Validation of a Dynamic Lettuce Growth Model for Greenhouse Climate Control

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ABSTRACT

*Validation results are presented of a dynamic crop growth model of lettuce (*Lactuca sativa L.*) previously used in a greenhouse climate optimization study. The model describes the dynamic behaviour of two state variables, the non-structural dry weight and the structural dry weight, as affected by the incident photosynthetically active radiation, the carbon dioxide concentration and the air temperature in the greenhouse. Model equations and parameters have been collected from the literature. Because in the control study the economic return of a lettuce cultivation was considered to be determined by total crop dry weight, the model's ability to describe the dynamic behaviour of the dry matter content of a lettuce crop has been evaluated. Comparison of simulations with data obtained in two growth experiments showed that the growth model was able to describe with satisfactory accuracy the dry matter production of lettuces cultivated according to standard horticultural practice.*

NOTATION

c	Constant
f	Mass rate of change (g m^{-2} s^{-1})
g	Conductance (m s^{-1})
r	Specific rate of change (s^{-1})
U	Model input
X	State variable

Subscripts

bnd	Boundary layer
car	Carboxylation
CO_2	Carbon dioxide concentration (ppm)
gr	Growth of structural material (g m^{-2} s^{-1})
K	Extinction coefficient
lar	Leaf area ratio
max	Saturation rate (g m^{-2} s^{-1})
nsdw	Non-structural dry weight (g m^{-2})
PAR	Photosynthetically active radiation (W m^{-2})
phot	Carbon dioxide photosynthesis (g m^{-2} s^{-1})
Q_{10}	Q_{10} factor
resp	Maintenance respiration (g m^{-2} s^{-1})
rt	Root
sdw	Structural dry weight (g m^{-2})
sht	Shoot
stm	Stomata
T	Temperature (°C)
α	Conversion of assimilated CO_2 to sugar
β	Yield factor
γ	Growth rate coefficient
Γ	CO_2 compensation point (ppm)
ε	Light use efficiency (g J^{-1})
τ	Ratio of root dry weight to total dry weight
ω	Density of CO_2 (g m^{-3})

INTRODUCTION

Growing crops in artificial enclosures like greenhouses provides an opportunity of cultivating exotic crops during winter and spring time by protecting them from unfavourable outdoor climatic conditions. Moreover, it facilitates the improvement of the quality as well as the quantity of crop growth by means of changing the environment in the greenhouse. For instance, for lettuce an average head weight increase of about 20% can be obtained when the carbon dioxide concentration in the greenhouse is raised from the ambient level of 350 ppm to 800 ppm (Hicklenton, 1988).

Generally speaking, a major aim of horticultural crop production is to produce crops such that best economic results are obtained. With respect to greenhouse climate control this suggests that the application of the climate conditioning equipment should be based on a trade-off between cost of operation and economic return. This is a typical optimal control

problem which was first defined in horticultural engineering research by Seginer (1989) and studied, for instance, by Van Henten & Bontsema (1991). In horticultural practice, optimal control is hardly recognized and climate control is merely based on intuition and blue-prints resulting from knowledge about plant growing.

Application of optimal control theory (Kirk, 1970) offers an opportunity to identify control strategies in which the benefits associated with the marketable produce and the costs associated with its production are balanced. This approach requires, among others, an appropriate model of the crop evolution in time as a function of the indoor climate. The development of such models requires insight into the biological process, and their successful application demands appropriate validation.

When it is the aim to apply a process model in a dynamic control scheme, model validation should emphasize the evaluation of the model's ability to describe the dynamic behaviour of the process variables relevant for control, as a function of the input variables.

In the control study by Van Henten & Bontsema (1991) economically optimal strategies of the air temperature and the ambient carbon dioxide concentration were derived for a lettuce cultivation using a growth model which described the dry matter accumulation of a lettuce crop as a function of the incident photosynthetically active radiation and the ambient temperature and carbon dioxide concentration. The economic return of the produce sold was considered to be determined by the dry weight of the crop at harvest time. A strong correlation was found between the economically optimal greenhouse climate strategies and the outdoor climate.

In this paper results are presented of a model validation of the lettuce growth model previously used in the control study by Van Henten & Bontsema (1991). The lettuce growth model was based on first principles from plant physiology, and the model equations and model parameters have been extracted from the literature.

In two experiments lettuces were grown according to standard horticultural practice, and data were collected of crop dry matter and the climatic conditions in the greenhouse, including the air temperature, the carbon dioxide concentration and the solar radiation at canopy level.

Using dynamic simulation, the ability of the model to describe the measured dry matter accumulation was evaluated. Furthermore, a sensitivity analysis with respect to variations in the model parameters was performed to obtain insight into the relative importance of the parameters in this model representation of lettuce growth.

The paper is organized as follows. First, the model equations and parameters are presented. Next, methodology and results of two validation experiments as well as the sensitivity analysis are described. Finally, the

results are analysed and implications for future research on greenhouse climate control are addressed.

THE MODEL

Dry weight is a major variable defining the state of the crop. Total plant dry weight (DW) is divided into two components, the non-structural dry weight (NSDW) and the structural dry weight (SDW) such that DW = NSDW + SDW. In the model it is assumed that, at a given time, the plant is completely defined by two state variables: X_{nsdw}, and X_{sdw} (Thornley & Hurd, 1974; Sweeney et al., 1981). The non-structural dry weight consists, for instance, of glucose, sucrose and starch. The structural dry weight is the remaining component of the total dry weight and represents the weight of structural components like cell walls and cytoplasm.

The crop growth model describes the dynamic behaviour of the two state variables non-structural dry weight X_{nsdw} (g m^{-2}) and structural dry weight X_{sdw} (g m^{-2}) on a square-metre soil basis with the equations

$$\frac{dX_{nsdw}}{dt} = c_{\alpha} f_{phot} - r_{gr} X_{sdw} - f_{resp} - \frac{1 - c_{\beta}}{c_{\beta}} r_{gr} X_{sdw} \tag{1}$$

$$\frac{dX_{sdw}}{dt} = r_{gr} X_{sdw} \tag{2}$$

where f_{phot} (g m^{-2} s^{-1}) is the gross canopy photosynthesis, f_{resp} (g m^{-2} s^{-1}) is the maintenance respiration, r_{gr} (s^{-1}) is the specific growth rate and c_{α} and c_{β} are parameters. The model is represented in Fig. 1 using a formalism which resembles the conventions for relational diagrams introduced by Ferrari (1982). The diagram illustrates the effect of the greenhouse climate on the dry matter production.

The growth rate of the non-structural dry weight (eqn 1) is determined by the gross canopy photosynthesis (f_{phot}), the rate with which non-structural material is used for growth of structural dry weight ($-r_{gr} X_{sdw}$), the maintenance respiration (f_{resp}), which provides energy to maintain cells and their biostructure and ionic gradients, and synthesis and respiratory losses due to growth ($-((1 - c_{\beta})/c_{\beta}) r_{gr} X_{sdw}$).

The factor c_{α} which converts assimilated CO_2, into sugar (CH_2O) is taken to be the ratio of the molecular weights of CH_2O and CO_2, i.e. 30/44 = 0·68. The yield factor c_{β} indicates the respiratory and synthesis losses of non-structural material due to growth. These losses are assumed to be proportional to the growth rate of the structural dry matter. According to Penning de Vries et al. (1974) the growth related losses are
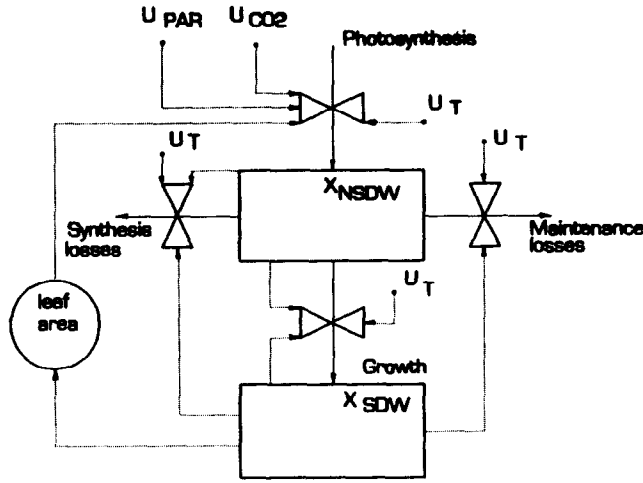
Fig. 1. Dynamic crop growth model of lettuce. U_{PAR} is the photosynthetically active radiation, U_T is the canopy temperature and U_{CO_2} is the carbon dioxide concentration in the greenhouse air.

strongly dependent on the chemical composition of the dry matter formed. This parameter was estimated at 0·8 for lettuce (Sweeney *et al.*, 1981).

The growth rate of structural dry matter (eqn 2) depends only on the rate at which the non-structural material is transformed into structural material. Translocation is neglected in this model. The specific growth rate r_{gr} (s^{-1}) describes the transformation rate of non-structural dry weight to structural dry weight. In accordance with Thornley & Hurd (1974) it is assumed that the specific rate of utilization of non-structural material for the construction of structural material depends on the ratio of non-structural dry weight to total dry weight, obeying the Michaelis–Menten equation. Furthermore the transformation of non-structural into structural material depends on the temperature (Sweeney *et al.*, 1981). This results in the following relation for r_{gr}:

$$r_{gr} = c_{gr,max} \frac{X_{nsdw}}{c_\gamma X_{sdw} + X_{nsdw}} c_{Q10,gr}{}^{(U_T-20)/10} \qquad (3)$$

where U_T (°C) is the canopy temperature and $c_{gr,max}$ (s^{-1}) is the saturation growth rate at 20°C. From measurements of Van Holsteijn (1981) $c_{gr,max}$ was estimated as 5×10^{-6} s^{-1}. According to Thornley & Hurd (1974) the parameter c_γ should have a value in the range 0·5–1·0. In this model a value of 1·0 is employed (Sweeney *et al.*, 1981). It should be mentioned that with this parameter choice the relative growth rate will never reach its maximal value $c_{gr,max}$ because generally the non-structural dry weight X_{nsdw} amounts to less than 25% of the total dry weight (Goudriaan *et al.*,

1985). As a consequence the quotient in eqn (3) will never obtain the value of 1·0. Therefore the interpretation of the saturation growth rate $c_{gr,max}$ is not very straightforward. $c_{Q_{10},gr}$ is the Q_{10} factor for growth which has a value of 1·6. For every temperature increase of 10°C the growth rate coefficient increases by a factor 1·6 (Sweeney *et al.*, 1981).

The maintenance respiration rate of the crop (f_{resp}) is described by

$$f_{resp} = (c_{resp,sht}(1 - c_\tau)X_{sdw} + c_{resp,rt}c_\tau X_{sdw})c_{Q_{10},resp}{}^{(U_T-25)/10} \quad (4)$$

where $c_{resp,sht}$ and $c_{resp,rt}$ (s^{-1}) are the maintenance respiration coefficients for the shoot and the root at 25°C expressed in the mass of glucose consumed per unit amount of structural dry matter present. The maintenance requirements for leaves and roots were set at 0·03 and 0·01 day^{-1} by Van Keulen *et al.* (1982). Assuming that the shoot is essentially composed of leaves this resulted in values of $3·47 \times 10^{-7}s^{-1}$ and $1·16 \times 10^{-7}s^{-1}$ for $c_{resp,rt}$ and $c_{resp,rt}$ respectively. $c_{Q_{10},resp}$ is the Q_{10} factor of the maintenance respiration which has a value of 2. The parameter c_τ expresses the ratio of the root dry weight to the total crop dry weight and is assumed to be constant. For lettuce grown in soil a value for c_τ of 0·15 has been reported (Lorenz & Wiebe, 1980; Sweeney *et al.*, 1981).

In accordance with Goudriaan & Van Laar (1978) and Goudriaan & Monteith (1990) gross canopy photosynthesis can be described by the empirical relation

$$f_{phot} = (1 - \exp(-c_K c_{lar}(1 - c_\tau)X_{sdw}))f_{phot,max} \quad (5)$$

in which $f_{phot,max}$ (g m^{-2} s^{-1}) is defined as the gross carbon dioxide assimilation rate of the canopy having an effective canopy surface of 1 m^2 per square-meter soil at complete soil covering. The geometrical and optical properties of the canopy with respect to incident radiation when the soil is not completely covered are accounted for by $(1 - \exp(-c_K c_{lar}(1 - c_\tau)X_{sdw}))$ in which $c_{lar}(1 - c_\tau)X_{sdw}$ represents the leaf area index. The extinction coefficient c_K has a value of 0·9 and 0·3 for planophile and erectophile canopies respectively (Goudriaan & Monteith, 1990). For a lettuce crop, being more a planophile than a erectophile crop, a value of 0·9 seems to be most suitable. The parameter c_{lar} (m^2 g^{-1}) is the structural leaf area ratio which is assumed to be constant in this model. Based on measurements of Lorenz & Wiebe (1980) and assuming that on average the non-structural dry weight accounts for 10% of total structural dry weight, c_{lar}, was estimated as 75×10^{-3} m^2 g^{-1}.

The response of canopy photosynthesis ($f_{phot,max}$) to photosynthetically active radiation and carbon dioxide concentration in the greenhouse air

is described by a rectangular hyperbola. The equation used by Acock *et al.* (1978) was extended to account for photorespiration and temperature effects on the light use efficiency as well as temperature effects on the carboxylation conductance in the leaf tissue.

$$f_{\text{phot,max}} = \frac{\varepsilon U_{\text{PAR}} g_{\text{CO}_2} c_\omega (U_{\text{CO}_2} - \Gamma)}{\varepsilon U_{\text{PAR}} + g_{\text{CO}_2} c_\omega (U_{\text{CO}_2} - \Gamma)} \tag{6}$$

in which ε (g J^{-1}) is the light use efficiency, Γ (ppm) is the CO_2 compensation point which accounts for photorespiration at high light levels, U_{PAR} (W m^{-2}) is the incident photosynthetically active radiation, U_{CO_2} (ppm) is the CO_2 concentration in the greenhouse air, g_{CO_2} (m s^{-1}) is the canopy conductance to CO_2 diffusion and c_ω (g m^{-3}) is the density of CO_2. At a temperature level of 15°C and an ambient pressure of 101·3 kPa, c_ω has a value of approximately $1·83 \times 10^{-3}$ g m^{-3}.

The CO_2 compensation point γ is affected by temperature according to the relation

$$\Gamma = c_\Gamma c_{Q_{10},\Gamma}^{(U_T - 20)/10} \tag{7}$$

in which c_Γ is the CO_2 compensation point at 20°C which has a value of 40 ppm, $c_{Q_{10},\Gamma} = 2$ is the Q_{10} value which accounts for the effect of temperature on Γ (Goudriaan *et al.*, 1985).

At high light levels the effect of photorespiration is only observable through the CO_2 compensation point. At low light levels, however, photorespiration has a pronounced effect on the light use efficiency. This effect has been accounted for by the relation

$$\varepsilon = c_\varepsilon \frac{U_{\text{CO}_2} - \Gamma}{U_{\text{CO}_2} + 2\Gamma} \tag{8}$$

in which $c_\varepsilon = 17·0 \times 10^{-6}$ g J^{-1} is the light use efficiency at very high CO_2 concentrations (Goudriaan *et al.*, 1985).

The canopy conductance g_{CO_2} (m s^{-1}) for diffusion of CO_2 from the ambient air to the chloroplast is determined by three series conductances. Two of them are of physical nature, the boundary layer conductance and stomatal conductance, and one is of chemical nature, the carboxylation conductance (Goudriaan *et al.*, 1985):

$$\frac{1}{g_{\text{CO}_2}} = \frac{1}{g_{\text{bnd}}} + \frac{1}{g_{\text{stm}}} + \frac{1}{g_{\text{car}}} \tag{9}$$

where g_{bnd}, g_{stm} and g_{car} (m s^{-1}) are the boundary layer conductance, the stomatal conductance and the carboxylation conductance, respectively.

Because $f_{\text{phot,max}}$ is defined as the assimilation rate of an effective canopy surface of 1 m² per square-metre soil, the canopy conductance may be replaced by the conductances of single leaves.

The boundary layer conductance of lettuce leaves can be estimated from the temperature difference between the leaves and the ambient air and the wind speed around the leaves. For an average wind speed of 0.1 m s^{-1} commonly encountered in the greenhouse, a temperature difference of 5°C and a characteristic length of a leaf of 0.075 m, the boundary layer conductance for CO_2 diffusion has a value of 0.007 m s^{-1} (Stanghellini, 1987).

The stomatal resistance depends on the physiological state of the crop. For a crop which is not subject to stress the stomatal conductance for CO_2, diffusion has a value of around 0.005 m s^{-1} during day time. The effects of temperature, carbon dioxide concentration, water vapour deficit and incident solar radiation on the stomatal conductance have been reported (Stanghellini, 1987). These effects are not accounted for in this model.

The carboxylation conductance shows an optimum response with respect to temperature. Complex biochemical models exist which describe these temperature effects on the chemical reactions taking place. For control purposes it is assumed that the effect of temperature on the carboxylation conductance may be simplified by the following polynomial:

$$g_{\text{car}} = c_{\text{car},1} U_T^2 + c_{\text{car},2} U_T + c_{\text{car},3} \qquad (10)$$

for a temperature between 5 and 40°C with the parameter values $c_{\text{car},1} = -1.32 \times 10^{-5}$, m s^{-1} °C^{-2}, $c_{\text{car},2} = 5.94 \times 10^{-4}$ m s^{-1} °C^{-1} and $c_{\text{car},3} = -2.64 \times 10^{-3}$ m s^{-1}. The carboxylation conductance has a maximum of 4.0×10^{-3} m s^{-1} at 17.5°C and zero values around 5 and 40°C.

With the model described so far it is possible to describe the evolution of the state variables X_{nsdw} and X_{sdw}. However, with eqns (1) and (2) it is also possible to predict other crop parameters which are related to the state variables. For instance, with a plant density of 18 plants per square metre, total plant dry weight is related to both state variables according to the relation

$$Y_{\text{dw}} = \frac{X_{\text{risdw}} + X_{\text{sdw}}}{18} \qquad (11)$$

Plant leaf area of the crop is assumed to be proportionally related to the amount of structural dry matter in the shoot:

$$Y_{\text{lai}} = \frac{(1 - c_\tau) c_{\text{lar}} X_{\text{sdw}}}{18} \qquad (12)$$

MODEL VALIDATION

In the dynamic lettuce growth model knowledge about physiological subprocesses determining crop growth has been combined. In two validation experiments the ability of this model to describe the evolution of crop dry weight as affected by the carbon dioxide concentration, air temperature and incident photosynthetically active radiation inside the greenhouse was investigated. An exact criterion of success of the validation is hard to define. Here, the criterion has been adopted that simulated growth should lie within the 95% confidence limits of the measurements for most of the time. Preferably, but more stringent, the model should be able to follow the general dynamic trend in the mean of the measurement data.

During two consecutive experiments plants were sown and raised at a nursery in peat blocks and then planted at a density of 18 plants per square-metre in a nutrient film technique (NFT) system in an experimental greenhouse with an area of 300 m². Because comparative studies of, for instance, Van Holsteijn (1981) revealed that different lettuce cultivars have distinct growth responses, in the two successive experiments different lettuce cultivars (*Lactuca sativa* L.) were used. In agreement with Dutch horticultural practice, during the autumn experiment which started 17 October 1991 cultivar 'Berlo' was used. In the second experiment, starting 21 January 1992, cultivar 'Norden' was employed. 'Norden' is frequently cultivated in winter and spring.

The greenhouse climate was controlled according to the rules followed in normal horticultural practice. During the first days of the cultivation period the day and night temperatures were kept at 14°C. Then the night temperature was lowered to 10°C whereas the day time air temperature setpoint was at least 14°C and increased dependent on the radiation level. During day time pure CO_2, was supplied to a maximum level of 750 ppm depending on the amount of global radiation and the opening of the ventilation windows. The nutrient solution had an EC of around 2·3 mS and a pH of around 6.

With a data logging system connected to the greenhouse climate computer, half-hour mean values of the indoor climate data were recorded. Both the air temperature and the global radiation at canopy level were measured at four spots in the greenhouse. In the simulation the averages of these measurements were used. It was assumed that photosynthetically active radiation accounts for 50% of total incident solar radiation (Spitters *et al.*, 1986). The average carbon dioxide concentration in the greenhouse was obtained from a mix of samples which were taken continuously at six places in the greenhouse. Measurements of the carbon dioxide
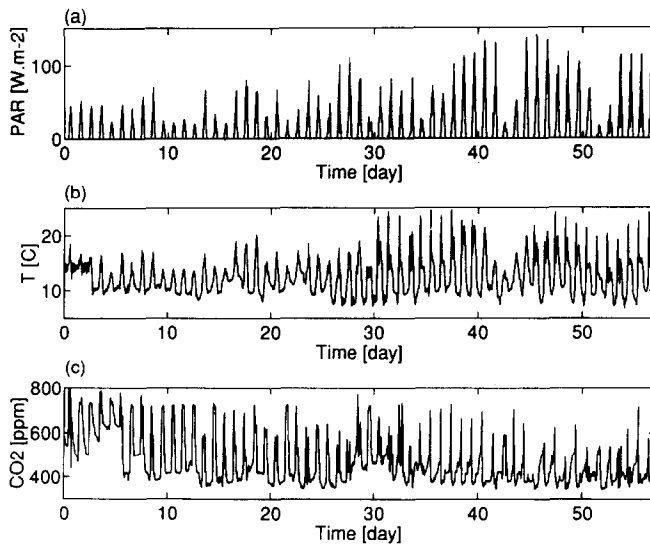
Fig. 2. Incident photosynthetic active radiation (a), air temperature (b) and carbon
dioxide concentration (c) in the greenhouse during validation experiment 2.

concentration, the air temperature and the photosynthetically active
radiation inside the greenhouse during the second experiment are shown
in Fig. 2. The greenhouse climate throughout the first experiment was
similar. However, the time sequence was a bit different due to the
inherent variability of the outdoor climate.

Every 5–7 days throughout the growing season, 20 plants were selected
at random and dry weight of both root and shoot as well as total leaf area
were determined destructively for each plant. Dry weights were obtained
after oven drying the plants at a temperature of 105°C for 24 h.

Using the recorded greenhouse climate data, crop growth during both
experiments was simulated. The canopy temperature used in the model
was assumed to be equivalent to the measured air temperature. Although
differences between the canopy and the air temperature occur throughout
the day, on average this assumption seems acceptable.

Because no separate measurements of the non-structural dry weight
and the structural dry weight were available, the initial conditions of the
state variables had to be estimated from the measurements of the total
dry weight at the planting date. Crop dry weight amounted to 2.70 g m^{-2}
and 0.72 g m^{-2} during the first and the second experiment respectively. It
was assumed by Sweeney et al. (1981) that at the planting date the ratio
of structural to total dry weight was 0.50. However, it was indicated by
Goudriaan et al. (1985) that the non-structural dry weight rarely exceeds
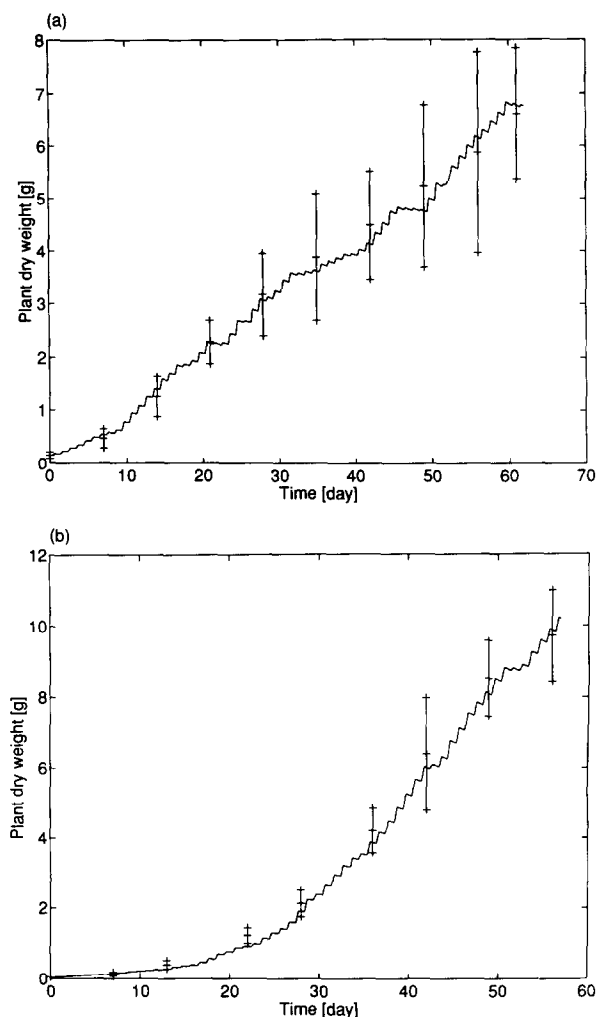25% of the total dry weight. In the simulations the initial values of

Fig. 3. Total plant dry weight versus time during (a) experiment 1 and (b) experiment 2. The continuous line represents the model predictions; the measured dry weight is denoted by + and the vertical bars indicate the 95% confidence limits of the measurements.

the state variables were calculated using a value of 0·75 for the ratio of structural dry weight to total dry weight.

In Fig. 3 the simulated plant dry weight as well as the weekly measurements during both experiments are presented. The vertical bars around the measurement points indicate the 95% confidence limits. The standard deviation in the measurements amounted to about 10% and 5% of the measured mean value during the first and the second experiment respectively. In both experiments the simulated dry matter accumulation lies within the 95% confidence limits of the measurements for most of the
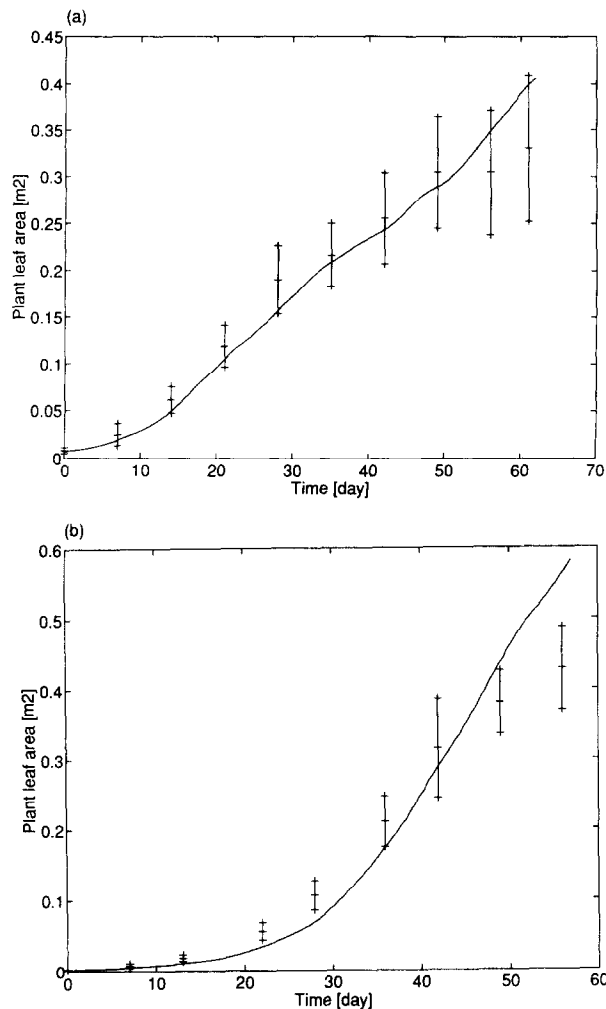
Fig. 4. Plant leaf area versus time during (a) experiment 1 and (b) experiment 2. The continuous line represents the model predictions; the measured leaf area is denoted by + and the vertical bars indicate the 95% confidence limits of the measurements.

time. Moreover, the simulated dry matter accumulation follows quite accurately the general trend in the mean measured crop growth although in the second experiment a slight underestimation is observed.

It can also be observed that the simulations of the dry matter content exhibit more dynamics than could be measured at an interval of 5–7 days.

Canopy photosynthesis and consequently crop growth strongly depend on the light interception by the canopy which is related to the amount of leaf area present. Figure 4 shows simulated and measured data of the leaf area. During the first experiment the model describes the mean

measured leaf area quite accurately although the model tends to over-estimate at the end of the growing period. Overestimation of the leaf area towards the end of the growing period was also encountered during the second experiment, but a significant underestimation was found during the early stages of growth.

PARAMETER SENSITIVITY

The ability of a model to describe the dynamic behaviour of the process considered is determined essentially by the model structure and the particular parameterization. Assuming that the structure of the lettuce growth model presented in this paper describes the fundamental processes governing lettuce growth, a sensitivity analysis of the model with respect to parameter variations was performed to obtain insight into the relative importance of the parameters in this model representation. Since sensitive parameters will explain most of the variation in the model simulation these parameters should be the subject of future modelling research when general application of this model is thought of.

Model sensitivity to changes in the parameters was evaluated using the sensitivity function according to France & Thornley (1984):

$$S_i = \frac{\partial Y_{dw}(T)}{\partial p_i} \frac{p_i}{T_{dw}(T)} \tag{15}$$

where S_i is the value of the sensitivity function for a variation of parameter i, $Y_{dw}(T)$ is the simulated dry weight at harvest time T using the original parameters, p_i is the original parameter value, ∂p_i is a small variation in parameter i while keeping the other parameters constant and $\partial Y_{dw}(T)$ is the difference between the simulated dry weight at harvest time with and without the parameter variation. Because the sensitivity analysis was performed with the objective of classifying the impact of parameter variations on the model performance, the relative instead of absolute parameter sensitivity was evaluated.

Obviously parameter variations may result in positive as well as negative values of S depending on their positive or negative influence on crop growth. If $S_i = 1$ then a given fractional change in the value of parameter i produces the same fractional change in the yield $Y_{dw}(T)$. Parameters with $S_i > 1$ have larger effects on yield, and vice versa.

In the simulations to obtain the parameter sensitivity, the climate data of the second experiment were used because these data covered a wider range of values than the data of the first experiment. For the parameter variations ∂p_i a value of 5% was used. Since c_ω and c_α are viewed as

TABLE 1
Model Sensitivity with Respect to Variations in the
Parameters in Decreasing Order of Magnitude

Parameter	S	Parameter	S
c_β	0·95	$c_{gr,max}$	0·14
c_ε	0·83	$c_{car,3}$	0·14
$c_{car,2}$	0·46	$c_{resp,sht}$	0·13
c_K	0·38	$c_{Q10,rgr}$	0·11
c_{lar}	0·38	g_{stm}	0·08
$c_{car,1}$	0·20	$c_{Q10,l}$	0·06
c_Γ	0·19	c_τ	0·06
g_{bnd}	0·16	$c_{resp,rt}$	0·00
$c_{Q10,resp}$	0·15		

physical constants, they have not been included in the analysis. Results are presented in Table 1.

The results presented in Table 1 show that two parameters play a major role in the determination of lettuce crop growth, namely the yield factor c_β which describes the conversion efficiency from non-structural dry matter to structural dry matter and the light use efficiency c_ε. The parameter $c_{car,2}$ determining the carboxylation conductance, and the extinction coefficient c_K and the leaf area ratio c_{lar} affect to a smaller extent the simulated crop dry weight at harvest time. The model sensitivity for variations in the other parameters seems to be relatively small.

Following the same procedure the model sensitivity with respect to variations in the initial conditions was determined. A 5% variation in the initial conditions of X_{nsdw} and X_{sdw} resulted in values of the relative sensitivity function of 0·02 and 0·11 respectively.

DISCUSSION

An economically efficient greenhouse climate control scheme balances the benefits associated with the marketable produce and the costs associated with its production. In the derivation of the control scheme, dynamic process models are used to predict the revenue of the control actions to be taken, and obviously the performance of the control algorithm when applied in practice is strongly influenced by the ability of the model to describe the dynamic behaviour of the process variables relevant for control. The validation study revealed that the model used in the control study of Van Henten & Bontsema (1991) describes with satisfactory

accuracy the general trend in the dry matter accumulation of a lettuce crop measured during two growth experiments. Simulated growth lies within the 95% confidence limits of the measurements for most of the time. Moreover, simulated growth follows quite accurately the general trend in the average measured dry weight production although during the second experiment a slight underestimation is observed.

During the early stages of growth, light interception by the canopy and consequently crop photosynthesis and growth is limited by the amount of leaf area present, which in this model is determined by the leaf area ratio c_{lar}. The relative importance of c_{lar} was confirmed by the sensitivity analysis. During the first experiment the measured leaf area ratio was observed to be constant, but it showed a declining trend during the second experiment. Underestimating the leaf area ratio and consequently the leaf area in the first weeks of the second experiment (Fig. 4b) may be a major cause for underestimating the dry matter accumulation throughout that period of time and this effect may have propagated during the rest of the growing period. In the last 2 weeks before harvest time, plant leaf area is overestimated by the simulation. At that stage of growth, due to morphogenetic adaptations of the crop, i.e. head formation, a change in the leaf area ratio can be observed (Bensink, 1971). The overestimation, however, does not affect the simulated crop dry matter production, because at that time the canopy is fully closed and any increase in the amount of leaf area does not contribute to an increased canopy photosynthesis (see eqn 5). These results emphasize the need for accurate parameterization of the leaf area ratio for an accurate description of growth before canopy closure.

Sensitivity analysis of the model with respect to parameter variations showed that two parameters particularly affect crop growth in this model representation, namely the yield factor c_β and the light use efficiency c_ε.

Sweeney *et al.* (1981) estimated the yield factor c_β as 0·8. Compared with the value of 0·72 (Van Keulen *et al.*, 1982) it seems relatively high. With respect to lettuce specifically, however, no other data for c_β were found in the literature.

The model sensitivity was evaluated using data of the second growth experiment. The light levels during this experiment were rather low. At low light levels the canopy photosynthesis is very sensitive to small changes in c_ε. At high light levels the effect of changes in c_ε will be much less distinct.

The sensitivity with respect to variations in the initial conditions is rather small compared with the model parameters, the structural dry weight having a bit more impact than the non-structural dry weight. Therefore, small measurement errors in the initial conditions do not seem

to have a very strong effect on the simulated crop growth when the harvest weight is considered.

In horticultural practice cultivars 'Berlo' and 'Norden' are considered to have different growth responses which make them particularly suitable for cultivation in the autumn and winter respectively. Different growth responses of distinct lettuce cultivars were reported by Van Holsteijn (1981). The arrangement of the two experiments did not allow for any experimental evidence about a difference between the two cultivars used. However, when the simulation of dry matter production is considered, the model was able to simulate crop growth of both cultivars equally well.

The results clearly demonstrate that simulated growth exhibits dynamics in the dry matter which could not be observed with a measurement frequency of 5–7 days. To verify these fast responses, crop dry weight should be sampled more frequently. Yet the measurements presented in Fig. 3 show a large variability in the measured plant dry weight. This is partly due to an evident variability present in a crop grown under practical circumstances, and to a certain extent a consequence of errors in the measurements of plant dry weight. Therefore it is arguable whether it is possible to validate these fast but relatively small responses found in the simulations, since they will be dominated by crop variability and measurement errors.

Besides, the overall impression of Fig. 3 is that crop growth acts as a kind of slow integrator of the input variables and is not extremely sensitive to large and rapid changes in the environmental conditions as shown in Fig. 2. This may signify the fact that from the control point of view, when crop growth is considered, fast transients in the greenhouse climate are not of major importance, although this was not verified in the literature on economically optimal greenhouse climate control (e.g. Seginer, 1989; Van Henten & Bontsema, 1991).

CONCLUSIONS

In this paper results have been presented of the validation of a dynamic lettuce growth model. The model was based on first principles of plant physiology and the model equations and parameters were collected from the literature. Since in the control study in which the model was employed crop dry weight was considered to be the process variable determining economic return of the cultivation, the validation emphasized the evaluation of the model's ability to describe the dynamic evolution of crop dry weight as determined by the model inputs, i.e. the photosynthetically active radiation, the plant temperature and the

ambient carbon dioxide concentration. In two validation experiments the model was able to simulate dry matter accumulation with a satisfactory accuracy; the simulations followed the general dynamic trend in the average of the measured crop dry weight. However, in the simulations crop dry weight exhibited some relatively small and fast fluctuations which could not be verified due to the sampling frequency of 5–7 days. Measurements should be done at least once a day to get insight into the fast dynamics of crop growth which are predicted by the model, although the large standard deviation of the measurements obtained in the experiments indicates that these small changes will be very hard to determine under practical circumstances.

Furthermore, simulations indicate that crop growth is not very sensitive to rapid changes in the greenhouse climate. This might indicate that from the control point of view when crop growth is considered, fast transients in the greenhouse climate are not of major importance.

A sensitivity analysis of the model with respect to parameter variations revealed that only two parameters mainly determine crop growth. The other parameters affect crop growth to a much smaller extent. Parameter sensitivity is an important item when evaluating the performance of the climate controller derived by, for instance, Van Henten & Bontsema (1991) using this model. This will be the object of future research.

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