much carbon the leaves are able to take up, which in turn is affected by the climate. The current understanding is that the environment has a greater effect on photosynthesis, causing a range of adaptations. We have characterized photosynthetic behaviour in several tomato cultivars and have detailed growth and environmental data produced in commercial production conditions.

Key questions:

1. What kind of effect do various photosynthetic adaptations have on source-sink balance?

2. Which aspects of photosynthesis are most relevant and how much would they have to change to have a noticeable effect?

3. Although growers have little control over light input, what else could be changed in the growing environment to reduce variability in production?

We aim to model the plant growth in a way that address question 1. We assume that in a glasshouse the temperature, carbon dioxide and water supply is optimal so that light is the rate-limiting factor in plant growth.

In Section 2 we propose a basic model for light-driven growth of a plant with leaf-development, flowering and fruit development all controlled by local sugar concentrations. This work was loosely based on the papers of Jones *et al.* [1] and Schepers *et al.* [3]. In Section 3 we illustrate some results which this model can produce, as well as performing some mathematical analysis to determine the growth rate of the plant. We consider the effects of varying some of the parameters within the model to show qualitatively the different types of behaviour that might be expected. We expect that following experiments the parameters could be fitted to experimental data, and the model used to predict plant responses to a variety of environmental lighting conditions. Finally in Section 4 we draw conclusions and make some suggestions for future work, based on our present understanding of the model and its predictions.

2   Modelling

We assume that temperature is adequately regulated, so that it is not a rate-limiting factor in the growth of the plants, and that there is no problem with carbon dioxide availability for photosynthesis. This leaves light-availability as the rate-determining factor governing plant growth and fruit development.
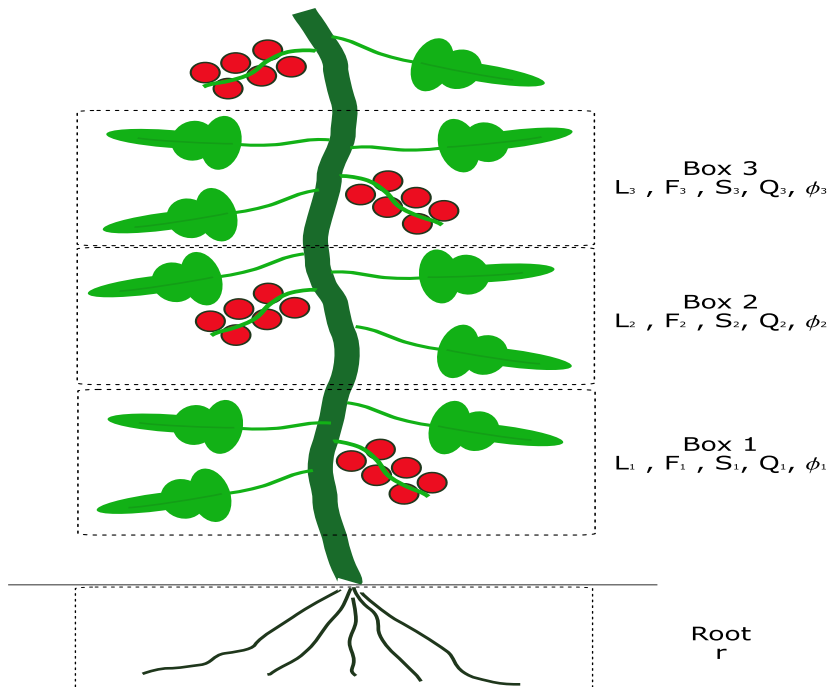

Figure 1: Illustration of tomato plant.

We start mathematically modelling the system by splitting the stem into discrete 'boxes', with each box containing three leaf branches and a potential flower/fruit branch. These

3

boxes or blocks will be labelled with the index i, with $i = 1, 2, 3, \ldots, h$, h being the maximum height of the plant. The box $i = 1$ corresponds to the lowest box, nearest to the roots as illustrated in Figure 1.

We assume that at the top of the stem new boxes appear, with zero size, thus we introduce a box size variable $\phi_i(t)$ as the size of box or block i relative to its maximum size (which we designate as $\phi = 1$). Hence we model the evolution of $\phi_i(t)$ by

$$\underbrace{\frac{\mathrm{d}\phi_i}{\mathrm{d}t}}_{\substack{\text{rate of change} \\ \text{of relative} \\ \text{box size}}} = \underbrace{k_p q_{i-1}}_{\substack{\text{sugar} \\ \text{in next} \\ \text{box down}}} \cdot \underbrace{(1 - \phi_i)}_{\substack{\text{room} \\ \text{for} \\ \text{growth}}}, \tag{1}$$

where the rate of growth depends on the availability of sugar, q_i, in the box *below* the growing box. For completeness, we define $\phi_0 = 1$, so that the base of the stem is fully developed.

We consider the development of the leaves and flower/fruit independently, and assume that each is dependent on a local sugar concentration. We assume that the sugar is transported both up and down the stem, and is used for leaf, fruit, stem and root growth. We define the amount of available sugar in box i as $q_i(t)$. The local sugar *concentration* is thus $s_i = q_i/\phi_i$.

For leaf development we postulate an equation of the form

$$\underbrace{\frac{\mathrm{d}L_i}{\mathrm{d}t}}_{\substack{\text{rate of change} \\ \text{of leaf} \\ \text{maturity}}} = \underbrace{\frac{k_1 \phi_i q_i}{q_i + \phi_i s_a}}_{\substack{\text{sugar-} \\ \text{dependent} \\ \text{growth}}} \cdot \underbrace{(1 - L_i)}_{\substack{\text{room} \\ \text{for} \\ \text{growth}}}. \tag{2}$$

The latter term prevents leaves growing arbitrarily large, and the former term describes how the growth rate depends on sugar-availability, this is via a function which increases with sugar, but saturates as sugar concentration increases to high levels ($s/(s + s_a) = q/(q + s_a \phi)$). This equation describes the growth of the variables L_i from zero to one.

For fruit development we postulate a similar equation, of the form

$$\underbrace{\frac{\mathrm{d}F_i}{\mathrm{d}t}}_{\substack{\text{rate of change} \\ \text{of fruit} \\ \text{maturity}}} = \underbrace{\frac{k_4 q_i F_i}{q_i + s_d \phi_i}}_{\substack{\text{sugar-} \\ \text{dependent} \\ \text{growth}}} \cdot \underbrace{(1 - F_i)}_{\substack{\text{room} \\ \text{for} \\ \text{growth}}} \cdot [\underbrace{(F_i - F_c)}_{\substack{\text{growth} \\ \text{away} \\ \text{from } F_c}} + \underbrace{k_8 (q_i - \phi_i s_c)}_{\substack{\text{initial} \\ \text{sugar-dep} \\ \text{growth/abort}}}]. \tag{3}$$

This is more complicated, since we assume that the variables $F_i(t)$ start at some nonzero but low level F_c, rather than $F = 0$. If at the point of setting, the sugar concentration $s = q/\phi$ is below s_c then the initial perturbation to F is negative, meaning that F will decrease, towards zero. This indicates fruit-abortion. However, if there is adequate

4

sugar, and $s > s_c$ then the initial perturbation makes $F > F_c$ and subsequently the fruit will grow, towards $F = 1$ with a rate which depends on the availability of sugar (and the rate k_4).

For sugar availabilities we include all the above usage terms, as well as transport between each box and its nearest neighbour above and below.

$$\underbrace{\frac{\mathrm{d}q_i}{\mathrm{d}t}}_{\substack{\text{rate of} \\ \text{change} \\ \text{of sugar}}} = D\big(\underbrace{q_{i+1} - q_i\frac{\phi_{i+1}}{\phi_i}}_{\substack{\text{transport} \\ \text{from/to next} \\ \text{higher box}}} \underbrace{- q_i + q_{i-1}\frac{\phi_i}{\phi_{i-1}}}_{\substack{\text{transport} \\ \text{from/to next} \\ \text{lower box}}}\big) - \underbrace{k_6 q_i}_{\substack{\text{background} \\ \text{decay} \\ \text{rate}}}$$

$$- \underbrace{k_5\frac{\mathrm{d}F_i}{\mathrm{d}t}}_{\substack{\text{flux to} \\ \text{fruit} \\ \text{development}}} - \underbrace{k_3\frac{\mathrm{d}L_i}{\mathrm{d}t}}_{\substack{\text{flux to} \\ \text{leaf} \\ \text{development}}} - \underbrace{k_7 k_p q_i (1 - \phi_{i+1})}_{\substack{\text{flux to} \\ \text{stem tip} \\ \text{growth}}}$$

$$+ \underbrace{k_2 I(t) L_i}_{\substack{\text{sugar} \\ \text{production} \\ \text{from light}}} \underbrace{. \exp\left(-k_s \sum_{n=i+1}^{h} L_n\right)}_{\text{shading}}, \qquad i = 2, ..., h-1. \qquad (4)$$

Whilst this equation is suitable for most blocks of the plant, the top and lowermost have modified equations since transport is then restricted. Thus for $i = 1$ and $i = h$ we find

$$\frac{\mathrm{d}q_1}{\mathrm{d}t} = D\left(q_2 - q_1\frac{\phi_2}{\phi_1} - q_1 + r\frac{\phi_1}{\phi_0}\right) - k_6 q_1 - k_5\frac{\mathrm{d}F_1}{\mathrm{d}t} - k_3\frac{\mathrm{d}L_1}{\mathrm{d}t}$$

$$-k_7 k_p q_1(1 - \phi_2) + k_2 I(t) L_1 \exp\left(-k_s \sum_{n=2}^{h} L_n\right), \qquad (5)$$

$$\frac{\mathrm{d}q_h}{\mathrm{d}t} = D\left(-q_h + q_{h-1}\frac{\phi_h}{\phi_{h-1}}\right) - k_6 q_h - k_5\frac{\mathrm{d}F_h}{\mathrm{d}t} - k_3\frac{\mathrm{d}L_h}{\mathrm{d}t} + k_2 I(t) L_h. \qquad (6)$$

Here, as noted after equation (1), $\phi_0 = 1$.

Analogously to the sugar content of each section of stem, q_i, we model the sugar content of the root. We introduce a variable $r(t)$ which could be thought of as $q_0(t)$ and allow transport of sugar both to and from the lowest compartment of the stem (q_1) and usage of sugar in the root at a rate k_r. Hence

$$\underbrace{\frac{\mathrm{d}r}{\mathrm{d}t}}_{\substack{\text{rate of change} \\ \text{of sugar} \\ \text{in root}}} = \underbrace{D\left(q_1 - r\right)}_{\substack{\text{transport} \\ \text{of sugar} \\ \text{from stem}}} - \underbrace{k_r r}_{\substack{\text{root's} \\ \text{uptake} \\ \text{of sugar}}}, \qquad (7)$$

Parameter	Explanation	Value
D	Sugar diffusivity	0.1
F_c	Fruit abortion threshold	0.1
k_1	Rate of leaf development	1
k_2	Rate of sugar production per leaf area per light unit	0.5
k_3	Rate of sugar usage for leaf development	1
k_4	Rate of fruit development	0.92
k_5	Rate of sugar usage for fruit development	1
k_6	Background sugar degradation rate	0.025
k_7	Rate of sugar usage for stem tip growth	0.01
k_8	Abortion inclination constant	0.1
k_p	Stem tip growth rate	1
k_r	Rate of uptake of sugar by root	1
k_s	Shading factor	0.25
s_a	Leaf growth saturation constant	1
s_c	Critical sugar concentration (for abortion)	0.1
s_d	Fruit growth saturation constant	1
h	Maximum height of plant (in number of boxes)	120

Table 1: Table of parameters.

This models the uptake of sugar by the root system; whilst the root system grows, we do not need a detailed model of its growth, it is sufficient to note that it acts as a sink for some of the sugar.

The initial conditions we use for the system (1)–(4) together with (7) are

$$L_i(0) = 0, \quad F_i(0) = F_c, \quad q_i(0) = 0, \quad s_i(0) = 0, \quad \phi_i(0) = 0, \quad r(0) = 1, \qquad (8)$$
$$\phi_1(0) = 1, \quad q_1(0) = 1, \quad L_1 = 0.1.$$

In order to start the numerical scheme, it is convenient to impose small values for $\phi_i(0)$ for all i; if this is chosen to be exponentially decaying, then this fixes the resulting speed of plant stem-tip growth. To avoid this situation, we choose initial conditions which decay faster than any exponential, namely $\phi_i(0) = 10^{-6} \exp(-i^2/100)$.

3 Results

3.1 Growth followed by severe loss of light

The first simulations we show are for a plant growing in good light, which after a certain length of time of normal growth experiences a prolonged period of low light (40% of initial intensity for times between 3000 and 6000), with normal good light conditions being reinstated towards the end of the simulation. The results are illustrated in Figures 2, 3 and 4; the parameters are as given in Table 1.
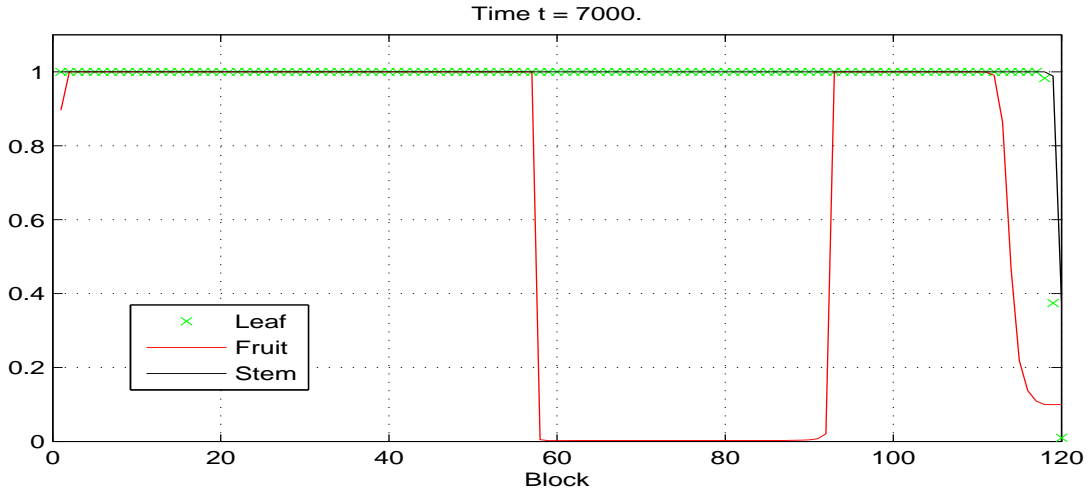
Figure 2: parameter values as in Table 1. At the start and end of the simulation the light is uniform and strong, allowing plant growth, and fruit setting; between times 3000 and 6000 the light is reduced to 40% of its initial value, reducing sugar production, allowing growth, but insufficient to allow fruit to set.

As the plant grows, we see the plant tip move to larger block numbers, with $\phi_i = 0$ in the region where the plant has yet to grow and $\phi_i = 1$ behind, where the stem is fully established, and a narrow region at the tip in which ϕ makes the transition from zero to one. Immediately behind this tip, we see a green curve, where L makes the transition from zero to one, indicating the growing of leaves. Further behind, is a red curve indicating the fruit. The situation at the end of a simulation is shown in Figure 2. In this figure, the red curve shows more complex behaviour, since between blocks 60 and 90, the light was reduced, and so fruit in these blocks was aborted due to the sugar level being too low.

The light reduction occurred between non-dimensional times of 2500 and 6000, and the effect on the total sugar in the plant is clearly seen in Figure 3. This graph shows the total sugar content, $S(t) = \sum_i q_i(t)$. We note a plateau of steady sugar concentrations, and hence steady growth between times 1000 and 2500, which is reestablished once the light is returned to normal at 6000; however, there is a lower plateau between 3500 and 6000 where the sugar level is too low for fruit to set. (Technically, in the model, the fuit setting in box i depends on the *local* sugar content q_i, not on the *global* availability S, but the effect is still present).

An important point to note in Figure 3 is the overshooting and undershooting as one moves from one plateau to the next. The first is due to the demand of sugar from the already set fruit when the light intensity is reduced, the plateau is higher than the initial minimum, since in the later growth fruit is aborted and so the demand for sugar is reduced. The peak at time 6000 is due to the increased light causing increased sugar production, and there being no fruit to use it since fruit has been aborted in the dark phase.
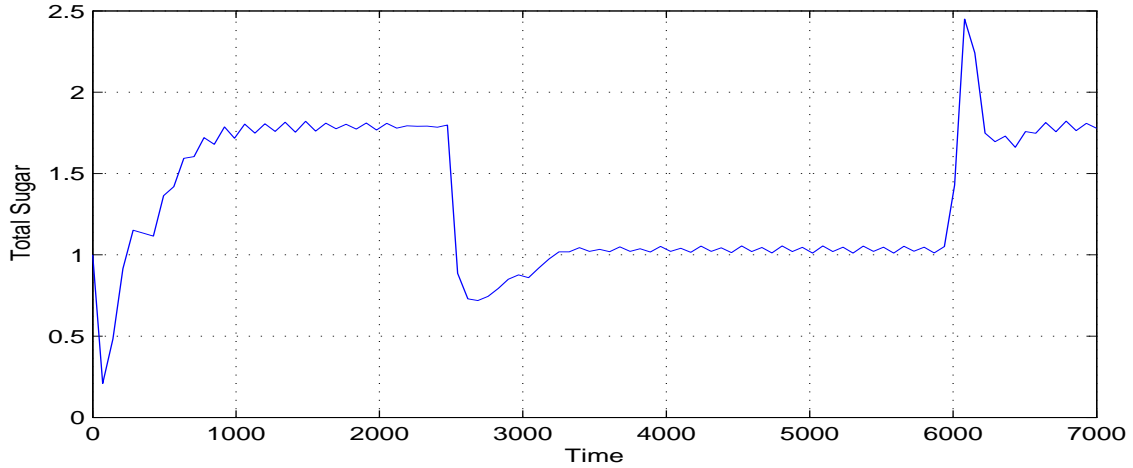
Figure 3: parameter values as in Table 1; light intensity as in Figure 2; hence between times 3000 and 6000 we observe a reduced sugar production, so a lower steady-state is reached. After the light resumes its original intensity at time 6000 we note a large spike in sugar levels, due to production returning to normal, but the plant having no fruit to develop.
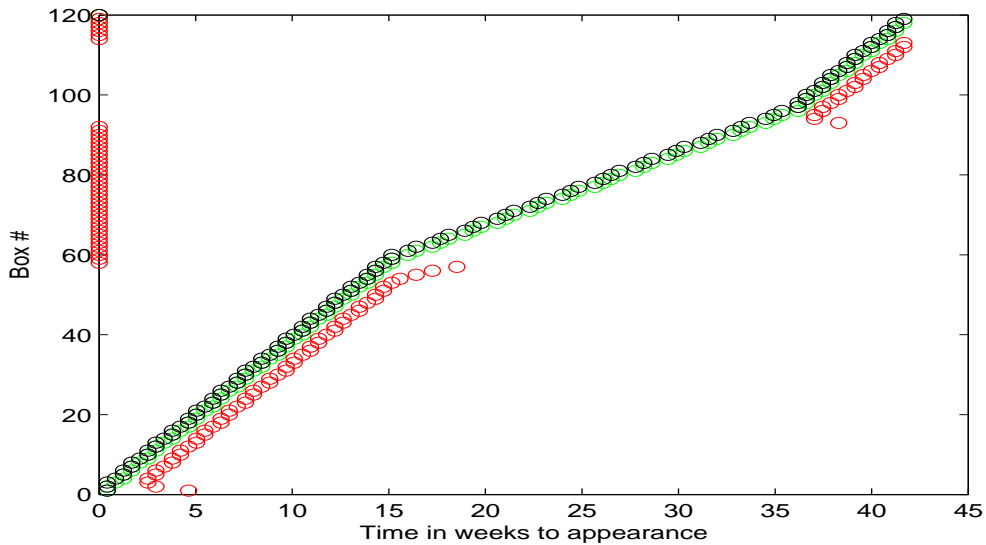

Figure 4: parameter values as in Table 1; light intensity as in Figures 2 and 3. Between weeks 15 and 35, the light intensity is reduced, leading to no fruit setting, and slow ripening of fruit already set. Once the original light intensity is reestablished fruit once again sets and ripens. During the relatively dark phase, the plant continues to grow, but at a slower rate.

All these results are summarised in Figure 4. This shows traces for the growing tip in black, and leaves in green, which are almost on top of one another. We observe slower growth in the dark phase between weeks 15 and 35 (which correspond to the nondimensional times of 2500 and 6000). The red curve shows the fruit setting at a later time, and in the dark phase, the aborted fruit is indicated by circles on the vertical axis.

8

At the start of the dark phase, some fruit is still produced, corresponding to fruit which was set in the light phase. After week 36, fruit resumes normal development.

3.2 Growth followed by slight loss of light

The dark phase in the above simulations might be interpreted as an extreme example. Here we modify the parameters slightly to show that more complex behaviour can be exhibited. Figure 5 shows oscillations between $F = 0$ and $F = 1$ in the dark phase of the simulation. This is more easily interpreted using Figure 6 below. The right-hand panel of Figure 5 shows the distribution of sugar through the stem at the end of the simulation. The plant is in a state of steady growth with ample light at this point. We see low sugar levels at the bottom of the plant, increasing to a peak just below the growing tip. Thus the plant concentrates sugar to the areas in which leaf, tip and fruit are developing. This predicted distribution ought to be fairly straightforward to verify experimentally.
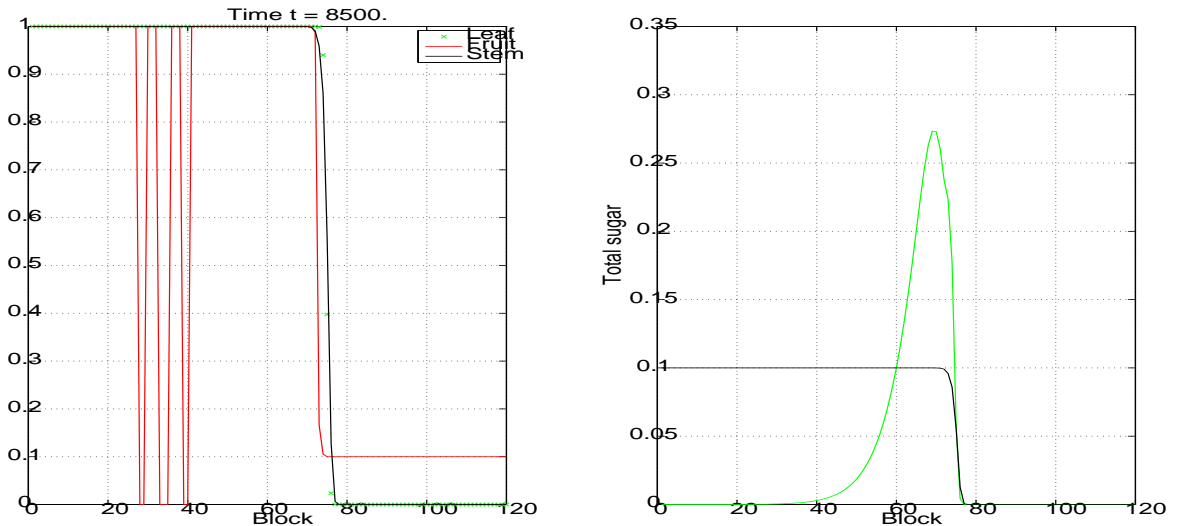

Figure 5: Illustration of plant growth with less severe dark phase. On the left: tip, leaf and fruit development at the end of the simulation; on the fright: sugar distribution through stem at end (green) and critical threshold for fruit abortion (black).

Figure 6 clearly shows the lower growth rate during the dark phase, but interestingly also sporadic setting and aborting of fruit during the dark phase. Clearly the light is not sufficient to maintain sugar levels high enough for all fruit to set, but once one or two fruiting branches have aborted, the drain on the reduced production of sugar means that there is sufficient for fruit on the next branch or two to set. However, the increased drain on sugar due to this fruit growing means that some later fruit is aborted. This leads to alternating setting and aborting of fruit during the dark phase.
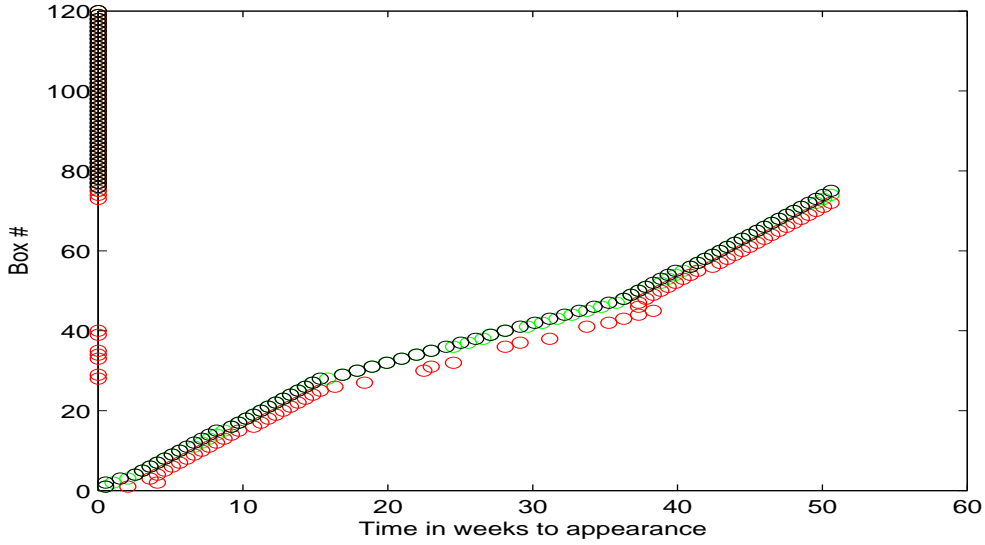
Figure 6: Illustration of plant growth with less severe dark phase between weeks 18 and 38.

Parameter	Value	Parameter	Value
k_1	1	D	0.1
k_2	0.3/0.75	s_c	0.1
k_3	1	s_d	1
k_4	0.92	s_a	1
k_5	1	F_c	0.1
k_6	0.025	k_p	1
k_7	0.01	k_r	1
k_8	0.1	k_s	0.25

Table 2: Table of parameter values used in the analysis of high and low ps species of plants.

3.3 Variation in PS

High-PS and Low-PS refers to the photosynthetic capacity of the leaves or overall output of photosynthesis. To model this variation in outputs across a range of species, we consider two types of plant, one with a larger value of k_2 and one with a lower value. We impose $k_2 = 0.75$ for the high ps case and $k_2 = 0.3$ for the low ps case. All other parameter values are given in Table 2. The results from the two cases are shown in Figures 7 and 8 respectively.

Figure 7 shows the case of a plant with high PS. In this simulation, between weeks 15 and 30, the intensity of the incident light has been reduced significantly. The effect of this is to reduce the amount of sugar produced. However, because this plant is effective at converting light to sugar, the sugar levels remain above the critical value needed for the fruit to set. The effects of the reduced sugar availability are two fold: firstly a slower growth of the plant, and a longer time it takes for the fruit to grow to maturity. This
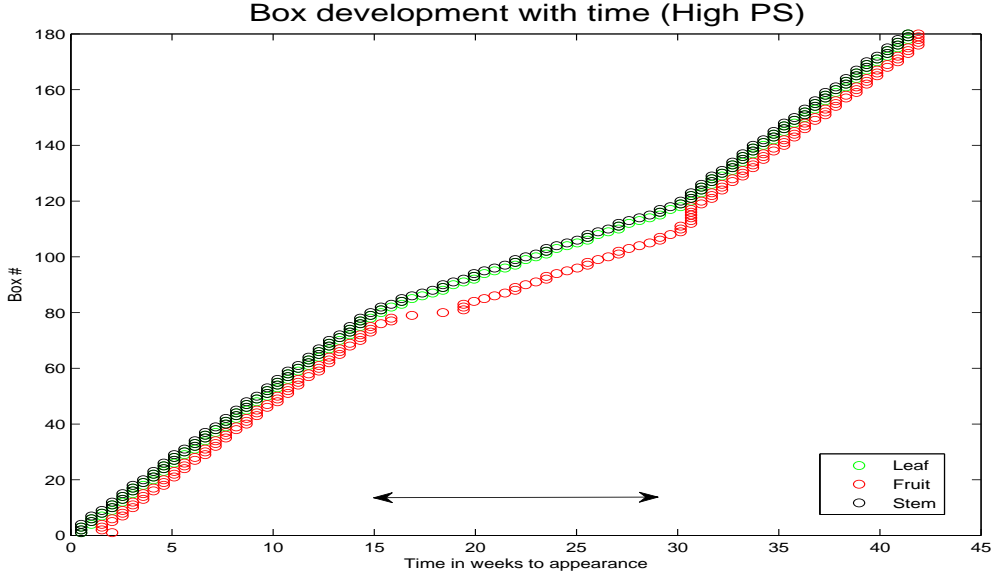
Figure 7: Simulation for the high ps strain of plant, with $k_2 = 0.75$; all other parameter values as in Table 2.

latter effect is deduced from the larger distance between the black/green trace and the red trace in the centre of Figure 7.

Similar light conditions hold in Figure 8, where we observe the effect on a low ps type of plant. The reduced sugar production gives rise to a slower growth of the plant in both bright and dark conditions. Furthermore, in the time of lower light, there is insufficient sugar present for the fruit to set develop, instead, it is aborted, as indicated by the red circles visible on the vertical axis. The fruit that develops in the time of lower light is fruit that has set in the bright conditions, and then taken a long time to grow to maturity due to the low sugar levels. Once light returns to the original levels, we note that plant growth resumes, fruit setting and development returns.

3.4 Theoretical analysis of tip growth speed

Biologically, it seems reasonable that the rate of plant growth is governed by what happens at the tip, and in problems involving diffusion and chemical reactions, it is common for the behaviour at the head of the wave to determine its speed. For example, in the Fisher-KPP equation [2]

$$u_t = Du_{xx} + u(1-u), \qquad \text{subject to} \quad \begin{array}{l} u \to 1 \text{ as } x \to -\infty, \\ u \to 0 \text{ as } x \to +\infty, \end{array} \tag{9}$$

the behaviour of $u(x)$ as $x \to \infty$ determines the wavespeed as follows. We assume the existence of a travelling wave, $u(x,t) = u(x - ct) = u(z)$, then $-cu' = Du'' + u - u^2$. Since $u \to 0$ in this limit, and we have a linear approximation for the behaviour of u, the assumed form for u is $u \sim e^{-\lambda z}$ as $z \to +\infty$, which implies $c = D\lambda + 1/\lambda$. The double root condition $dc/d\lambda = 0$ implies $\lambda_c = \pm 1/\sqrt{D}$ hence $c_c = 2\sqrt{D}$.
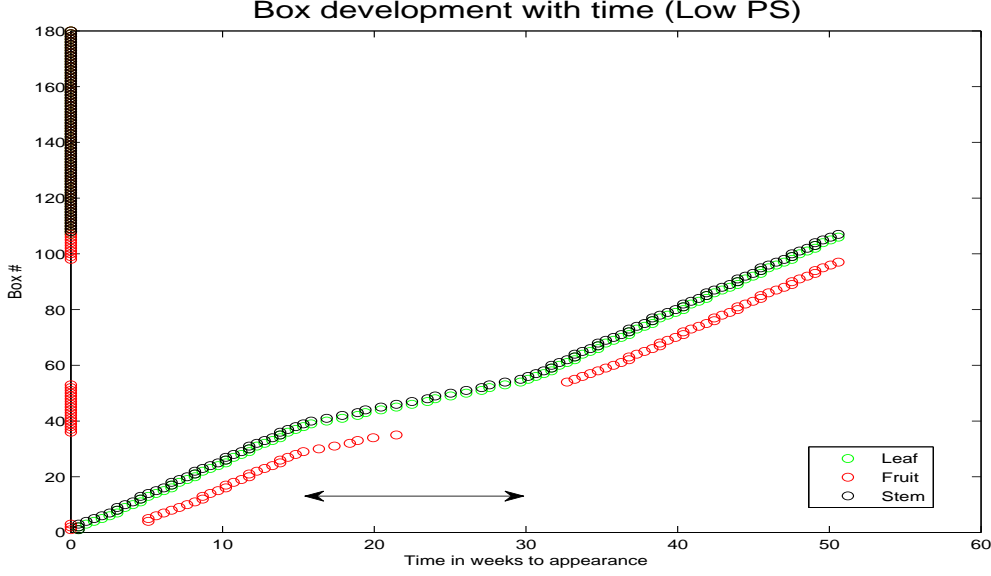
11

Figure 8: Simulation for the low ps strain of plant, with $k_2 = 0.3$; all other parameter values as in Table 2.

We perform a similar analysis on the system of equations (1)–(4), firstly assuming a travelling wave solution with speed v, and then looking at the small amplitude asymptotics for $q, L, \phi \ll 1$ together with $F - F_c \ll 1$ as $n \gg 1$ which corresponds to $z = n - vt \to +\infty$. From the leading order terms of (1)–(4) we find

$$-v\,\phi'(z) = k_p q(z-1), \tag{10}$$

$$-v\,L'(z) = \frac{k_1 \phi(z) q(z)}{q(z) + s_a \phi(z)}, \tag{11}$$

$$-v\,F'(z) = \frac{k_4 q(z) F_c}{q(z) + s_d \phi(z)} (1 - F_c)[(F(z) - F_c) + k_8(q(z) - s_c \phi(z))], \tag{12}$$

$$-v\,q'(z) = D\left(q(z+1) - q(z)\frac{\phi(z+1)}{\phi(z)} - q(z) + q(z-1)\frac{\phi(z)}{\phi(z-1)}\right) - k_6 q(z)$$
$$-\frac{k_5 k_4 q(z) F_c (1 - F_c)}{q(z) + s_d \phi(z)}[F(z) - F_c + k_8(q(z) - s_c \phi(z))] - \frac{k_3 k_1 \phi(z) q(z)}{q(z) + s_a \phi(z)}$$
$$-k_7 k_p q(z) + k_2 I L(z), \tag{13}$$

hence ϕ, q, L, $F - F_c$ are proportional to each other and all decay at the same rate. We assume that $L(z) \sim \overline{L} \mathrm{e}^{-\lambda z}$, $q(z) = \overline{q} \mathrm{e}^{-\lambda z}$, $\phi(z) = \overline{\phi} \mathrm{e}^{-\lambda z}$ and $F(z) = F_c + \overline{F} \mathrm{e}^{-\lambda z}$ with the same λ in each expression to obtain relationships between the prefactors $\overline{\phi}$, $\overline{L}$, $\overline{F}$, $\overline{q}$ and λ as follows

$$\overline{\phi} = \frac{k_p \overline{q}\,\mathrm{e}^{\lambda}}{v\,\lambda}, \quad \overline{L} = \frac{k_1 \overline{\phi}\,\overline{q}}{(\overline{q} + s_a \overline{\phi})\,v\,\lambda}, \quad \overline{F} = \frac{k_4 \overline{q}\,F_c\,(1 - F_c)\,[\,\overline{F} + k_8(\overline{q} - s_c \overline{\phi})]}{(\overline{q} + s_d \overline{\phi})\,v\,\lambda}, \tag{14}$$

$$v\lambda = -k_6 - \frac{k_5 k_4 F_c (1 - F_c)[\overline{F} + k_8(\overline{q} - s_c \overline{\phi})]}{\overline{q} + s_d \overline{\phi}} - \frac{k_3 k_1 \overline{\phi}}{\overline{q} + s_a \overline{\phi}} - k_7 k_p + \frac{k_2 I \overline{L}}{\overline{q}}. \tag{15}$$

This system of four equations should be interpreted as being for the unknowns $\overline{L}$, $\overline{\phi}$, $\overline{F}$ in terms of $\overline{q}$ (which should be eliminated from the system and so remains indeterminable);

12

this leaves the final equation to determine $v(\lambda)$. However, it is not clear that this functional relationship can rewritten as an explicit formula for v in terms of λ.

The last equation of (14) implies

$$\frac{\overline{F}}{\overline{q}} = \frac{k_4 k_8 F_c (1 - F_c)(\lambda v - s_c k_p e^\lambda)}{\lambda v (\lambda v + s_d k_p e^\lambda) - \lambda v k_4 F_c (1 - F_c)}, \tag{16}$$

which means that (15) can be rewritten as

$$\lambda v (\lambda v + k_6 + k_7 k_p) = \frac{k_1 k_p e^\lambda (k_2 I - k_3 \lambda v)}{\lambda v + s_a k_p e^\lambda} - \frac{\lambda v k_4 k_5 k_8 F_c (1 - F_c)(\lambda v - s_c k_p e^\lambda)}{\lambda v + s_d k_p e^\lambda - k_4 F_c (1 - F_c)}. \tag{17}$$

One noteworthy property of this equation is that it does not depend on D — the rate at which sugar diffuses up the stem. This is effectively a quartic polynomial for v in terms of λ.

$$\begin{aligned} \lambda v (\lambda v &+ k_6 + k_7 k_p)(\lambda v + s_a k_p e^\lambda)(\lambda v + s_d k_p e^\lambda - k_4 F_c (1 - F_c)) \\ &= k_1 k_p e^\lambda (k_2 I - k_3 \lambda v)(\lambda v + s_d k_p e^\lambda - k_4 F_c (1 - F_c)) \\ &\quad - \lambda v k_4 k_5 k_8 F_c (1 - F_c)(\lambda v - s_c k_p e^\lambda)(\lambda v + s_a k_p e^\lambda). \end{aligned} \tag{18}$$

Note that we have not had to take continuum limits to obtain this result, keeping the discrete differences means that this equation is transcendental, due to the presence of e^λ terms as well as polynomial terms in λ.

If we assume that the light intensity is large, that is $I \gg 1$, then $v \gg 1$ also, with $v \sim I^{1/3}$, and the dominant balance gives

$$\lambda^4 v^4 = k_1 k_p e^\lambda k_2 I \lambda v, \tag{19}$$

hence $v = \lambda^{-1} (k_1 k_2 k_p I e^\lambda)^{1/3}$. This relationship gives $\lambda = \lambda_c = 3$ as a repeated decay rate and hence the expected speed is $v_c = v(\lambda_c)$ is given by

$$v_c = \tfrac{1}{3} e (k_1 k_2 k_p I)^{1/3}. \tag{20}$$

That this should depend on k_2 and k_p is entirely to be expected since they determine the efficiency of sugar production from light and the tip growth rate respectively. However, the strong dependence on the leaf-growth rate is less expected.

If one attempts a similar calculation based on the assumption that the light intensity is small, then one requires $v \sim I$ but the expression for $v(\lambda)$, namely

$$\lambda v = \frac{k_1 k_2 k_p I (s_d k_p e^\lambda - K_4)}{[s_d k_p e^\lambda - k_4 F_c (1 - F_c)][k_1 k_2 k_3 + s_a k_p (k_6 + k_7 k_p)] - k_4 k_5 k_8 k_p^2 s_d s_a F_c (1 - F_c) e^\lambda}, \tag{21}$$

is of a form which prevents $dv/d\lambda = 0$ being solved. Hence we discount this possibility, leaving (20) as our main result.

13

3.5 Other analysis

More accurate calibration of the model may be achieved by considering the proportion of sugar that goes into each fruit, leaf and stem, and root growth, previously determined to be approximately 70/20/10 respectively. From the model described above, and equation (4) in particular, the instantaneous flux of sugar into leaf, fruit, and stem growth can be calculated respectively by

$$Q_L(t) = \sum_i k_3 \frac{\mathrm{d}L_i}{\mathrm{d}t} = k_3 k_1 \sum_i \frac{\phi_i(t)q_i(t)(1 - L_i(t))}{q_i(t) + s_a\phi_i(t)}, \tag{22}$$

$$Q_F(t) = \sum_i k_5 \frac{\mathrm{d}F_i}{\mathrm{d}t} = k_5 k_4 \sum_i \frac{q_i(t)F_i(t)(1 - F_i(t))}{q_i(t) + s_d\phi_i(t)}[F_i(t) - F_c + k_8(q_i(t) - s_c\phi_i(t))], \tag{23}$$

$$Q_G(t) = \sum_i k_7 \frac{\mathrm{d}\phi_i}{\mathrm{d}t} = k_7 k_p \sum_i q_{i-1}(t)(1 - \phi_i(t)). \tag{24}$$

Assuming that the plant is growing steadily, all the variables (L, F, q, ϕ) then follow a travelling wave solution of the form $L_i(t) = L(z) = L(i - vt)$ etc., where v is the speed of the wave, that is, the rate at which the plant tip is growing. We then have

$$Q_L = k_1 k_3 \int \frac{\phi(z)q(z)[1 - L(z)]}{q(z) + s_a\phi(z)} \mathrm{d}z = k_3 \int -v\frac{\mathrm{d}L}{\mathrm{d}z}\mathrm{d}z = -vk_3[L]_0^h = vk_3, \tag{25}$$

$$Q_F = k_4 k_5 \int \frac{q(z)F(z)[1 - F(z)]}{q(z) + s_d\phi(z)}[F(z) - F_c + k_8(q(z) - \phi(z)s_c)]\mathrm{d}z = vk_5, \tag{26}$$

$$Q_G = k_7 k_p \int q(z)(1 - \phi(z + 1))\mathrm{d}z = vk_7, \tag{27}$$

here we have assumed that the variables L, q, ϕ, F are following a travelling wave solution as the plant grows in steady light. Since the ratios of sugar going into fruit, leaf, tip-growth are 70, 20, 10 we have

$$\frac{k_5}{k_3 + k_5 + k_7} = 0.7, \qquad \frac{k_3}{k_3 + k_5 + k_7} = 0.2, \qquad \frac{k_7}{k_3 + k_5 + k_7} = 0.1. \tag{28}$$

Such a relation helps determine some of the parameters in the model.

4 Conclusions

First let us recap the three questions posed in the introduction, namely

1. What kind of effect do various photosynthetic adaptations have on source-sink balance?

2. Which aspects of photosynthesis are most relevant and how much would they have to change to have a noticeable effect?

3. Although growers have little control over light input, what else could be changed in the growing environment to reduce variability in production?

In response to Question 1, our model has included parameters which describe the production, transport and usage of sugar from leaves through the stem to fruit and stem-tip. Across a range of species there will be different values for these parameters indicating varying priorities which plants put on the aspects of plant growth. In some leaf development (k_1) will be more important at the cost of aborted fruit, in others stem-tip growth (k_p) will be reduced in order to maintain fruit growth (k_4). The model accounts for varying levels of photosynthesis (k_2). Each of these has an associated cost in terms of sugar (k_3, k_5, k_7).

In response to question 2, the dominant requirements for photosynthesis are light, carbon dioxide, water and temperature. We have assumed that all except the first are present in adequate quantities, so have not really investigated this effect fully. All our rate parameters should be dependent on temperature, with an Arrhenius rate law being the most obvious way of including temperature. The inclusion effects relating to the availability of carbon dioxide and water would require modelling these concentrations around the plant, and into the leaves through the leaves' stomata. This would require considerable extra modelling work.

In response to Question 3, we have provided a model which, if fitted to a variety of species, would enable the stability of each to varying light levels to be assessed. Furthermore, some parameters in the model enable the growing environment to be controlled. For example, the removal of leaves from the plant will affect the shading factor k_s.

We have illustrated that the model can produce a variety of behaviours, both in response to light conditions, and that different species of plants can exhibit differing responses to the same light source. These results are shown in the first parts of Section 3. Later parts of that section show how to use the model to predict the flux of sugar to various processes in the plant, and to predict the overall speed of growth of the plants, which depends on almost all the parameters in a complicated manner.

4.1   Future work

Clearly the most immediate need for a deeper investigation of the model is a calibration of the model to some real data. The main purpose of this would be to identify sensible parameter values; however, fitting to several species would help highlight how plants differ in their response to variations in light levels. Understanding this would enable the plants stability or robustness to assessed, and it would then be possible to assert that whilst Species A may not have as high a yield as species B in optimum conditions, when subject to realistic variations in light, A would outperform B.

Whilst the model presented here has been developed using intuition and understanding of the tomato plant, the model could be adapted to other species, such as peppers, cucumbers. This might require the refining of the model to address specific behaviours

of other plants. One feature we have ignored so far is the effect of harvesting of fruit from the lower branches as the plant continues to grow.

Another practise we have ignored is the removal of lower leaves, although this has partly been taken into account through the shading effect of upper leaves, which reduces the sugar production in lower leaves. The main reason for lower leaf removal is believed to be prevention of disease, and the spread of disease is another issue which we have so far ignored.

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