CHAPTER 4

Roses are unselfish:
a greenhouse growth model to predict
harvest rates

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ABSTRACT. We consider the question of how rose production in a greenhouse
can be optimised. Based on realistic assumptions, a rose growth model is de-
rived that can be used to predict the rose harvest. The model is made up of
two constituent parts: (i) a local model that calculates the photosynthetic rate
per area of leaf and (ii) a global model of the greenhouse that transforms the
photosynthesis of the leaves into an increase in mass of the rose crop. The
growth rate of the rose stems depends not only on the time-dependent ambient
conditions within the greenhouse, which include temperature, relative humid-
ity, CO_2 concentration and light intensity, but also on the location and age
distribution of the leaves and the form of the underlying rose bush supporting
the crop.

KEYWORDS: Rose production model, advection equation, stem density func-
tion, global and local leaf photosynthesis

1. Introduction

The production of roses has become more competitive and commer-
cialised over the last few decades. While the rose grower's own experience
remains the key to producing a large rose harvest, qualitative and quan-
titative modelling of the biochemical processes in rose plants is becoming
increasingly important in optimising rose production even further.

In this article, we develop a simplified mathematical model for rose pro-
duction to predict the total mass of rose crop produced per square metre of
greenhouse per week, depending on the climatic conditions inside the green-
house. The goal of our model is to tune these conditions in such a way that
the harvest of roses is maximised.

Rose stems grow by assimilating CO_2 from the air. This is done in
the leaves and is called photosynthesis. In the greenhouse, rose stems are
cut once they have reached a certain length and, when a rose is harvested,
it (obviously) stops assimilating. The CO_2-assimilation and, therefore, the
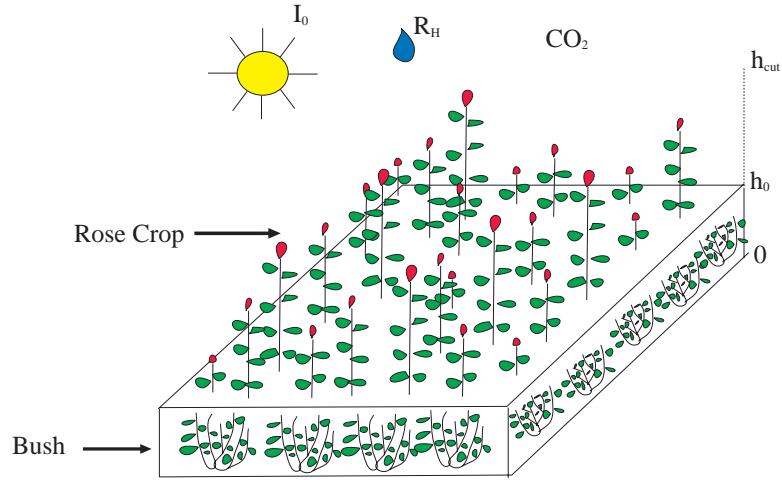growth of the roses is influenced by several environmental factors. Some of

FIGURE 1. A rose plant is divided into a bush part below supporting the crop above, which consists of the stems to be harvested when they reach height h_{cut}.

these can be controlled by the rose-grower, for example by using heaters, opening or closing the windows and putting up blinds for shade. These actions, in turn, alter the CO_2-concentration in the air C_a (by ventilation), the relative humidity R_H, the temperature in the greenhouse T_a, and the light intensity I_0 (see figure 1).

To model the rose plants in the greenhouse, we assume that the plants can be divided into two constituent parts. The lower part is the 'bush' that supports the upper part or the 'crop', see figure 1. We assume that the bush has height h_0 and that it is not harvested but has leaves that assimilate. The crop on the other hand consists of stems, each with a rose bud on top, that are harvested once they reach a certain height h_{cut}. They are then cut at the level $h = h_0$ so that the harvested stems all have length $h_{cut} - h_0$. As mature plants are cut, new stems begin to grow from the top of the bush appearing at a rate proportional to the total photosynthetic rate in the greenhouse. We ignore at present the part of the acquired photosynthetic energy that is used for maintenance and storage, and assume that the photosynthesis in the crop and bush is entirely used to increase the mass of stems in the crop.

The model can be split into two distinct levels. The first level is concerned with the biological process inside a leaf, in other words the local photosynthesis. The other level handles modelling the greenhouse as a whole and here the global CO_2-assimilation of all the rose plants and the resultant harvest are taken into account. We make realistic and sometimes simplifying assumptions based on biological observations. As the photosynthesis in a leaf depends on the age of the leaf, we have to know where the young and

old leaves are positioned on a rose plant. For this reason we assume that stems grow vertically, and that new leaves grow at the top. Thus, we find the older leaves on the lower part of the stem and the younger ones near the bud. We also suppose that the leaves, and therefore the leaf area, are distributed uniformly along the stem. In other words, the leaf area of each stem is proportional the stem's length.

One of the essential assumptions on which the global model is built is the so-called 'unselfishness principle'. The principle says that any energy gained by photosynthesis of a single leaf, either located on a stem or within the bush, contributes equally to the growth of all the stems, large and small. Hence, a taller stem, which has more leaves, will assimilate more CO_2 and produce more energy than a shorter one but their combined energy will be shared equally between them. As a result, every stem grows at the same speed, independent of its own photosynthetic rate. This assumption reflects both real data and the observation that a single rose plant, possessing a number of rose stems of differing heights, acts as a single entity; in this way young stems can develop quickly, even though they do not possess a large leaf area.

Based on the principles stated above, a global rose production model has been constructed that resolves the rate of change in height distribution of rose stems (see section 2). The state of the crop at any given instant of time is uniquely determined by a stem density function $d(h, t)$, describing the number of stems per area of greenhouse as a function of height h and time t. The dynamics of d are given by a linear advection equation and the unselfishness principle implies that the relevant advection speed is a function of time only. The growth or advection rate is found by calculating the total net photosynthesis of a square metre of rose plants. This is determined by adding the local photosynthetic contribution from each leaf in the rose crop and rose bush. As the leaf's local photosynthetic rate depends both on its age and on the amount of light it receives (affected by shading from higher leaves), an ability to model the age and height distribution of leaves is important. The total photosynthesis produced per square metre follows, in turn, by integration of the local photosynthesis rate over all the leaf ages and heights in both the rose crop and the bush, weighted by the leaf area distribution. In our model, the leaf distributions of the rose crop and the bush are treated separately. Indeed, two different approaches to model the total photosynthesis of the bush are given with their respective advantages and disadvantages.

To close the global rose production model, we must also model the local photosynthesis to obtain the photosynthetic rate of a single leaf as a function of height and leaf age; this is done in section 3. The local model used is a simplified version of the models developed by Harley *et al* (1992) and Kim

and Lieth (2001). Of course, the global model can be equally well coupled to other local models of leaf photosynthesis.

Given the necessary simplifications, several proportionality constants appear as parameters in the global model. These parameters must be determined either by direct measurement of the rose plants or by fitting them to given harvest data. In section 4, we describe how the estimation of these parameters can be accomplished. The model should then, in principle, be able to aid the rose grower to optimise the weekly amount of harvested roses. However, adequate testing of the model by numerically fitting the parameters to real data is still in progress.

The outline of the article is the following. In section 2, the global mathematical model for rose growth is developed. The simplified local leaf model used for photosynthesis is then described in section 3. The combination of the local and the global model contains seven unknown parameters. In section 4, we argue how these parameters can be estimated by direct measurements on a rose plant, and also from the harvest data. Finally, we summarize the theory and discuss directions for future work in section 5.

2. Global rose production model

The rose plants growing in a greenhouse can be separated into two parts: the rose stems, which are harvested, and the rose 'bush' below that contains the body of the rose plants supporting each individual stem (see figure 1). The rose bush is not harvested and lies between $h = 0$ and $h = h_0$. Its leaves assimilate energy that contributes to the growth of the crop. The rose stems growing vertically out of the rose bush are, at a given time, of different heights. As each rose plant consists of a mixture of mature and young rose stems, rose stems of different heights are taken to be distributed evenly throughout the greenhouse.

2.1. A representation of the greenhouse. The mathematical model for rose production is based on the following assumptions, which agree with the rose growers experience and simplify the mathematical modelling:

i. The principle of unselfishness: roses are unselfish, meaning that any biomass gained through photosynthesis of a single leaf is equally distributed among all the stems, large and small. In other words at any fixed time, every stem grows at the same speed $v(t; d)$, independent of its own photosynthesis production.

ii. All stems grow vertically.

iii. All stems start at height h_0. The appearance (sprouting) of new stems depends on the climatic conditions and is therefore assumed to be proportional to the photosynthetic rate.

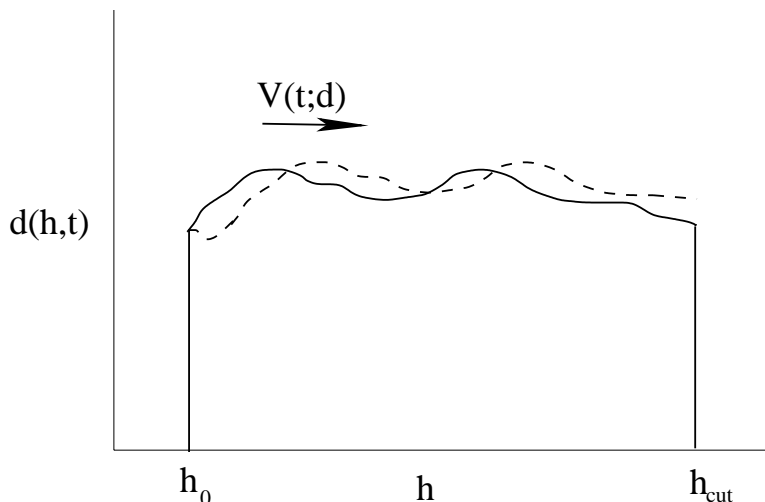iv. Stems are cut at a height h_0 and harvested when they exceed height $h > h_{cut} > h_0$.

FIGURE 2. The state of the rose crop can be expressed by a stem density function $d(h, t)$ representing the distribution of stems of differing heights per square metre of greenhouse area. The dynamics of $d(h, t)$ is governed by an advection equation and the unselfishness principle implies that the advection speed is independent of h.

v. All new leaves appear at the top of a stem, implying that the leaves closest to the rose bud are the youngest.
vi. Both mass and leaf area of a stem are proportional to the length of the stem and uniformly distributed along it.

For the dimensions of all occurring quantities and constants we refer to tables 1 and 2.

The state of the greenhouse is given by a stem density function $d = d(h, t)$ for $h > h_0$ such that the number of stems of lengths between h and $h + \mathrm{d}h$ per square metre of greenhouse is $d(h, t)\mathrm{d}h$ (see figure 2).

2.2. The advection equation for the stem density function d. The unselfishness principle (assumption i) implies that this density function is advected by a growth rate $v = v(t; d)$, which is independent of h and will be determined later. Hence, we obtain

$$(1) \qquad\qquad \partial_t d + v\, \partial_h d = 0,$$

where $\partial_t = \partial/\partial t, \partial_h = \partial/\partial h$ denote partial derivatives with respect to time t and height h.

The boundary condition at $h = h_0$ represents the creation of new stems from the rose bush (provided there is enough light such that $v(t; d) > 0$). By assumption iii, the appearance of new stems at h_0 is proportional to the

Symbol	*Quantity*	*unit*
h	height	m
h_0	starting height of stems	m
h_{cut}	cutting height	m
d	stem density distribution	m^{-3}
v	growth velocity	$m\ s^{-1}$
P_{net}	total net photosynthesis rate	$\mu mol\ m^{-2}s^{-1}$
H	harvest rate	$kg\ m^{-2}s^{-1}$
M	crop mass	$kg\ m^{-2}$
N	number of stems	m^{-2}
ρ	leaf area density	m^{-1}
q	age density distribution	$m^{-1}s^{-1}$
a	leaf age	s
I	photosynthetic photon flux density	$\mu mol\ m^{-2}s^{-1}$
T_{max}	average growth time of rose (6 to 8 weeks)	s
τ	Length of growing season (6 months)	s

TABLE 1. Dimensional quantities used in the global greenhouse model
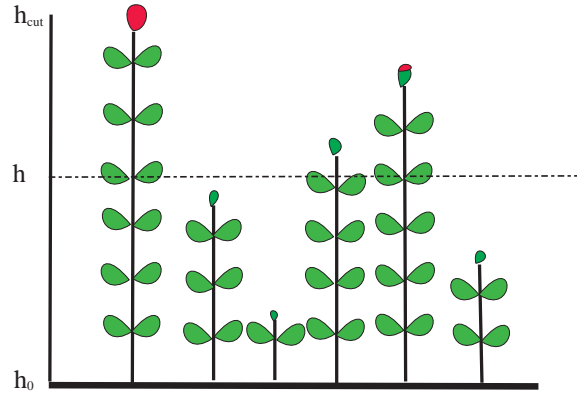
FIGURE 3. At a certain height h all rose stems of heights greater than h contribute to the leaf area density $\rho(h)$. Smaller rose stems do not.

rate of photosynthesis $P_{net}(t;d)$:

$$(2) \qquad\qquad\qquad d(h_0, t) = k_2\, P_{net}(t;d).$$

This net photosynthetic rate P_{net} represents the biochemical intake or loss of CO_2 per square metre of greenhouse and will be determined later.

Assumption iv implies that the harvest rate $H(t)$ per square metre of greenhouse is given by

$$(3) \qquad\qquad H(t) = k_3\, v(t;d)\, (h_{cut} - h_0)\, d(h_{cut}, t),$$

where k_3 is the mass of a rose per unit length. It is straightforward to alter the model to a situation where the roses larger than h_{cut} are harvested at discrete times and not continuously (see Appendix A).

2.3. Determining the growth speed v. The mass of crop in the greenhouse is again proportional to k_3 and the first moment in h of the stem density function

$$(4) \qquad\qquad M(t) = k_3 \int_{h_0}^{h_{cut}} (h - h_0)\, d(h, t)\, \mathrm{d}h,$$

where the stem density is properly weighed by the stem length $(h - h_0)$ in order to obtain the mass (that is, following assumption vi). Differentiating (4) and integrating the r.h.s. by parts gives

$$\frac{dM}{dt} = -k_3\, v(t; d) \int_{h_0}^{h_{cut}} (h - h_0)\, \partial_h d(h, t)\, \mathrm{d}h$$

$$= k_3\, v(t; d) \int_{h_0}^{h_{cut}} d(h, t)\, \mathrm{d}h - k_3\, v(t; d)\, (h_{cut} - h_0)\, d(h_{cut}, t)$$

$$(5) \qquad = k_3\, v(t; d)\, N(t) - H(t),$$

where the integral over $d(h, t)$ is the total number of stems per square metre and given here as

$$(6) \qquad\qquad N(t) = \int_{h_0}^{h_{cut}} d(h, t)\, \mathrm{d}h.$$

The net photosynthetic rate P_{net} is proportional to the change in productive mass plus the harvest rate, and by using (5) we can subsequently obtain the growth rate $v(t; d)$:

$$(7) \qquad\qquad k_1\, P_{net}(t; d) = \frac{dM}{dt} + H(t) = k_3\, v(t; d)\, N(t)$$

$$(8) \qquad\qquad \Longleftrightarrow \quad v(t; d) = \frac{k_1\, P_{net}(t; d)}{k_3\, N(t)}.$$

2.4. The leaf density functions. In order to calculate P_{net} from the local photosynthesis model, we require information about the distribution of leaf area, leaf age and light intensity (photon flux density) with respect to height.

The density function $\rho(h, t)$ is defined so that $\rho(h, t)\, \mathrm{d}h$ yields the area of leaves with stem lengths between h and $h + \mathrm{d}h$ per square metre of greenhouse. It is related to $d(h, t)$ by

$$(9) \qquad\qquad \rho(h, t) = k_4 \int_{h}^{h_{cut}} d(\zeta, t)\, \mathrm{d}\zeta.$$

| Symbol	Constant	unit
k_1	mass production per CO_2 intake	$kg \ \mu mol^{-1}$
k_2	birth rate of stems	$s \ \mu mol^{-1} \ m^{-1}$
k_3	stem mass per unit length	$kg \ m^{-1}$
k_4	leaf area of a stem per unit length	m
k_5	inverse average growth velocity	$s \ m^{-1}$
k_6	light absorption coefficient	–
k_7	ratio of leaf area in bush to leaf area in crop (rose stems)	
k_8	contribution of bush second model	–

TABLE 2. Parameters in the global greenhouse model
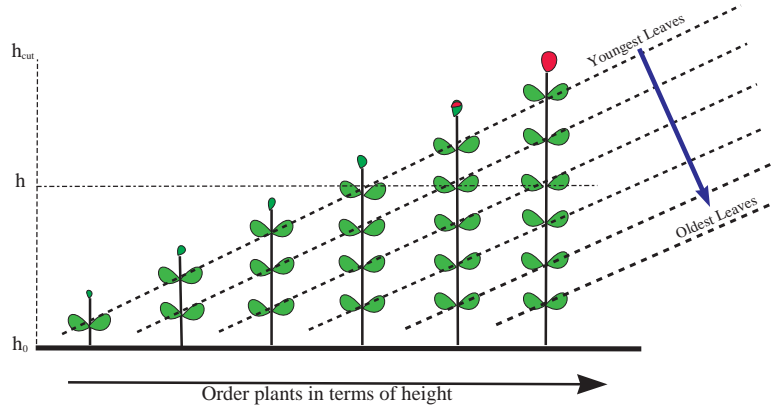
FIGURE 4. Placing the rose stems in order of size is a useful guide to calculate the age distribution of leaves at a given height h. The sketch depicts the situation where the growth velocity is approximated to be constant to simplify the age density distribution.

The integration limits are chosen as h and h_{cut} because all the rose stems of heights greater than h contribute to the leaf area density at h; figure 3 provides a more graphical explanation why.

The age density distribution $q(t, a, h)$ is defined so that $q(t, a, h) \, \mathrm{d}h \, \mathrm{d}a$ yields the leaf area of age between a and $a+\mathrm{d}a$ located between the heights h and $h+\mathrm{d}h$ per square metre of greenhouse. Under the simplifying assumption that the age of a leaf is proportional to its distance from the top of the stem we find that the leaves of age a at height h belong to stems of height $h + \frac{a}{k_5}$ (see figure 4). The parameter $k_5 = T_{max}/(h_{cut} - h_0)$ is the inverse average growth rate of a typical stem. The time T_{max} indicates the average total growth time of a stem from its first appearance on the bush to harvest; T_{max} differs for each type of rose and each growth season. Thus

$$q(t, a, h) = c \, d \left(h + \frac{a}{k_5}, t \right).$$

Using the fact that $\rho(h,t) = \int_0^{Tmax} q(t,a,h)\mathrm{d}a$ we can determine the proportionality constant c to obtain

(10)
$$q(t,a,h) = \frac{k_4}{k_5}\, d\left(h + \frac{a}{k_5}, t\right).$$

Of course, the assumption of a constant growth velocity for the branches is in contradiction with our model assumptions. We use it, however, for the determination of the age distribution in order to avoid the highly complex nonlinear integrodifferential equation for v which would result if v itself would be used there. The assumption can be justified by the fact that T_{max} is large compared to the time scale on which the photosynthesis varies.

2.5. The light penetration. The top leaves of the tallest rose stems receive all the light available. However, the amount of light reaching the lower leaves of the mature plants and of the newer stems is diminished by the amount of leaf coverage above. The isotropic nature of the greenhouse means that all leaves at the same height have approximately the same amount of shade. The change in light intensity $I(h)$ as function of h is thus taken to be proportional to $\rho(h)$ and $I(h)$, leading to

(11)
$$\frac{dI(h)}{dh} = k_6\,\rho(h)\,I(h), \quad I(h_{cut}) = I_0, \quad \Longleftrightarrow \quad I(h) = I_0\,e^{-k_6\int_h^{h_{cut}}\rho(\zeta)\,\mathrm{d}\zeta}.$$

The assumed age distribution of the leaves of the rose stems and the change in light intensity at each height now enable us to calculate the net photosynthesis produced by the rose crop per square metre of greenhouse, as follows

(12)
$$P_{crop}(t;d) = \int_{h_0}^{h_{cut}} \int_0^{Tmax} q(t,a,h)\,P(t,a,h)\,\mathrm{d}a\,\mathrm{d}h.$$

Here $P(t,a,h)$ is the local photosynthesis rate per unit area for a leaf at height h and age a under given exterior climatic conditions (that is, temperature, relative air humidity, light intensity, and CO_2-concentration) at time t, as predicted by the local leaf model described in section 3.

2.6. The photosynthesis in the bush. While P_{crop} represents the major source of biomass for the roses in the greenhouse, the rose bush below h_0 also contains leaves and produces an additional seasonally-varying contribution to the net growth rate. We take two different approaches in modelling the rose bush, although other models are possible.

For the first approach it is assumed that the number of leaves in the rose bush, $h < h_0$, is some given ratio k_7 of the number of leaves in the crop above, for a given type of rose in a given season. These leaves within the bush are taken to be uniformly distributed between $h = 0$ and $h = h_0$. Furthermore, it is assumed that the leaves' ages are distributed uniformly

throughout the bush from newly created leaves to leaves roughly as old as the length of an entire growing season τ; here the season is assumed to last roughly six months (winter and summer). From these assumptions, the leaf area density within the bush can be written as

$$(13) \qquad \rho(h < h_0) = \frac{k_7}{h_0} \int_{h_0}^{h_{cut}} \rho(\zeta) \mathrm{d}\zeta.$$

The amount of light reaching these bush leaves can then be determined from the solution to equation (11) for $0 < h < h_{cut}$. Furthermore, the uniform age and height distribution of leaves in the bush leads to the expression

$$(14) \qquad q_{bush}(t, a, h) = \frac{k_7 \int_{h_0}^{h_{cut}} \rho(\zeta) \mathrm{d}\zeta}{h_0 \, \tau},$$

for the age density distribution, which is constant in both a and h. The net rate of photosynthesis of the bush can subsequently be found, as for the crop, by integration over all leaf ages and heights,

$$P_{bush}^{(1)}(t; d) = \int_0^{h_0} \int_0^{\tau} q_{bush}(t, a, h) \, P(t, a, h) \, \mathrm{d}a \, \mathrm{d}h$$

$$(15) \qquad = \frac{k_7 \int_{h_0}^{h_{cut}} \rho(\zeta) \mathrm{d}\zeta}{h_0 \, \tau} \int_0^{h_0} \int_0^{\tau} P(t, a, h) \, \mathrm{d}a \, \mathrm{d}h.$$

In the second approach, the above model of the bush is simplified. Now, we assume that the leaves in the bush all have a mean age $\tau/2$ and a mean height $h_0/2$; again τ is the length of an entire growing season. Introducing another constant k_8 to represent the leaf area in the bush, we obtain

$$(16) \qquad P_{bush}^{(2)}(t) = k_8 \, P(t, \tau/2, h_0/2)$$

for the net rate of photosynthesis of the bush.

Both of these approaches to model the bush have their advantages and disadvantages. The first approach is more realistic compared to the second one since the bush is taken to have a similar leaf distribution as the crop. However, this model breaks down when all of the crop is harvested at the same time. In that case, the parameter k_7 limits to infinity and renders the bush model invalid. This scenario is realistic for certain rose types, like the variety "Sweet Unique", where all the roses are harvested at once particular instant. In addition, determining the parameter k_7 from the greenhouse data or relating it to the other parameters is non-trivial, so that implementation of the model may be more difficult compared to the second approach.

In the second approach on the other hand, the structure of the bush is simplified too much. More realistically, the bush consists of leaves with different ages and height like in the first approach. An advantage of this approach is, however, that k_8 can be estimated more readily from the harvest data, see section 4.

Finally, the total net photosynthetic rate is the sum of the net crop photosynthesis from (12) and the net bush photosynthesis from either (15) or (16), depending on the approach taken for modelling the bush, leading to

$$(17) \qquad P_{net}(t; d) = P_{crop}(t; d) + P_{bush}(t; d).$$

In order to use our model to predict rose production, seven parameters k_i with $i = 1, \ldots, 6$ and either k_7 or k_8 must be estimated, for each rose type and for each season, using real harvest data with corresponding climate information measured inside the greenhouse.

3. Local leaf model for photosynthesis

It is important to emphasize that the production model described in section 2 is closed once only we have a model for the local photosynthesis in a leaf. Presently, we will use a version of the photosynthesis rose leaf model of Harley *et al.* (1992) and Kim and Lieth (2001).

Following Harley *et al.* (1992) and Kim and Lieth (2001), the photosynthetic rate in a unit area of leaf at height h and with age a, is given by

$$(18) \qquad P(t, a, h) = min\{A_v, A_j\} - R_d.$$

Here A_v and A_j are the rate of Rubisco limited photosynthesis and the rate limited by RuBP regeneration respectively, while R_d is a threshold CO_2 consumption or dark respiration, for example due to losses at night, which we take constant at $R_d = 0.82 \, \mu mol/(m^2 \, s)$ (cf. Hartley *et al.*, 1992). The existence of the dark respiration term R_d implies that $P(t, a, h)$ can be less than zero at height h and a. However, any local losses can be compensated by a positive global photosynthesis rate elsewhere due to the unselfishness principle. Both P_{net} and $P(t, a, h)$ are expressed in terms of a CO_2-rate per square metre of greenhouse, which is $\mu mol \, CO_2/(m^2 \, s)$.

The photosynthesis rates A_v and A_j depend on the intercellular CO_2-concentration C_i, as is shown in figure 5: the photosynthesis stops in conditions of too little intercellular CO_2 (i.e. if $C_i < \Gamma_*$). For increasing values of C_i, the photosynthetic rate allowed by RuBP regeneration increases faster than the Rubisco limited photosynthesis rate, but the latter attains a higher value V_{cmax} than the former.

The formula for Rubisco limited photosynthesis A_v is given by (Kim and Lieth, 2001)

$$(19) \qquad A_v = V_{cmax} \frac{C_i - \Gamma_*}{C_i + \kappa} \qquad with \quad V_{cmax} = V_m \, g(T) \, f(a),$$

where V_{cmax} is the maximum rate of carboxylation and C_i the intercellular CO_2-concentration, and $g(T)$ and $f(a)$ represent the dependence on leaf temperature T and leaf age a. The remaining unknowns are constants,
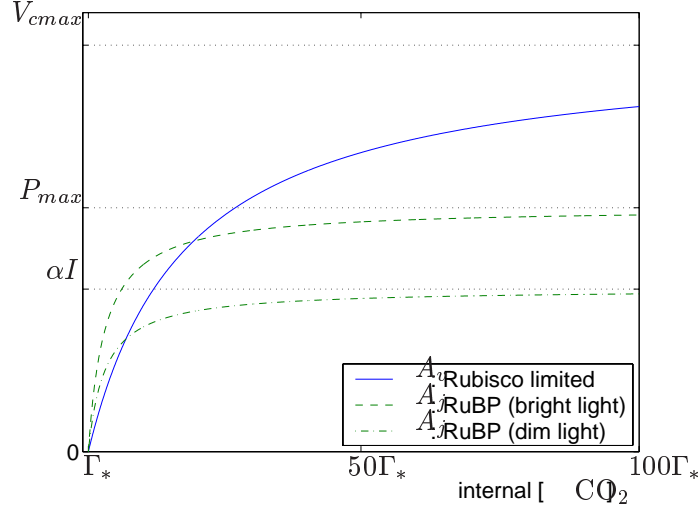
FIGURE 5. The C_i-dependence of photosynthesis rates A_v and A_j.

defined and given in table 3; see also Harley *et al.* (1992) and Kim and Lieth (2001). The RuBP limited photosynthetic rate A_j is

$$A_j = \frac{C_i - \Gamma_*}{4\,(C_i + 2\,\Gamma_*)} J \tag{20}$$

with the potential electron transport rate J given by

$$J = \frac{8\,\alpha\,I\,P_{max}}{\alpha\,I + P_{max} + \sqrt{(\alpha\,I + P_{max})^2 - 4\,\alpha\,I\,P_{max}\,\theta}} \tag{21}$$

with

$$P_{max} = P_m\,g(T)\,f(a). \tag{22}$$

Here $I = I(h)$ is the photosynthetic flux density given in (11) at height h above the ground. We note that when $P_{max} \gg \alpha\,I$ the potential rate $J \approx 4\,\alpha\,I$, which means that when $\alpha\,I$ is sufficiently small the production is limited by the lack of light. Inversely, when $P_{max} \ll \alpha\,I$ the potential rate $J \approx 4\,P_{max}$, which means that when $\alpha\,I$ is sufficiently large, any increase in the amount of light has no additional influence on the rate of photosynthesis.

The temperature dependence $g(T)$ and age dependence $f(a)$ of the photosynthesis rates V_{cmax} and P_{max} are shown in figure 6. These dependencies are described by the formula

$$g(T) = \frac{4\,(T - T_o)\,(T_d - T)}{(T_d - T_o)^2} \quad \text{and} \quad f(a) = (a/a_{opt})\,e^{(1 - a/a_{opt})}. \tag{23}$$
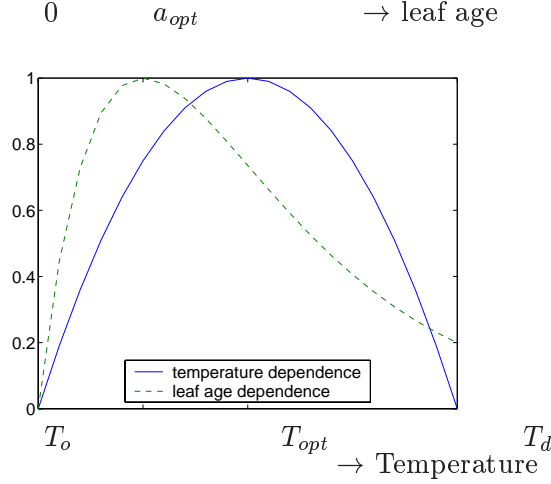
FIGURE 6. The temperature and leaf age dependence of local photosynthetic rates V_{cmax} and P_{max}

This temperature dependence $g(T)$ is chosen, instead of the one in Harley *et al.* (1992) and Kim and Lieth (2001), because it includes a minimum and maximum temperature T_o and T_d, respectively, below and above which the photosynthesis production is zero, respectively. The age dependence $f(a)$ follows from Lieth and Pasian (1990).

The intercellular CO_2-concentration is

$$(24) \qquad C_i = C_a - \beta \frac{P(t,a,h)}{g_s}, \qquad g_s = g_0 + g_1\, P(t,a,h)\, R_H/C_a$$

where the ambient CO_2-concentration is given in $\mu mol CO_2/(mol\ air)$, R_H is the relative humidity, g_s is the stomatal conductance to H_2O in $mol\ H_2O/(m^2\ s)$, g_0 is the minimal stomatal conductance to H_2O in $mol\ H_2O/(m^2\ s)$, and $\beta = 1.6$. Note that (24) is the quasi steady-state solution of

$$(25) \qquad \frac{\partial C_i}{\partial t} = g_s(C_a - C_i) - \beta P(t,a,h),$$

expressing the effects of consumption of CO_2 by photosynthesis and conduction of CO_2 by the leaf stomata. Note also that the intercellular concentration C_i is lower than the ambient one, provided $P(t,a,h) > 0$. For an increasing production $P(t,a,h)$ the concentration C_i is decreasing, while for increasing ambient humidity R_H the concentration C_i is increasing.

Constant	definition	value
R_d	dark respiration	$0.82\,\mu mol\,CO_2/(m^2\,s)$
V_m	-	$94.3\,\mu mol\,CO_2/(m^2\,s)$
Γ_*	CO_2 compensation point	$44\,\mu mol\,CO_2/mol$
κ	-	$730\,\mu mol\,CO_2/mol$
P_m	-	$56.6\,\mu mol\,CO_2/(m^2\,s)$
α	quantum efficiency	$0.055\,mol\,CO_2/(mol\,photon)$
θ	curvature factor	0.7
T_o	lower temperature bound	$10\,^oC$
T_d	upper temperature bound	$48.6\,^oC$
a_{opt}	optimum age	$28.01\,days$
g_0	minimum stomatal conductance	$0.18\,mol\,H_2O/(m^2\,s)$
g_1	-	6.71
β	conversion factor CO_2/H_2O	1.6

TABLE 3. Definitions and given values of the constants used in the leaf photosynthesis model.

The leaf temperature T and the ambient temperature T_a are related by linearizing the expression on page 232 of Jones (1992)

$$(26) \quad T = T_a + [4 - (2/45)\,T_a]\,I_0/(1380) - [1 + (6/45)\,T_a]\,(1 - R_H)/0.7$$

with I_0 expressed as $\mu mol\,photons/(m^2 s)$ and R_H taking some value between 0 and 1.

The calculation of the photosynthesis rate $P(t, a, h)$ requires the solution of a quadratic equation, since the intercellular CO_2-concentration C_i and the stomatal conductance g_s both depend on $P(t, a, h)$. However, in various asymptotic limits, the equation for $P(t, a, h)$ can be linearised, simplifying the calculations (see Appendix A.2).

4. Parameter estimation from harvest data

In the model, we have introduced seven parameters: $k_1, \cdots, k_6$ and either k_7 or k_8. These parameters need to be estimated.

The rose grower can directly estimate k_4 by measuring the average leaf area per metre of stem. Similarly, the average growth speed $V = (h_{cut} - h_0)/T_{max}$ can be found from the stem height desired $(h_{cut} - h_0)$ and the average length of the growth cycle of such a rose stem T_{max} for the current season; the reciprocal of $V = 1/k_5$ determines k_5 as required.

We determine k_3 by averaging (3) in time. After simplifying and rearranging, we find

$$(27) \qquad k_3 = \frac{\bar{H}}{V\,(h_{cut} - h_0)\,D_{cut}}$$

where $\bar{H}$ is the average harvest of stems per square metre of greenhouse, V is the average of $v(t; d)$ and D_{cut} is the average of $d(h_{cut}, t)$. A relation

between k_1 and k_2 is obtained by averaging $d(h_0, t) = k_2 \, P_{net}$ and $k_1 \, P_{net} = k_3 \, v(t; d) \, N(t)$. Using (27), our simplification gives

$$(28) \qquad\qquad k_2 = k_1 \, \frac{D_0 \, D_{cut} \, (h_{cut} - h_0)}{\bar{H} \, \bar{N}}$$

with D_0 the average of $d(h_0, t)$ and $\bar{N}$ the average of $N(t)$.

In the first approach to model the bush, a rough estimate of k_7, the ratio of the leaf area in the bush to that of the crop, needs to be provided by the rose grower.

In the second approach, we take $k_8 = \kappa \, k_4 / k_5$. It now turns out that it is only necessary to obtain the combinations $\kappa_1 = k_1 \, k_4$, $\kappa_2 = k_2 \, k_4$ and $\kappa_6 = k_6 \, k_4$.

Finally, the parameters k_1 and k_6 (or κ_1 and κ_6) are obtained by fitting them to the weekly harvest data, given the measured time series for the ambient climate.

The roses in the greenhouse considered are of the variety "Red Berlin", planted in May 1999 on a total surface of $8480 \, m^2$. The data consists of the number of harvested stems per square metre of greenhouse and the harvested grams per stem over 56 weeks, from week one 2001 until week four in 2002. In addition, time series data of the ambient conditions are provided over the same period. These quantities are all measured and recorded at irregular times, ranging from a few minutes to one hour or more. The resulting ambient light intensity can also be determined from the data using the information on the incoming sunlight, the intensity of any additional artificial light sources, and the screen settings (screens are used to shield roses from too much sunlight). By averaging we can subsequently find $\bar{H}$ and $\bar{N}$.

5. Conclusion and discussion

We have considered the question of optimising rose production in a greenhouse. A rose production model has been constructed that consists of a local and a global model coupled together. In this model, rose growth depends naturally on the time-dependent ambient conditions given by the temperature, the relative humidity, the CO_2-concentration, and the light intensity.

The global model is governed by an advection equation for the stem density function $d(h, t)$. The key assumption used is the unselfishness principle, which implies that the photosynthetic energy produced in the leaves is distributed evenly among the stems, and hence that the advection speed $v(t; d)$ is an explicit function of time only. Other simplifying assumptions used are that any new leaves appear at the top of the stem and that the mass and leaf area are uniformly distributed along the stem. Consequently, the leaf area distribution is directly proportional to the stem density function. It is shown that v can be determined from the net photosynthetic rate, which is

the sum of the photosynthetic rate in the bush below height $h < h_0$ and the photosynthetic rate in the rose crop between heights h_0 and h_{cut}.

The net photosynthetic rate depends on the local photosynthesis in a leaf as well as the ambient climate. A local model adapted from the biological literature (Harley *et al.*, 1992, Kim and Lieth, 2001) is then used to determine this local photosynthetic rate which is a function of leaf age and height.

The total model contains seven unknown parameters that can be estimated from direct measurements on the rose plants, the average harvest and weekly harvest data, as well as from the time series data of the ambient climate in the greenhouse.

This article describes the theory behind our model. Future research is required to test and validate the model. The first necessary step is to estimate the model's parameters by using the greenhouse data provided for the rose variety "Red Berlin" over 56 weeks in the years 2001 and 2002. Subsequently, we can attempt to optimise the rose production by running the model in forecasting mode. During this comparison between model and data, we anticipate further model improvements may be required, such as solving the nonlinear integral equation for the advection speed and the inclusion of a storage mechanism for photosynthetic energy.

It is quite clear that some of our modelling assumptions are an oversimplification of the real situation. One major drawback in our approach seems to be the fact that the only measure for the development of a rose stem is given by its accumulation of biomass due to photosynthesis. This is not very realistic, as can be seen for example from the seasonal differences in the thickness of the harvested rose stems. In particular, the process of blossoming, which is a crucial guide to when the rose stem should be cut, is not modelled at all. Moreover, various bush models are possible, corresponding to the different ways the rose bush supporting the stems can be allowed to grow (or not) in the greenhouse. However, we hope that our approach via stem, leaf, and age density functions will prove flexible enough to be used as a basis for more complex and precise models. Such improvements, together with the continuation of the work on parameter estimation, form an intriguing challenge for further research in optimising rose production.

A. Appendix

A.1. Numerical methods. In this appendix, we describe how we (numerically) integrate the rose production model forward given the ambient climate. We illustrate the method for a slightly different scenario to the one described in section 2, where all the rose stems with a length greater then $h_{cut} - h_0$ are harvested at certain specific times (discrete) instead of continuously.

A.1.1. Advection equation. In summary, the complete mathematical model is given by

$$(29) \qquad \partial_t d + \frac{k_1 \, P_{net}(t; d)}{k_3 \, \int_{h_0}^{h_{max}} d(\zeta, t) \, \mathrm{d}\zeta} \, \partial_h d = 0$$

with boundary conditions

$$(30) \qquad d(h_0, t) = k_2 \, P_{net}(t; d) \qquad \text{when} \quad v(t; d) > 0, \quad \text{and}$$

$$(31) \qquad h_{max}(t) = max(h_{cut}, \int_{h_{max}(0)}^{t} v(\gamma; d) \, \mathrm{d}\gamma).$$

Irrespective of the up- and downwind cases $v(t; d)$ remains similar, but when $v(t; d) = k_1 \, P_{net}/(k_3 \, N(t)) < 0$ with $N(t) = \int_{h_0}^{h_{max}} d(h, t) \, \mathrm{d}h$ we have $h_{max} < h_{cut}$ and the crop length decreases. Since (29) is an advection equation, it requires a boundary condition at $h = h_0$ when $v > 0$, and it has a moving boundary condition at $h = h_{max}$ when $v < 0$. We assume that the conditions are such that $h_{max} > h_0$.

Define $x = (h - h_0)/(h_{max} - h_0)$, then (29) becomes

$$(32) \qquad \partial_t d + \left(\frac{v - x \, \dot{h}_{max}}{h_{max} - h_0} \right) \partial_x d = 0 \quad \implies \quad \partial_t d + u \, \partial_x d = 0$$

with $x \in [0, 1]$ and $u = (v - x \, \dot{h}_{max})/(h_{max} - h_0)$. When $v < 0$, we note that $d(x = 1, t)$ is the last value $d(1, t')$ at time t' when v became zero. When $h_{max} = h_{cut}$ we have $dh_{max}/dt \equiv \dot{h}_{max} = 0$ and (32) is just a rescaled version of (29).

We used a second-order up- or downwind scheme depending on the sign of u to spatially discretise x in the interior and use a first-order up- or downwind scheme at the left-or right boundary, respectively. Using $N + 1$ grid points from $x \in [0, 1]$ we arrive at a system of ordinary differential equations. A variable time stepping scheme for ordinary equations from Matlab is used (i.e. `ode15`).

A.2. A linear expression for the local photosynthetic rate. In the limits where $C_i \gg \Gamma_*$ and $C_i - \Gamma_* = \epsilon$ with $\epsilon \ll 1$, the expression for the photosynthetic rate becomes linear. This can be seen by considering the limiting behaviour of A_v in (19) and A_j in (20) and by approximating

$C_i \geq C_{ia} = \max[C_a - \beta\, P(h,a)/g_0, C_a - \beta\, C_a/(g_1\, R_h)]$. Then, we can simplify (18) to give

$$(33) \qquad P(t,a,h) = \min\left\{ V_m\, g\, f, V_m, \frac{C_{ia} - \Gamma_*}{\Gamma_* + \kappa}, J/4, J\,\frac{C_{ia} - \Gamma_*}{12\,\Gamma_*} \right\} - R_d,$$

which is linear in $P(t,a,h)$. The net photosynthesis $P_{net}(t;d)$ as a function of time t follows from (17) and (33) by using the climate data. Linear interpolation is used to find the climate values at times t between given data points.

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