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Influence of canopy architecture and parameters of leaf level photosynthesis on dry matter production in greenhouse cucumber

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Highlights: Productivity of crops highly depends on structural and physiological parameters. Using a FSPM we analyzed the sensitivity of key parameters revealing the strong influence of structural differences as well as the dominant role of light and stomatal control on the physiological parameters.

Keywords: L-System, photosynthesis, canopy structure, modeling

INTRODUCTION

Indeterminately growing plants like cucumbers (*Cucumis sativus* L.) are continuously producing new fruits. In these crops, variations in yield and individual fruit growth depend on the plant arrangement and plant density (Kahlen, 2007; Wiechers et al., 2011a). The photosynthetic activity of the leaves is one of the key physiological processes in plants determining dry matter production, driven by the available quantity of light as one of the major environmental factors (Chenu et *al.*, 2005). The model of leaf photosynthesis developed by Farquhar and coworkers (Farquhar et al., 1980) is capable of predicting the rate of photosynthesis for a variety of environmental factors like: CO_2 concentration, light, temperature and relative humidity (von Caemmerer, 2000). In the Farquhar model, the stomatal conductance (g_s) and the internal conductance (g_i) are major influences on the apparent rate of photosynthesis. The model contains multiple input variables, parameters, constants and equations for which different methods of parameterization are proposed (e.g. Sharkey et al., 2007; Dubois et al., 2007). A combination of the Farquhar model and a model of stomatal conductance (g_s) (Ball et al., 1987) was developed to simulate the photosynthesis of single leaves (Kim and Lieth, 2003). To be able account for the strong variability of leaf photosynthesis over the plant, a leaf level model needs information about the plant and canopy structure. A precise description of the plant structure is of special importance in vertically trained row canopies like greenhouse cucumber with their discontinuous canopy structures, which causes the spatial distribution of light to be highly uneven and variable with time (Wiechers et al., 2011b). Besides the rate of photosynthesis the rate of respiration also plays a major role for the determination of plant productivity. Commonly the concept of growth and maintenance respiration has been used to account for respiration in plant models (Amthor, 2000). Thus, to simulate the environmental influences on the yield formation and the development of individual organs, models which are capable of accounting for interactions between organ based physiological processes and plant morphology influenced by the canopy structure are essential (Fourcaud et al., 2008).

The objective of this study is to gain a better understanding of the importance of the key structural and physiological based factors of plant productivity. Therefore, we extended the established L-Cucumber (Kahlen et al., 2008) model to analyze the influence of structural and physiological factors on dry matter production.

SIMULATIONS

The capability to track structural changes is analyzed by simulating four canopies with different plant spacing's, a dense and a wide variant of both, a row canopy and an isometric canopy (Table 1).

Table 1. Plant spacing of the four measured and simulated canopy architectures

Distance (m)	Sparse Isometric (I1)	Dense Isometric (I2)	Sparse Row (R1)	Dense row (R2)
In row	1.08	0.54	0.54	0.27
Between row	0.93	0.93	1.86	1.86

Into the existing dynamical FSPM L-Cucumber (Kahlen et al., 2008) the model of leaf photosynthesis (Kim and Lieth, 2003) based on own measurement for cucumber was implemented. The model parameterization was not changed for the simulations of the four canopy structures. Main functional traits considered in this study are parameters of the photosynthesis like the maximum rate of electron transport (J_{max}), the maximum rate of carboxylation (V_{cmax}), g_s and g_i. Hourly leaf level light intensities were calculated with the radiosity based Caribu light model (Chelle et al., 1998). To avoid artifacts due to overestimations of the vegetative plant part the maximum leaf size and the specific leaf area (SLA) of the four canopy structures were taken as input in to the model. Plant morphology only differed due to the shade avoidance adaption of the leaves. Simulations were run until day 47 after transplanting with daily measured light and temperature values of the actual experiments as input. Detailed information about assimilate partitioning of the model can be found elsewhere (Wiechers et al., 2011a). Simulation results were compared to data of non-destructive measurements of the vegetative and fruits plant parts as well as final harvest data of four different canopy architectures.

RESULTS AND DISCUSSION

Differences in canopy architecture nearly doubled the final fruit dry mass in the experiment (Fig. 1). We implemented individual coefficients for growth respiration of fruits (30 %) and vegetative parts (10 %), related to the newly produced dry matter, as well as a maintenance respiration coefficient for the fruit part (2 %), related to the standing dry mass. Figure 1 shows exemplarily the close simulation of the measured dry matter production per plant in the different plant architectures for the row canopies. Maintenance respiration of the leaves was assumed to be covered by the respiration term of the Farquhar model. The low respiration coefficients of the fruits can be explained by the relatively low physiological activity of the fruit tissue and the excluding of photosynthetic activity of fruits by the model (Schapendonk & Challa, 1981; Marcelis & Baan Hofman-Eijer, 1995a, b). The maximum deviation of the simulations ranged between 15 % overestimation and 11 % underestimation for the final fruit dry mass. The bigger deviations at the end of the simulation can be related to change in fruit growth due to a topping of the plants (downwards arrows in Fig. 1).

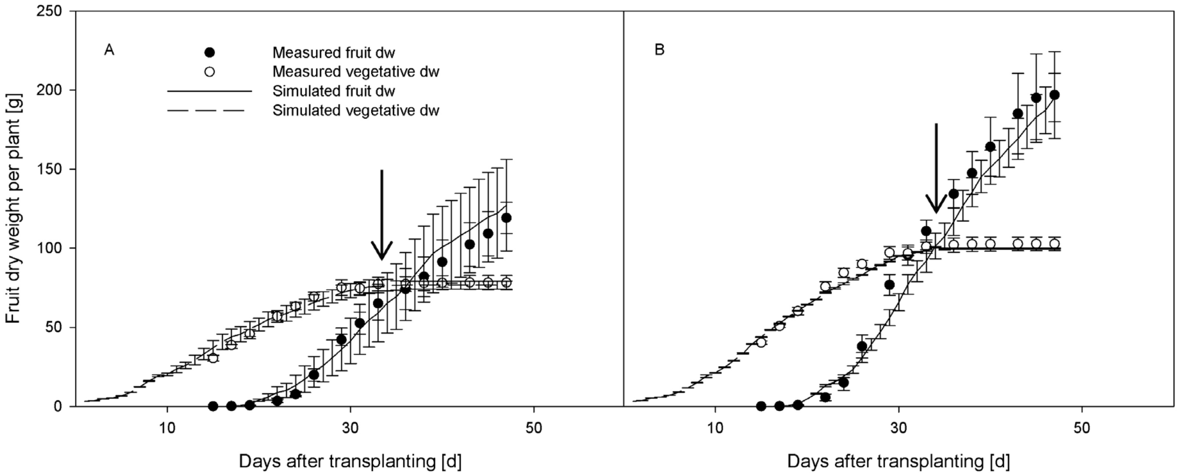

Figure 1. Measured and simulated fruit and vegetative dry weight (dw) per plant in a row canopy with 2 plants per m² (A) and 1 plant per m² (B). Downward arrows indicate topping. Error bars represent standard deviations.

Analyzing the impact of key parameters of leaf level photosynthesis shows clear differences in the sensitivity of a change of individual parameters (Table 2). Starting from the parameterization for cucumber four scenarios for each parameter were simulated with -20 %, -10 %, +10 %, +20 % change of the parameter. Internal conductance and maximum rate of carboxylation were less sensitive to a change of the parameter value compared to changes in the stomatal conductance and the maximum rate of electron transport. The results are in line with the common knowledge that the canopy productivity is mainly influenced by the availability of light and the regulation by the stomata (Trouwborst et al., 2010).

Table 2. Average change (%) over four canopy architectures of internal conductance (g_i), stomatal conductance (g_s), maximum rate of electron transport (J_{max}) and maximum rate of carboxylation (V_{cmax}) per 10 % change of parameter on the final fruit dry weight (FFDW) .

	Change in FFDW (%) per 10% change of parameter			
Parameter	g_i	g_s	J_{max}	V_{cmax}
Mean	0.65	2.83	4.17	0.70
SD	0.60	0.25	0.99	0.91

Extending the existing L-Cucumber model with an implementation of a leaf level model of photosynthesis shows that the presented FSPM provides the possibility to account for physiological factors and factors induced by the spatial structure of the plant and the canopy, which are necessary for an accurate estimation of plant productivity. Relating the physiological changes to the structural differences clearly emphases the importance of a precise description of the plant structure.

Further simulations extending the set of parameters and their interaction should strengthen the usability of the model for analysis of the impact of the different plant parameters on dry matter production. Thus, the FSPM could serve as a tool to analyze the impact of environmental control strategies on productivity for greenhouse production.

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