

Simulating Growth and Development of Tomato Crop

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Abstract

Crop models are powerful tools to test hypotheses, synthesize and convey knowledge, describe and understand complex systems and compare different scenarios. Models may be used for prediction and planning of production, in decision support systems and control of the greenhouse climate, water supply and nutrient supply. The mechanistic simulation of tomato crop growth and development is described in this paper. The main processes determining yield, growth, development and water and nutrient uptake of a tomato crop are discussed in relation to growth conditions and crop management. Organ initiation is simulated as a function of temperature. Simulation of leaf area expansion is also based on temperature, unless a maximum specific leaf area is reached. Leaf area is an important determinant for the light interception of the canopy. Radiation shows exponential extinction with depth in the canopy. For leaf photosynthesis several models are available. Transpiration is calculated according to the Penman-Monteith approach. 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 growth respiration. Partitioning of assimilates among plant organs is simulated based on the relative sink strengths of the organs. The simulation of plant-nutrient relationships starts with the calculation of the demanded concentrations of different macronutrients for each plant organ with the demand depending on the ontogenetic stage of the organ. Subsequently, the demanded nutrient uptake is calculated from these demanded concentrations and dry weight of the organs. When there is no limitation in the availability at the root surface, the actual uptake will equal the demanded uptake. When the root system cannot fulfil the demand, uptake is less, plant nutrient concentration drops and crop production might be reduced. It is concluded that mechanistic crop models accurately simulate yield, growth, development and water and nutrient relations of greenhouse grown tomato in different climate zones.

INTRODUCTION

Models are powerful tools to test hypotheses, synthesize and convey knowledge, describe and understand complex systems and compare different scenarios. Crop models can be used to identify the desired growth conditions, explore effects of growth conditions related to the introduction of new technologies as well as identify the target traits of a crop that are particularly important for a specific environment. Models have been used in decision support systems, greenhouse climate and fertigation control, and prediction and planning of production.

Models predicting growth and yield have been developed for a large number of crops including tomato (Dayan et al., 1993; Gary et al., 1995; Heuvelink, 1995a; Marcelis et al., 1998; Cooman, 2002; Cooman and Schrevens, 2003; Dai et al., 2006; Boote and Scholberg, 2006).

In this paper, the main processes of a mechanistic crop model for tomato are analysed. The modeling concepts are based on the models TOMSIM (Heuvelink, 1999) and INTKAM (Gijzen, 1994; Marcelis et al., 2000). Processes addressed are leaf area

expansion, light interception, photosynthesis, respiration, fruit set, dry matter partitioning, transpiration, and water and nutrient uptake.

SIMULATION OF CROP GROWTH

A mechanistic crop growth model considers the main crop physiological processes (Fig. 1). The first process to be considered is the light interception by leaves. The calculated light interception depends mainly on leaf area of the crop and light incidence on the crop. Subsequently photosynthesis rate is calculated followed by calculations of the photosynthate use for respiration, conversion into structural dry matter (DM), the partitioning of DM among the different plant organs, and, finally, the fresh weight from the dry weight. Transpiration is calculated in parallel to calculations of photosynthesis. Also, nutrient demand and uptake are calculated.

Leaf Area

Leaf area is the most important factor that determines the fraction of incident radiation absorbed by the canopy. Leaf area formation rate is simulated as a function of number of stems per m^2 , temperature and light intensity. In addition, the variety or root stock may affect leaf area expansion. Sub-optimal water and nutrient supply may limit leaf area expansion (see paragraph on water and nutrient uptake). Furthermore, the amount of leaf area of a tomato crop is affected by pruning of lower old leaves and sometimes some very young leaves.

A leaf area index of 3 to 4 (m^2 leaves m^{-2} floor) appears to be optimal for tomato because then already about 90-95% of the visible light is intercepted by the canopy (Heuvelink et al., 2005). Measurements at seven commercial farms in the Netherlands showed that in the summer season light interception was on average 90% with values varying between 86 and 96%.

Two approaches are predominantly used in crop models to simulate leaf area index: 1) leaf area is described as a function of plant developmental stage (or accumulated temperature sum); and 2) leaf area is computed from simulated leaf dry weight (Marcelis et al., 1998). In tomato, the initiation rate of leaves is primarily determined by temperature, while leaf area per leaf is also affected by assimilate supply, which depends on radiation (Heuvelink and Marcelis, 1996). Due to these effects of assimilate supply the first approach does not give reliable results in greenhouse production, where the correlation between temperature and radiation is lower than in open field situations. In the second approach, first leaf dry weight is calculated and then multiplied by the specific leaf area (SLA). However, SLA is far from constant during a growing season (Heuvelink, 1999) and tends to be negatively correlated with the radiation level. More appropriate is to combine the two approaches as first presented by Gary et al. (1995). Leaf area increase is potential if SLA of the whole canopy is smaller than the maximum SLA (SLA_{max}). Potential leaf area increase is computed as the product of the potential weight of new leaf material and the minimum SLA (SLA_{min}). If the actual SLA is greater than SLA_{max} (if the leaf is thinner than permitted), leaf area increase is equal to the product of the weight of new leaf material and SLA_{max} . SLA_{max} is a constant, and SLA_{min} is made dependent on the day of the year as described by Heuvelink (1999).

Light Interception

Crop production is often linearly related to cumulative intercepted radiation, although environmental conditions, such as CO_2 concentration and temperature, may affect this relationship. In many cases, a linear relation between production and cumulative incident radiation is also found. Cockshull et al. (1992) observed over the first 12 weeks of harvest a fresh tomato production of 2 kg/100 MJ of incident solar radiation. Penning de Vries and Van Laar (1982) showed that the slope of the relationship between cumulative gross CO_2 assimilation and cumulative intercepted photosynthetically active radiation increased with latitude (range 0 to 60°) when all other conditions were the same. This means that crop production in the tropics can be much lower than at higher latitudes

on days with the same daily light integral. The difference is mainly explained by the fact that, in the tropics, the same daily light integral is realized by a shorter day length than at higher latitudes, but with higher maximum light intensity, at which photosynthesis is less efficient. Heuvelink (1995b) observed for tomato grown in greenhouses in Northern Europe that total plant dry matter production was 2.5 g/MJ incident PAR inside the greenhouse. This author estimated values from literature at 3.0-3.3 g MJ⁻¹ PAR in Northern Europe. In experiments in tropical low land in Indonesia, we estimated light use efficiency at approximately 2.1 g MJ⁻¹ incident PAR inside the greenhouse (Elings and Impron, unpublished).

The absorption of radiation can be simulated from the principle that absorption of radiation increases with increasing leaf area, but that mutual shading decreases the interception. This assumption leads to exponential extinction of radiation and is equivalent to the law of Lambert-Beer (Marcelis et al., 1998; Papadopoulos and Pararajasingham, 1997). Radiation absorption by the canopy ($I_{abs,L}$ radiation absorbed by the overlying LAI) can be approximated by

$$I_{abs,L} = (1-\rho) I_o (1-e^{-k * L})$$

in which ρ stands for canopy reflection coefficient, I_o for the radiation level at the top of the canopy, k for the extinction coefficient, and L for leaf area index. Typical values for ρ and k are 0.07 and 0.7, respectively (Marcelis et al., 1998).

In general, however, k will be different for each radiation direction in relation to the position and geometry of leaves. Because direct and diffuse radiation have different extinction profiles in the canopy and because of light saturation of photosynthesis, the solar beam (direct flux) should be singled out from the rest of the incoming radiation (diffuse flux). Hemming et al. (2008) and Heuvelink and Gonzalez-Real (2008) showed that when all radiation would be made diffuse (by using specific greenhouse covers or screens) a substantial (up to 10%) yield improvements are possible. Recently new so-called functional-structural models have been developed that simulate both the three-dimensional structure of plants as well as functioning, i.e. the physiological processes (Vos et al., 2007). This allows predicting more precisely effects of different row structures on plant functioning, distribution of leaf positions and geometries of leaves, different colours and positions of light sources. Also for tomato such models have been constructed (de Visser et al., unpublished data; Dong et al., 2007).

Photosynthesis, Respiration and Transpiration

Modelling of photosynthesis can be done largely independent of plant species, which only differ in parameter values of leaf photosynthetic properties. Detailed models of crop photosynthesis simulate leaf photosynthesis separately for shaded and sunlit leaves as a function of depth in the (multi-layered) canopy taking into account the direct and diffuse components of light. Biochemical type of models (Farquhar et al., 1980) has proven to be very suitable for leaf photosynthesis and it accounts for the major determining factors of light, CO₂ concentration and temperature. The most important factor determining photosynthesis is the light intensity; photosynthesis usually shows a saturation type of relationship to light intensity. Especially in greenhouses where CO₂ might be depleted or be enriched, models should also include effects of CO₂ on photosynthesis. Within a broad range (about 15-25°C) effects of temperature on gross photosynthesis are limited (Farquhar et al., 1980); at lower and higher temperatures photosynthesis may reduce substantially. Low air humidity may lead to stomatal closure resulting in reduced photosynthesis (Bakker, 1991).

Simultaneously with the simulation of leaf photosynthesis, leaf transpiration can be calculated. The Penman-Monteith equation is widely accepted for calculating transpiration (Stanghellini, 1987; Marcelis, 1989). Simulation of leaf transpiration includes calculation of temperature and energy balance of the leaf. This requires information on visible, near infra red and thermal radiation (from and to heating pipes, greenhouse roof and soil), vapour pressure deficit of air and air temperature. Moreover,

values of the stomatal and boundary layer conductance of the leaf are required. Boundary layer conductance depends on the leaf size, presence of leaf hairs and wind speed (Stanghellini, 1987).

In most crop growth models, respiration is subdivided in growth and maintenance respiration (Amthor, 1989). Net assimilate production results from the difference between canopy gross photosynthesis and maintenance respiration. Maintenance respiration is calculated as the product of dry weights of the different plant organs and their maintenance coefficients (specific respiratory costs for maintenance), which increase with increasing temperature (Amthor, 1989). However, this approach likely leads to overestimation of respiration in a large tomato crop that has old stem parts that have relatively low respiration requirements. Therefore, Heuvelink (1995a) made the maintenance coefficients dependent on the relative growth rate of the crop. Growth respiration is usually calculated as the product of dry weight growth rate of the different plant organs and a growth coefficient (specific respiratory costs for growth of each organ). There is reasonable consensus concerning the simulation of growth respiration (Thornley and Johnson, 1990). As the simulation of maintenance respiration is still an area of great uncertainty. Some authors (Gifford, 1995) have proposed to simulate total crop respiration as a constant fraction of the gross photosynthesis, as this gives reasonable results in several situations. In greenhouse grown tomatoes, De Koning (1994) estimated that this fraction was on average 22%.

The maximum photosynthesis rate (P_{\max}) varies during a cropping season. This variation can for 80% be explained by the radiation level in the preceding week (unpublished data). The P_{\max} at of the lower leaves was about 35% lower than that of top leaves. The lower P_{\max} at lower canopy depth is probably due to adaptation to lower light levels (Hogewoning et al., 2008). As light levels are low at the lower leaves in the canopy, the consequences of lower P_{\max} on crop photosynthesis are minimal.

Dry Matter Partitioning

Partitioning of dry matter among the various plant organs, and in particular, towards the fruits is not constant over time. The fraction of dry matter partitioned to the fruits is an important determinant of yield and balance between vegetative and generative growth rates. Growers are continuously searching for a proper control of this balance. Dry matter partitioning towards individual trusses is simulated on the basis of the concept of sink strengths as described by Heuvelink (1996) and Marcelis (1994). The fraction of assimilates partitioned to an organ (f_i) is proportional to the ratio between its potential growth rate (sink strength, S) and that of all plant parts together (ΣS).

$$f_i = S / \Sigma S$$

Sink strength can be defined as the potential demand or potential capacity of an organ for assimilate accumulation. Potential growth rate is quantified as the growth rate under conditions of non-limiting assimilate supply (Marcelis, 1996). The potential growth rate of a tomato fruit depends on its developmental stage (temperature sum from anthesis) (Heuvelink and Marcelis, 1989) and shows cultivar variation (De Koning, 1994). The potential growth rate of a truss of fruits depends on the number of fruits on the truss and the potential growth of each individual fruit. Consequently, the fraction of dry mass partitioned to fruits plotted versus number of fruits shows a saturation-type of curve (Heuvelink, 1997). A low number of fruits per truss may strongly limit fruit production. This often occurs in tropics: for instance Kleinhelz et al. (2006) observed a maximum ratio of fruit to total plant dry weight of 0.3, whereas Cockshull et al. (1992) and De Koning (1994) reported values of about 0.7 for Northern Europe. A low number of fruits per truss may be caused by poor fruit set, which may occur if pollination is poor due to, for example, the absence of bumble bees or vibration of flowers (use of electric bee). At high (>25°C daily temperature) and at low (<18°C daily temperature) temperature fruit set is sub-optimal (De Koning, 1994; Peet et al., 1997; Sato et al., 2006; Van der Ploeg and Heuvelink, 2007). Furthermore, a low source-sink ratio may limit fruit set (Bertin et

al., 1995). Therefore, fruit set may be limited in temperate climate zones by a low source/sink ratio and in hot tropics by high temperatures. This will negatively affect the partitioning of dry matter to the fruits. A crop model that predicts fruit yield under all these conditions should include the simulation of these effects on fruit set. For optimal development of a tomato plant, a stable source-sink ratio is needed. When the source is high due to for instance high radiation, the number of sinks should also be high. A very efficient method to increase the number of sinks (fruits) per m^2 is to increase the number of stems per m^2 (more plants per m^2 or more stems per plant). This is already applied by growers in countries, such as the Netherlands, where additional stems are retained during the summer period increasing stem density from about 2.5 to about 4 stems/ m^2 . Roughly we estimate that at solar radiation levels above 15 MJ m^{-2} at least 4 to 5 stems/ m^2 are needed to balance source and sink strength. Kleinhelz et al. (2006) observed the highest fruit growth at 8 stems/ m^2 for tomatoes grown in humid tropics of Thailand. Under these conditions a high stem density may have also favoured the micro climate in the canopy.

Formation and harvest or removal of trusses and leaves is calculated as a function of temperature (De Koning, 1994). Fresh weight growth of plant organs is obtained by dividing the dry weight of the organs by the dry matter content. Dry matter content of vegetative parts is assumed to be constant, while dry matter content of fruits is calculated as a function of day of year, temperature and EC of the nutrient solution (De Koning, 1994).

Water and Nutrient Uptake

Water uptake of the crop is calculated from transpiration and fresh weight growth as long as water availability is unlimited or it can be calculated based on the difference in water potential in the plant and the rooting medium (Marcelis, 1989; Elings et al., 2004).

The demand for nutrients mainly depends on the growth of the different plant organs as determined by factors other than nutrition (e.g. plant development, light intensity, temperature) (Le Bot et al., 1998). Nutrient demand is calculated for each organ as the product of dry weight growth and maximum nutrient concentration as described by several authors (Mankin and Fynn, 1996; Kläring et al., 1997; Bellert et al., 1998; Marcelis et al., 2005). The maximum nutrient concentration is the concentration that is reached when nutrient availability is not limiting. The maximum concentration of each macro-nutrient is modelled for individual trusses, leaves, and stems parts associated with a truss, and roots as a whole. These concentrations usually show an ontogenetic change. For each organ, the demanded nutrient concentration can be described by an initial linear increase or decrease with thermal time followed by a constant value; this relationship can be described by 3 parameters: minimum and maximum concentration and a slope (Marcelis et al., 2003; Elings et al., 2004).

When there is no limitation in water and nutrient availability, simulated nutrient uptake by the plant will equal its demand. The model can be coupled to an elaborate substrate model that determines whether the root system can meet the demand for water and nutrients and that calculates the nutrient uptake rates (Heinen, 2001; Elings et al., 2004). Instead of using an elaborate substrate model, water and nutrient uptake can also be calculated as the product of the demanded uptake and a reduction factor, where the reduction factor depends on humidity and nutrient concentrations in the substrate.

Shortage of nutrients in the rooting medium leads to low nutrient concentrations in the plant. Low nutrient concentrations in the plants are simulated to affect leaf photosynthesis, leaf area development, and dry matter partitioning. This concept was applied by Elings et al. (2004) and Marcelis et al. (2003).

VALIDATION OF THE CROP GROWTH MODEL

The tomato simulation described in this paper is mainly based on the models INTKAM and TOMSIM. These models have been validated under a wide range of conditions in experimental greenhouses with different plant densities, planting dates, temperatures, light levels, CO₂ concentrations etc. (Heuvelink, 1995a, 1996).

The models have also been proven to accurately simulate tomato production and transpiration in commercial farms in the Netherlands (52°N) including closed greenhouses (Heuvelink, 1999; Heuvelink et al., 2008; Elings and Voogt, 2008; Figs. 2 and 3). The same model was capable of simulating accurately crop growth and dry matter partitioning of a tomato crop in tropical low land.

CONCLUSIONS

Mechanistic crop models have been developed that accurately simulate yield, growth, development and water and nutrient relations of greenhouse grown tomatoes in different climate zones. In particular, total gross canopy photosynthesis and production of total plant dry matter in relation to growth conditions are well predicted. Partitioning of dry matter between vegetative and generative growth can be simulated well if the number of fruits per truss is correctly estimated. However, under conditions that evoke poor fruit set, the simulation of fruit set appears to be a weak point of the models. Simulation of transpiration and nutrient uptake is improved if the model can be calibrated on the basis of historical data. Furthermore, acclimation of plant processes to prevailing growth conditions is still poorly understood nor quantified. Many crop models do not yet consider product quality. It is now to incorporate modelling of fruit quality in crop growth models (Heuvelink et al., 2004; Struik et al., 2005).

The development of crop models is now that advanced that models are used by growers and advisers to support the decisions to be made on crop management. Models are also part of the climate and fertigation control system. For this latter purpose, on-line feedback from plant sensors or crop registrations is important (Marcelis et al., 2000).

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Figures

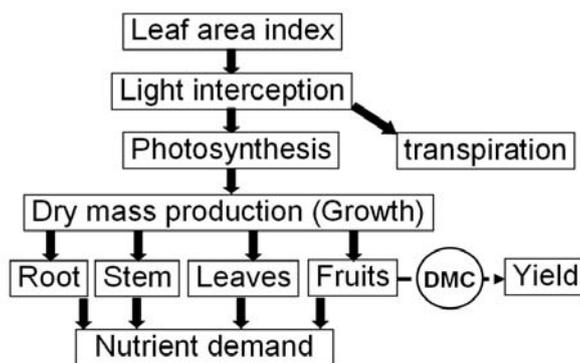


Fig. 1. Schematic representation of the major calculation steps of a crop growth model.

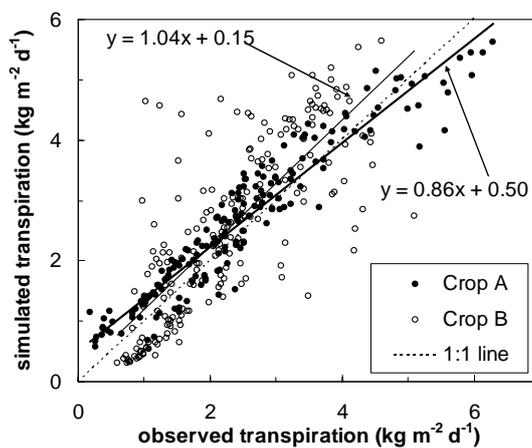


Fig. 2. Validation of simulation of daily transpiration of two tomato crops (crop A and B) (from Elings and Voogt, 2008).

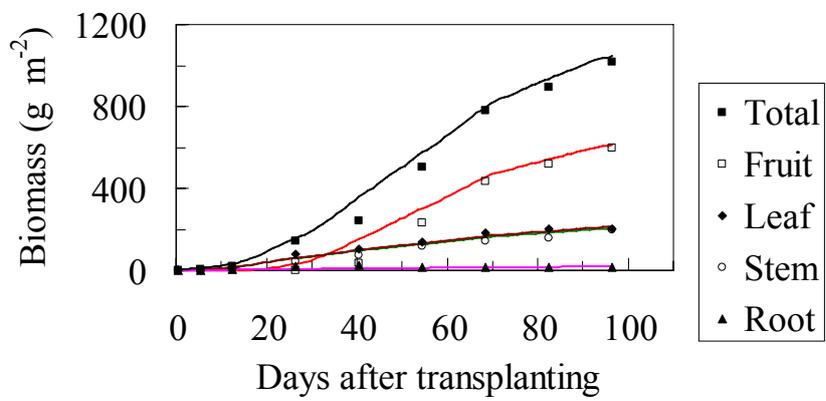


Fig. 3. Validation of simulation of dry matter production of greenhouse grown tomatoes tropical low land of Indonesia (1°S, altitude 25 m). Symbols are measurements and lines are simulations. Inputs to the model were climate data and plant density.