

## Modelling Dry Matter Production and Partitioning in Sweet Pepper

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### Abstract

**Models predicting growth and yield have been developed for a large number of crops. This paper describes a dynamic, mechanistic model for sweet pepper, addressing issues such as leaf area expansion, dry matter partitioning and validation.**

Leaf area formation and organ initiation are simulated as a function of temperature sum. Light absorption and photosynthesis are calculated for a multi-layered uniform canopy. Leaf photosynthesis is calculated for the various leaf layers according to the biochemical model of Farquhar, and integrated to canopy photosynthesis. Net assimilate production is calculated as the difference between canopy gross photosynthesis and maintenance respiration. The net assimilate production is used for growth of the different plant organs and for growth respiration. Fruit set is simulated as a function of source and sink strength and temperature. Assimilate partitioning between vegetative parts and individual fruits is simulated on the basis of the concept of sink strengths. The sink strength of each individual fruit is calculated as a function of its temperature sum from anthesis. The sink strength of the vegetative parts is calculated as a function of temperature only.

A wide range of experimental data show that leaf area is linearly related to the temperature sum from planting. The model was validated on the basis of six experiments in The Netherlands and France. Simulation of dry matter production and partitioning under a wide range of conditions showed that model results agreed well with measurements. Some directions for further improvements are discussed.

### INTRODUCTION

Models are powerful tools to test hypotheses, to synthesize knowledge, to describe and understand complex systems and to compare different scenarios. Models may be used in decision support systems, greenhouse climate control and prediction and planning of production.

Often descriptive and explanatory models are distinguished. Descriptive models, also called statistical, regression, empirical or black-box models, reflect little or none of the mechanisms that are the cause of the behaviour of a system, whereas explanatory models consist of a quantitative description of these mechanisms and processes (Penning de Vries et al., 1989). Explanatory models contain sub-models at least one hierarchical level deeper than the response to be described, e.g., crop photosynthesis and leaf area expansion are processes one hierarchical level below crop growth. Although the explanatory crop growth models in horticulture do, to some extent, reflect physiological processes, they do not incorporate all knowledge on biochemical mechanisms at the cellular level. On the other hand, if they did, the models would be impossible to manage and use for predictions and for analysis at the crop level.

Models predicting growth and yield have been developed for a large number of crops, including a few models for sweet pepper (e.g., Marcelis et al., 1998; Buwalda et

al., 2006; Schepers et al., 2006). Developmental aspects such as fruit set and abortion, but also leaf area expansion are generally weak points of models. Furthermore, models are seldomly thoroughly validated. This paper describes a dynamic, mechanistic model for sweet pepper, addressing issues such as leaf area expansion, fruit set, dry matter partitioning and its validation in six experiments.

## MATERIALS AND METHODS

In total eight experiments were conducted. Exp. 1 and 2 were used only for model calibration. Exp. 3 to 8 were used for model validation. However, Exp. 3 to 8 were also used for calibrating leaf area expansion. Although model validation should be done on different data as the data for model development and calibration, we choose to use data of all experiments for calibrating the simulation of leaf area expansion. Hence the simulation of leaf area expansion could not be validated; on the other hand if we had used only Exp. 1 and 2 for calibrating the simulation of leaf area expansion the model parameters would have been almost similar.

All experiments were performed with sweet pepper (*Capsicum annuum* L.) grown on rockwool with drip irrigation in Venlo type glasshouses in Wageningen, The Netherlands (latitude 52°N; Exp. 1-5) or in Carquefou France (latitude 47°N; Exp. 6-8). Per location each experiment was in a different year, except for Exp. 2 and 4 which were in the same year. Cultivation was as much as possible comparable to standard practices of growers, but some treatments were out of the range of standard cultivation practice of growers. Plants were pruned to two main stems per plant.

Exp. 1. 'Mazurka' (red fruits) was grown at three different planting densities: 1.56, 3.12 and 4.63 plants per m<sup>2</sup>. The crop was planted on January 10 and ended on July 3, 1996.

Exp. 2. 'Red Spirit' (red fruits) was grown at 3 different planting densities: 2.5, 3.8 and 5.0 plants per m<sup>2</sup>. The crop was planted on December 13, 2001 and ended on September 4, 2002.

Exp. 3. 'Mazurka' (red fruits) was grown at 3 different temperatures: average temperatures were 19, 22 and 25°C. The crop was planted on January 15 and ended on June 5, 1997.

Exp. 4. 'Meteor' (red fruits) was grown at three different CO<sub>2</sub> concentrations: 380, 580 and 780 ppm. As this experiment was performed in a greenhouse with mechanical cooling a very stable climate could be realized with constant CO<sub>2</sub> concentration during day time. The crop was planted on February 7 and ended on June 19, 2002.

Exp. 5. 'Solution' (red fruits) was planted on February 11 and the experiment ended on July 8, 2003.

Exp. 6-8. 'Triple 4' (green fruits) was grown in 3 subsequent years (2003-2005). Planting was each year on December 17 and experiments ended in September/October. In these experiments there were also fertigation treatments. However, as these treatments had no major effects on crop growth only the reference treatments of these experiments are shown (for more details see Marcelis et al., 2005 and Brajeul et al., 2006).

## MODEL DESCRIPTION

A mechanistic model for sweet pepper was developed that simulates leaf area expansion, dry and fresh weight growth of plant organs, flower formation, fruit set and fruit harvest. The model in fact also simulates plant-water relations and plant-nutrient relations, as described by Marcelis et al. (2005) and Brajeul et al. (2006). These parts of the model are not considered in this paper and the simulation runs shown assumed no limitation in availability of water or nutrients.

The model is primarily based on the INTKAM model for simulation of plant-water relations and dry matter production (Gijzen, 1994). The simulation of dry matter partitioning, fruit set and fruit growth is primarily based on the cucumber model of Marcelis (1994). The model consists of routines for greenhouse radiation transmission, radiation interception by the crop, leaf and canopy photosynthesis, respiration, dry matter production, dry matter partitioning among plant organs (roots, stem, leaves and individual

fruits), fruit set and fruit harvest. Greenhouse radiation transmission, radiation interception, photosynthesis and transpiration are calculated with short time intervals (e.g. one hour). The time step of calculation of dry matter production, partitioning, fruit set and fruit harvest is one day.

Light transmission is calculated for Venlo-type glasshouses according to Bot (1983). Interception of PAR radiation is calculated for a multi-layered uniform canopy (Goudriaan and Van Laar, 1994), assuming a spherical leaf angle distribution. The light interception is calculated separately for diffuse and direct light (Goudriaan and Van Laar, 1994). Leaf gross photosynthesis is calculated with the biochemical model of Farquhar et al. (1980) at 5 depths in the canopy. Stomatal conductance was calculated as a function of light intensity, temperature, air humidity and CO<sub>2</sub> concentration, according to Nederhoff et al. (1992). Canopy photosynthesis is computed from these leaf photosynthesis calculations by using the Gaussian integration method (Goudriaan and Van Laar, 1994).

Leaf area expansion was closely related to the temperature sum (Fig. 1). Leaf area expansion per main stem is simulated as a linear function of temperature sum from planting (with base temperature of 10°C). Leaf area data from many different experiments could all be well described by one linear relationship (Fig. 1). Even for different temperatures, planting densities and CO<sub>2</sub> concentrations the same regression line was valid. In all these experiments plants were grown with two main stems per plant. A few data from experiments (data not shown) where three main stems per plant were retained, showed that the simulation should be based on leaf area per main stem rather than the leaf area per plant. It has been observed in more crops that leaf area expansion can be determined by temperature sum, but usually assimilate supply also affects the leaf area expansion (e.g. Marcelis, 1993; Gary et al., 1995). Heuvelink and Marcelis (1996) showed that assimilate supply had no effect on the number of leaves in pepper. In addition, treatments like leaf or fruit removal which changed the source/sink balance had no effect on area per leaf. However, when plants were grown in a climate chamber at different light levels, the area per leaf was higher at higher light level (Heuvelink and Marcelis, 1996). The present data on sweet pepper grown in greenhouses indicate that leaf area expansion can be well predicted by a model that only considers the temperature sum from planting.

Net assimilate production results from the difference between canopy gross photosynthesis and maintenance respiration. Maintenance respiration is calculated as a function of dry weights of the organs and temperature, according to Spitters et al. (1989). The temperature effect is described by a Q<sub>10</sub> of 2 (doubling of respiration per unit dry weight with an increase in temperature of 10°C).

Assimilate partitioning between vegetative parts and individual fruits is simulated on the basis of the concept of sink strengths, as described by Marcelis (1994). In this concept the fraction of assimilates partitioned into an organ is calculated as the ratio between its potential growth rate (sink strength) and that of all plant parts. Dry matter gain of an organ is calculated as the amount of assimilates partitioned into each organ divided by the assimilate requirements for dry matter production. Based on data of Marcelis and Baan Hofman-Eijer (1995) the potential growth rate of each fruit is calculated as a function of its temperature sum from anthesis by using the Richards function. The potential growth rate of the vegetative parts is calculated as a function of temperature only.

Rates of formation of flowers and leaves are calculated as a function of temperature. Fruit set in sweet pepper was shown to depend largely on the source/sink ratio and temperature until about 2 weeks from anthesis of a flower, but being most susceptible during the first week after anthesis (Marcelis et al., 2004). Therefore, fruit set was simulated similarly as fruit set in cucumber by Marcelis (1994). The number of non-aborting fruits younger than 10 days from anthesis was calculated as a function of the source strength, sink strength and temperature (higher number of young non-aborting fruits at higher source strength, lower sink strength and lower temperature). This simulation of fruit set was calibrated on the data of Exp. 1. In the model fruits were

harvested when a threshold temperature sum from anthesis was reached. We used different threshold values for green and red fruits, but no further distinction was made for the different cultivars.

Input to the model are planting date, planting density, number of main stems per plant, colour of the harvested fruits, transmission of the greenhouse under diffuse weather conditions, and hourly values of global radiation outside the greenhouse and inside climate (temperature, air humidity and CO<sub>2</sub> concentration). The most relevant output variables of the model are dry weight of the different plant organs (roots, stems, leaves, fruits), number of fruits set and harvested, dry and fresh weight of harvested fruits.

## RESULTS AND DISCUSSION

Temperature had a strong effect on the rate of development of the plant (e.g. large increase in formation rate of leaves). However, the effect on total dry matter production was very small (Fig. 2, Exp. 3). The model predicted a similar response of the plant to temperature. According to the model the cumulative crop gross photosynthesis increased from 2092 to 2212 g CH<sub>2</sub>O m<sup>-2</sup> when temperature increased from 19 to 22°C. This was partly due the increased leaf area formation and therefore better light interception in the beginning of the growing season. A further increase of temperature hardly affected the simulated crop gross photosynthesis (2199 g CH<sub>2</sub>O m<sup>-2</sup> at 25°C). At increasing temperature the maintenance respiration strongly increased from 628 g CH<sub>2</sub>O m<sup>-2</sup> at 19°C, to 705 g CH<sub>2</sub>O m<sup>-2</sup> at 22°C and 798 g CH<sub>2</sub>O m<sup>-2</sup> at 25°C. The high maintenance respiration at the highest temperature counteracted the high gross photosynthesis such that the net crop photosynthesis was similar for the highest and lowest temperature, while the intermediate temperature showed a slightly higher net crop photosynthesis compared to the lower and higher temperature. These simulation results agreed rather well with observations, except that at the final harvest the observed dry weight at the highest temperature was somewhat lower.

Increasing the CO<sub>2</sub> concentration from constant 380 to 580 ppm, increased dry matter production considerably, while a further increase to 780 ppm resulted only in a slight increase (Fig. 2). Model results agreed with these measured effects. Simulated total dry matter production of the other four experiments agreed with observations. The absolute value of the relative difference between simulated and measured final plant dry weight was on average 4.0% (for all treatments and experiments the difference ranged from -7% to +8%, with an average of +0.1%).

Cumulative fruit production was also simulated quite well in all experiments (Fig. 3). In Exp. 3 the model over-estimates the partitioning into the fruits at high temperatures, which was mainly because of an over-estimation of fruit set. Despite the fact that dry matter partitioning into the fruits initially was under-estimated by the model in all treatments of the CO<sub>2</sub> experiment (Exp. 4), the model well predicted the observations that at higher CO<sub>2</sub> concentrations the fraction of dry matter partitioned into the fruits increases.

Sweet pepper is characterized by large fluctuations in fruit yield, even under constant climate conditions. Dynamic variations in source-sink balance, fruit set and assimilate partitioning are main determinants of these production fluctuations (e.g. Heuvelink et al., 2004; Marcelis et al., 2004). The model simulates strong fluctuations in source-sink ratio, fruit set and fruit harvest during a growing season (data not shown). The concepts of simulation of fruit set and partitioning in relation to the source-sink balance appears to be a powerful one in several crops (e.g. Bertin and Gary, 1993; Marcelis, 1994; Heuvelink, 1996). Furthermore, individual plants show quite some variation and there seems to be variation among individual flowers and fruits. Current research aims at obtaining a crop growth model that can also simulate inter- and intra-plant variation in fruit set by using the statistical technique of survival analysis (Wubs et al., 2007).

As validation of the model was done in France as well as in The Netherlands and as even the three Dutch validation experiments were done in three different glasshouse facilities (and the calibration experiments were done in a fourth glasshouse facility), it

indicates that the model can simulate plant dry matter production, as well as the partitioning into the fruits satisfactorily when hourly climate data are available as well as data on planting density and planting date.

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## Figures

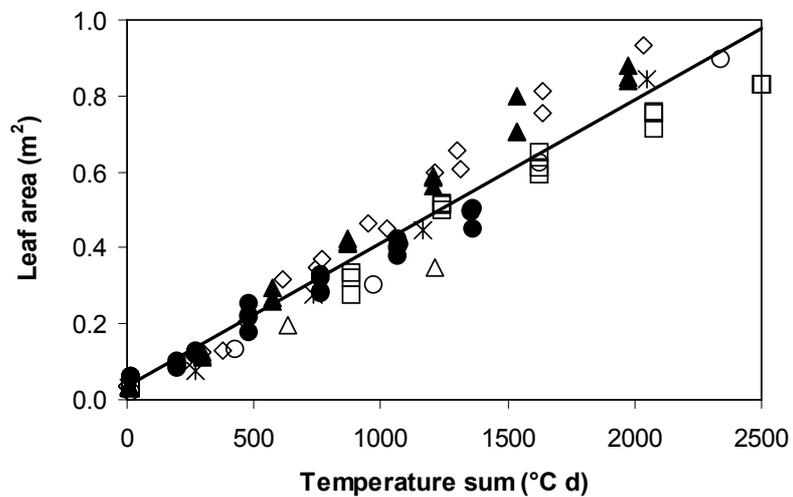


Fig. 1. Leaf area of sweet pepper plants (m<sup>2</sup> per main stem) plotted as a function of temperature sum (°C d) from planting. Data are derived from 8 experiments (Exp. 1 – Exp. 8). Per experiment a different symbol was used.

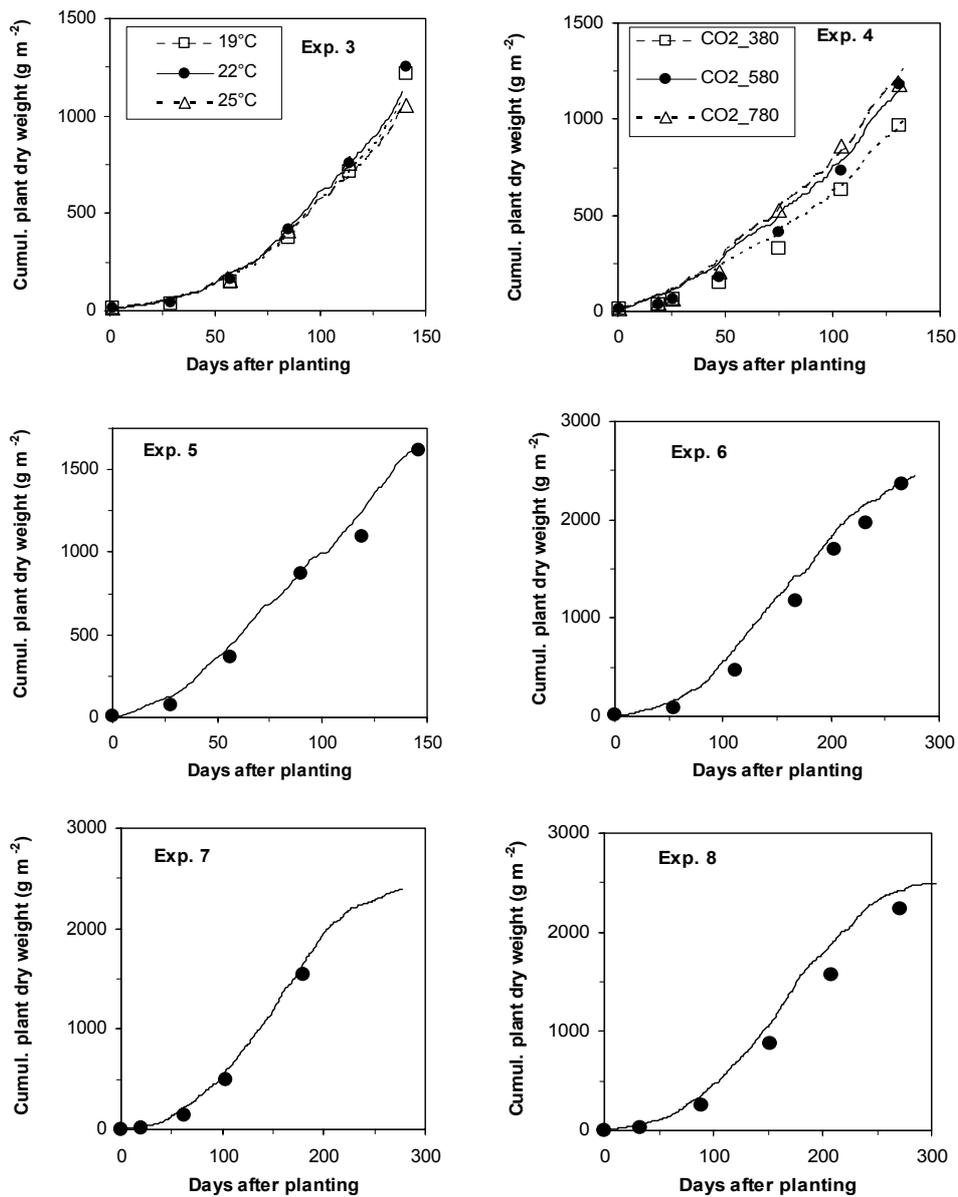


Fig. 2. Simulated (lines) and observed (symbols) cumulative plant dry weight of sweet pepper crops in six experiments. Weights include leaves, stems, fruits and harvested fruits, but not roots. In Exp. 3 plants were grown at three different temperatures (19, 22, 25°C), in Exp. 4 at three different CO<sub>2</sub> concentrations (380, 580, 780 ppm).

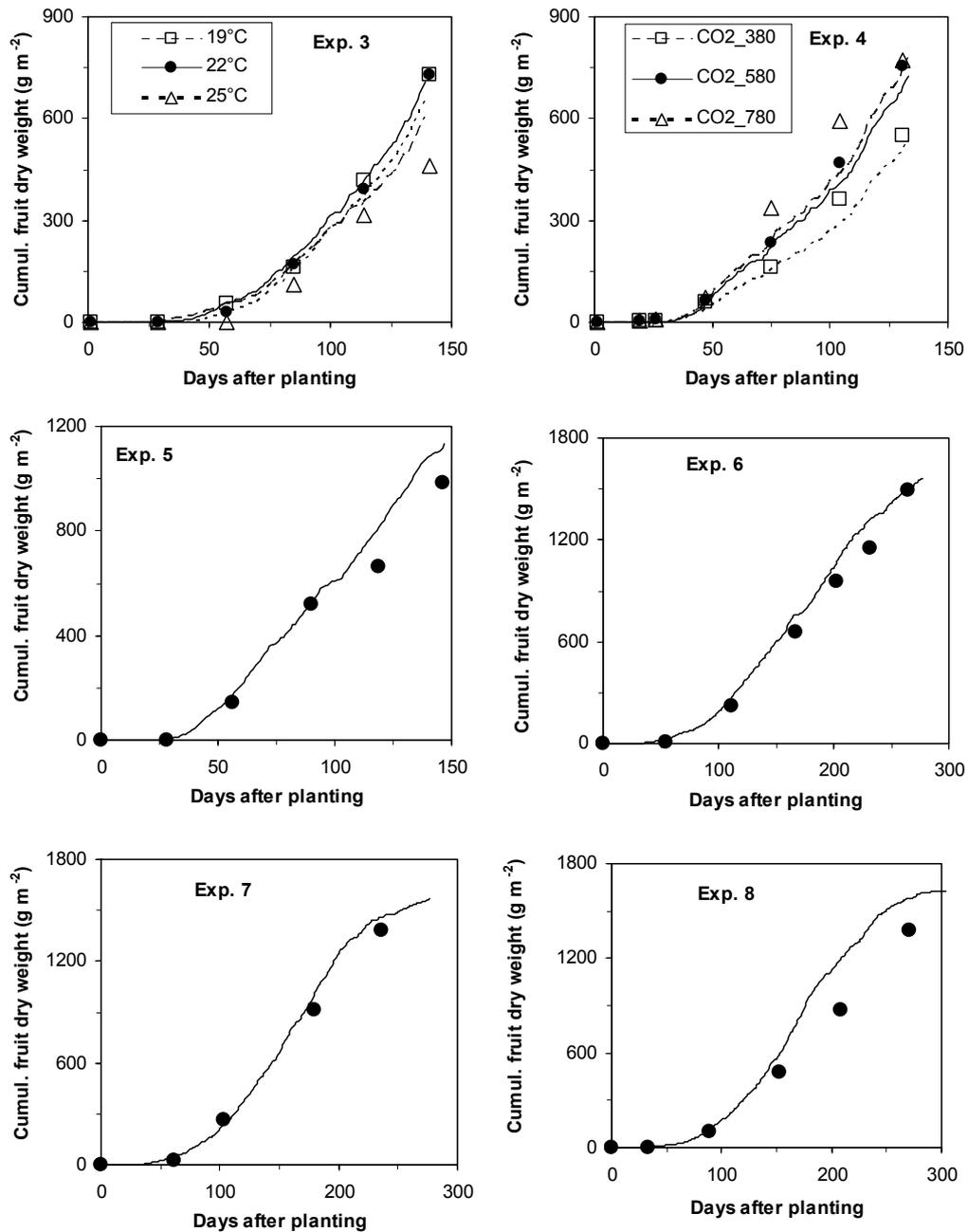


Fig. 3. Simulated (lines) and observed (symbols) cumulative fruit dry weight of sweet pepper crops in six experiments. Weights include harvested fruits. In Exp. 3 plants were grown at three different temperatures (19, 22, 25°C), in Exp. 4 at three different CO<sub>2</sub> concentrations (380, 580, 780 ppm).