Towards a 3D Structural Tomato Model for Calculating Light Interception

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Abstract
    A number of physiological tomato models have been proposed the last decades, their main challenge being the correct simulation of fruit yield. For this, an accurate simulation of light interception, and thus photosynthesis, is of primary importance. Light interception is highly dependent of the canopy structure which is affected amongst others by distance between plant rows, distance of plants within the row, leaf pruning and crop variety. In order to simulate these processes, a functional structural tomato model for the simulation of light interception on an individual leaf basis is proposed. The 3D model was constructed using L-systems formalism. For the architectural part of the model, manual measurements of leaf length, width, angle of the leaf main stem to plant stem and leaf orientation were conducted. The diurnal pattern of leaf orientation was also tested. The architectural model was coupled with a nested radiosity model for light calculation. Area per individual leaflet served as input of the light module for calculation of reflection, absorption and transmission of light. The model was used to test different crop planting scenarios on their effect on light interception. Results were then compared with light simulation for a totally homogeneous canopy.

INTRODUCTION

    A number of tomato models have been proposed over the years (e.g., Gary et al., 1995; Marcelis et al., 1998, 2009; Heuvelink, 1999; Boote and Scholberg, 2006). These models offer an accurate description of plant growth and its interactions with the environment providing a useful tool in our understanding of plant functioning. Although they make a distinction between different plant organs, they do not consider the plant structure in space. Especially functions like light interception, environmental plant adaptation, competition within and between species for light or nutrients, and assimilate allocations cannot be easily explained if plant structure in space is not taken into account.
    Functional-structural plant models (FSPM) or virtual plant models (Hanan, 1997; Sievänen et al., 2000; Godin and Sinoquet, 2005; Vos et al., 2007) are terms used to refer to models explicitly describing the development in time of the 3D architecture or structure of plants as driven by physiological processes. These physiological processes are the result of environmental factors. Functional-structural plant models were proposed the last decade as a means to investigate the function of plant structure in plant development combining traditional plant modeling with a 3D structure (Vos et al., 2007). For light extinction in particular the knowledge of how the plant develops in space is essential. So the use of such a model for light calculations would probably improve our knowledge of light distribution inside the crop canopy.
    Light extinction inside a plant canopy can reach up to 60% while for a crop canopy the light extinction can be up to 90% (Valladares, 2003). This variation in incident light availability inside the crop canopy induces extensive structural and physiological modifications. Average light conditions also have a big effect on plant photosynthetic capacity (A_{max}), which typically decreases two- to four times from top to the bottom of the canopy (Meir et al., 2002). The aim of this study is to explore the

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structural variations inside the tomato plant canopy and use this to develop a structural plant model for tomato. Subsequently, the structural plant model is used to test different plant spacing scenarios and their effect on light distribution inside the canopy.

MATERIALS AND METHODS

Plant Measurements
1. Experimental Set-Up. The experiment was carried out in a high-wired tomato 'Aranca' crop in a glasshouse of Improvement Center (52°N, Bleiswijk, the Netherlands). Plants were planted in the greenhouse at the end of January. The rows in the greenhouse were northeast-southwest oriented. Two rows of plants were planted in each gully. The distance between the two rows of one gully was 50 cm, the path width was 110 cm and the distance between 2 plants on the same row was 0.53 m. Plant height was 2.60 m. The plants were grown in rockwool (Grodan, type Expert). The greenhouse air was enriched with pure CO_2 at 400 ppm during day time. The lowest leaves were removed every week and plants were lowered such that plant height remained the same throughout the experiment.
2. Structural Plant Measurements. For a complete picture of plant development, detailed measurements of the 3D stem and leaf geometry were manually performed on 3 plants every other week. Measurements were performed for six weeks from 2 July to 13 August 2008. A protractor and a ruler were used for the measurements. The measurements included leaf angle, leaf length, leaf width and leaf orientation. In our experiment we defined leaf angle as the angle of leaf petiole to the horizontal where it is attached to the stem (Boonen et al., 2002). The rosette at the top of the plants with leaves smaller than 2 cm was considered as first node. Digitization of the plants was attempted with the use of a Fastrak 3D digitizer (Polhemus Inc, Colchester, VT, USA) but was not always possible. This was probably due to a powerful disturbance of the magnetic field of the digitizer due to metallic parts (heating pipes) positioned inside the canopy.

The plant was divided in three zones (upper, middle and lower zone) and the above mentioned structural plant characteristics were measured. Every zone had a length of 90 cm except the lowest one that had a length of 80 cm. Measurements were carried out weekly on 3 randomly picked leaves per zone in 13 replicate plants. Tomato composite leaf consists of a large terminal leaflet and up to 8 lateral leaflets, which can also be compounded. Many smaller leaflets or folioles may be interspersed between the larger leaflets depending on the cultivar (Atherton and Rudich, 1986). In our cultivar the leaf was composed of a big terminal leaflet, 3 pairs of larger leaflets and two pairs of smaller leaflets alternately placed. So, in addition to measurements on angles of main composite leaves (see above), angles of all leaflets were measured for 10 randomly selected leaves in each plant level, in order to determine a relationship between leaflet angle and leaflet position in the leaf. Leaflet angle was defined as the angle between the leaflet petiole and the leaf petiole. Angle of leaflet blades could not be measured with our method, mainly because they showed a convex shape which is hard to quantify. The model therefore assumed a fixed angle between leaflet petiole and leaflet blade thus changing blade orientation with petiole angle. Since the angle of leaves to the horizontal directly affects the flux of solar radiation per unit area (Falster and Westoby, 2003), measurements to establish the diurnal pattern of the leaf angles were also made. Leaf angles of 15 plants were measured early in the morning (09:00 hours) and in the afternoon (15:00 hours).
3. Light Measurements. Incident light was measured with the use of Sunscan (Delta-T, UK). The sensor was positioned perpendicular to the plant row. Measurements were taken every 25 cm from top to the bottom of the canopy, in 8 different positions in the greenhouse.

Model Description
The model consisted of two modules:

1. Structural Module. In this module the spatial development of the plant was described in the L-studio software (University of Calgary, Canada) in terms of symbols according to L-systems formalism (Lindenmayer and Prusinkiewicz, 1990). The plant was structured as a number of phytomers in deferent developmental stages. A phytomer is defined as the basic structural unit which for our model consisted of an internode and a composite leaf. Relationships of leaf angle to node number, leaf length to node number and leaf width to node number as well as leaflet area to leaf area and leaflet angle to petiole node number were determined by regression analysis. These relationships where used as input for the development of the structural part of the model. Leaflets were represented with rectangular shapes in the model in an approximation of their real shape. Plant and row spacing also served as an input. The basic simulation unit of the model included 20 identical plants (5 plants per row, 4 rows).

2. Light Module. A nested radiosity model (CARIBU) developed by Chelle and Andrieu (1998) and modified by Evers et al. (2005) and De Visser et al. (2007), was used for light calculations. The module calculates light reflection, absorption and transmission of photosynthetic active radiation (PAR) per polygon (here: leaflet). Multiple light scattering on every surface was taken into account. The nesting implies that a user-defined part of 3D space is used for the full radiosity model, which outcomes are nested, i.e., multiplied, using a turbid medium approach to mimic an infinite plant canopy. Reflectance and transmittance coefficients for the upper and lower side of the leaf were input in the model. Output values of light interception were given for leaflet as well as leaf level. Model calculations were performed at diffuse light conditions by forty three virtual directional light sources that were symmetrically arranged at the hemisphere.

Lambert-Beer

In many crop models Lambert-Beer's law (Monsi and Saeki, 1953) is used for the simulation of PAR interception. According to the law it can be shown that in an assumed uniform and infinite canopy of randomly distributed, absorbing leaves, the amount of photosynthetically active radiation intercepted (I) by a crop can be given by the following equation:

$$I = (1-\rho)*I_0*(1-e^{-k*L})*100 \tag{1}$$

where ρ stands for canopy reflection coefficient, I_0 is the radiation level at zero canopy depth, L the leaf area index of the canopy, and k is the light extinction coefficient. Extinction coefficient was set to 0.65 as reported by Papadopoulos and Pararajasingham (1997) and confirmed by our own measurements (data not shown).

Statistical Analysis

Statistical analysis was performed with Genstat 11 software (VSN International Ltd., Herts, UK). Differences of leaf angle, length and width between three plant heights were tested with Linear Mixed Model (REML). Leaf angles were compared between morning and afternoon with General Linear Models, repeated measurement analysis. Curves for leaflet angle to leaf petiole and for light interception to LAI were fitted with Regression Analysis. Goodness of fit was estimated by coefficient of determination (R^2). Statistical differences between curves were tested, by testing the statistical differences between the coefficients of the regression curves. P was 0.05.

RESULTS AND DISCUSSION

Structural characteristics of tomato leaves were monitored at three different depths in the canopy (Fig. 1). In the upper part of the plant, leaves had on average a slightly positive angle to the horizontal, while leaves in the middle and lower part of the canopy showed a negative angle to the horizontal. The negative value of -25° found in our experiment corresponds to the mean value used in the tomato model of Higashide (2009). Length and width were smallest in the top part of the canopy, as these leaves were not yet

full-grown. There was no statistically significant difference in leaf size between middle and lower part of the canopy. However, the blades attached to the petioles were not monitored and might have shown differences within the canopy.

Leaflet angles diminished from a maximum of 40° for the most proximal leaflet to 0° for the most distal leaflet to the stem (Fig. 1D). Leaflet angle showed no statistically significant differences between the three different canopy levels implying that the leaflets' angle is in fact an internal characteristic of the plant and dependent only on the position of the leaflet on the leaf. This result was also confirmed by measurements on other experiments (data not shown).

Leaf angle differed significantly between morning and afternoon only for the upper leaves (average leaf angles were -3.1 and -7.6° for morning and afternoon subsequently) (Fig. 2). A diurnal pattern was not observed at the middle and lower leaves. Forseth (1990) observed no diurnal changes in leaf angles to the horizontal of a number of species (for example cotton, beans, *Solanum*), but he did find significant changes of the plant angle to the azimuth. He also linked this azimuth movement to an increase in light interception and a proportional increase of productivity. Although Forseth does not differentiate leaf angle behavior between different canopy depths, his work is an indication that measurements of only leaf angle to the horizontal is not adequate to conclude about a diurnal pattern on tomato leafs. Leaf angle changes can also be linked to turgor loss of plant cells due to daily transpiration. So further research is needed as for the causes of this behavior on upper tomato leafs.

The above described structural measurements were used to develop a structural tomato model. The accuracy of the model was tested against measured values of light interception. In general the difference of the measured values versus the calculated values was of maximum 4%. The model was used to test three different crop planting scenarios and compare them to results of the Lambert-Beer equation which is currently used in most crop models for light simulation. The three different planting scenarios consisted of: (i) Normal practice: planting distances were the same as the ones found in the experiment (50 cm between the two rows of one gully and 110 cm of path). (ii) Big path: the distance between the rows in the same gully was reduced to 15 cm and the path width increased to 145 cm width. (iii) Even-distance rows: the plants were equally distributed in space (distance between plants in the same gully as well as across the pathway was equal to 80 cm). In order to test the accuracy of the tomato's model light calculations, the light interception of a completely homogeneous crop was compared to Lambert-Beer calculations (Fig. 3). Plant density was 4.1 plants per m^2 in all scenarios, with 1 stem per plant. It was assumed that plant size and structure was the same in all scenarios.

In general, row structures led to higher light interception in the upper part of the plants (LAI≤1.5) and lower interception in the lower part compared to homogeneous crop simulation. Light reaching the deeper part of the crop increased with path width and resulted in 30% light reaching soil level in our "big path" treatment. In accordance Papadopoulos and Pararajasingham (1997) reported that light penetration increased and therefore light interception decreased with the increase of plant spacing in a crop. Similar effects have also been reported in other crops such as corn (Stewart et al., 2003). Cournède et al. (2007), in their structural model concluded that deviations in calculations of light interception from Lambert-Beer law were mainly due because the latter assumes an even distribution of the leaf angles. The assumption of an even leaf distribution nevertheless has been challenged in the past. Maddonni et al. (2001) reported that in case of row structure the leaf orientation is changed and it is biased in being positioned perpendicular to the row. In our simulations the k-factor (extinction coefficient) inside the canopy increased from top to the bottom. This increase is in accordance with measured value of previous experiments (data not shown) and is directly linked with the decrease of leaf angle. In practice leaf angles are not constant but are dependent on the planting strategy. Toler et al. (1999) found that the k factor is dependent on the row distances and is decreasing with increasing row spacing. It could be argued that changes in k factor in relation to plant spacing are because of morphological changes in plants and mainly

orientation and leaf angle. The calculation of k factor from our model simulation shows that even if the structural characteristics of the plant stay the same, average k factor decreases with the increase of plant spacing (Fig. 4B). The extinction coefficient calculated for even-distance rows showed no differences to the one of homogeneous canopy. Nevertheless further increase of the path between the rows led to a decrease of the k factor, a decrease that reached 50% in case of the "big path" treatment.

CONCLUSIONS

In traditional physiological models, the extinction coefficient is generally used as a constant without taking into account its sensitivity to structural characteristics of the plant. Nevertheless, from our model simulations it is clear that the extinction coefficient changes not only with canopy depth but also with the increase of the row spacing. These changes in extinction coefficient can directly be linked to plant structural characteristics such as leaf angles and have a direct effect on light interception of the crop canopy. In this context the use of a structural model possesses an advantage for the calculations of light interception by the crop compared to traditional models. Furthermore such a model can be used to predict the effect of plant pruning or planting strategies to light interception.

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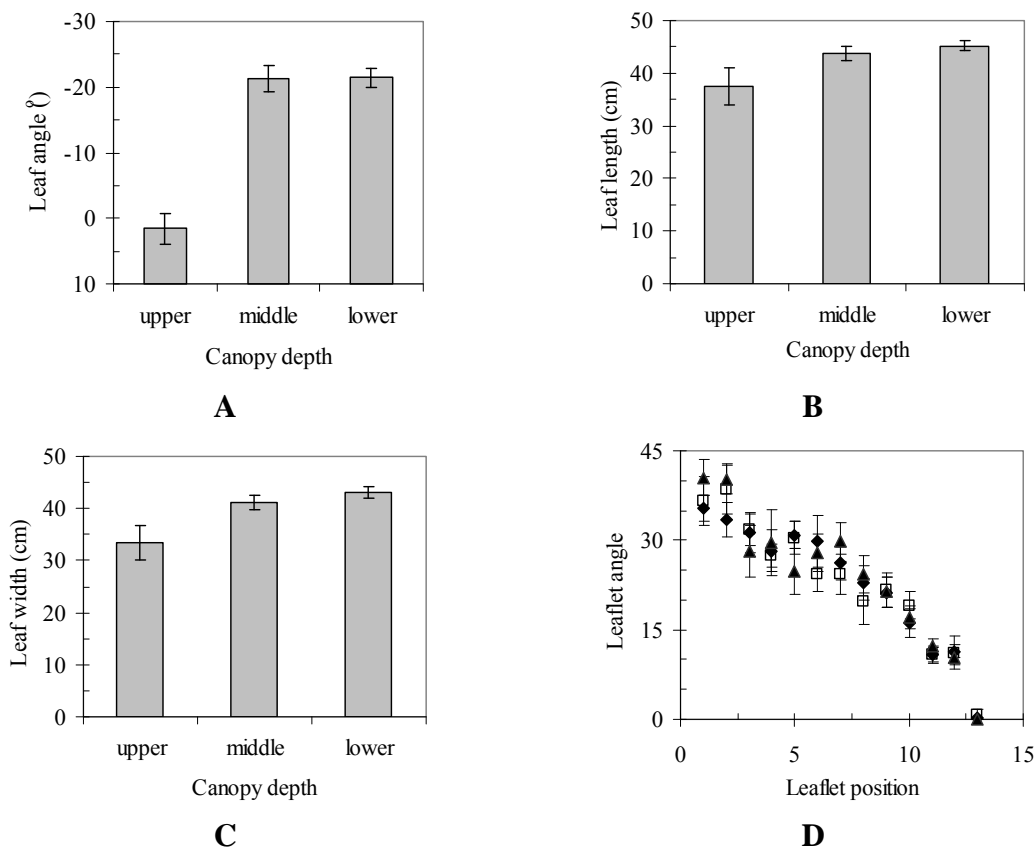
Fig. 1. Structural measurements for three different depths in a tomato canopy. Mean values of leaf angle to the horizontal (A), leaf length (B) and leaf width (C) are presented for the three different canopy depths as well as the relation between leaflet angle to leaf petiole and leaflet position (1 is most proximal leaflet to the stem) for top (■), middle (♦) and lower leaves (▲) (D). Error bars represent s.e. of the mean. Data are averages of 5 weeks, 13 plants per week. Data for graph D are averages of 10 leafs per canopy level.
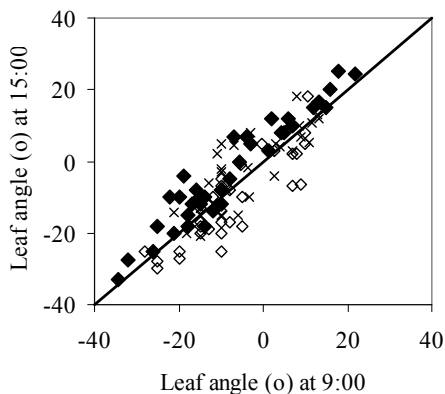

Fig. 2. Comparison of leaf angle (angle to the horizontal) in the morning (09:00 hours) and afternoon (15:00 hours) at three different heights of the canopy. Symbols ♦, ◊, and × refer to upper, middle and lower part of the plant consequently. The line is 1:1.
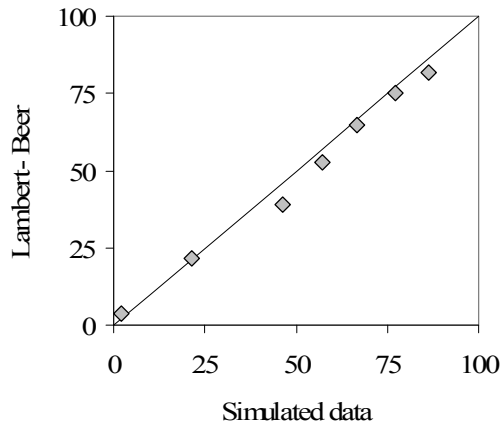
Fig. 3. Comparison of simulation data for a totally homogeneous canopy and Lambert-Beer law calculations for a canopy with the same. Data points are from the top (0 interception) to the bottom of the canopy (100).
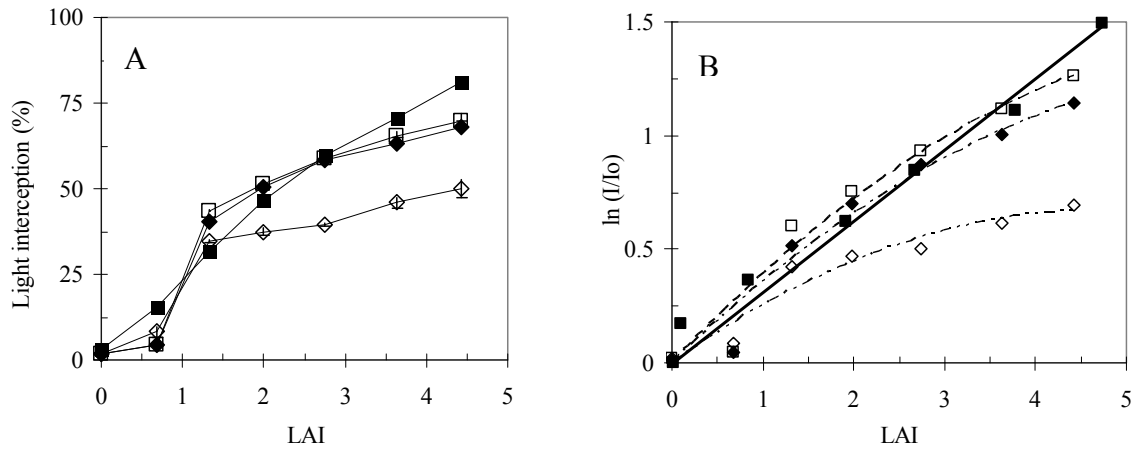

Fig. 4. A. Calculated light interception for different canopy structures. Light interception was calculated by structural model for plants grown in rows with path width of 110 (♦), 80 (□) and 45cm (◊). Plant density was always 4.1 m^{-2}. The ■ symbols correspond to calculation from Lambert- Beer; B. Average extinction coefficients k for the different treatments. LAI refers to cumulative leaf area from top to bottom of plant canopy.