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Revealing the relative importance of photosynthetic limitations in cucumber canopy

Tsu-Wei Chen[1*], Michael Henke[2], Katrin Kahlen[3], Pieter H.B. de Visser[4], Gerhard Buck-Sorlin[5], and Hartmut Stützel[1]

[1]Institute of Biological Production Systems, Leibniz Universität Hannover, Herrenhäuser Straße 2, 30419 Hannover, Germany, [2]Department Ecoinformatics, Biometrics and Forest Growth, Georg-August University of Göttingen, Göttingen, Germany, [3]Geisenheim University, Von-Lade-Straße 1, 65366 Geisenheim, Germany, [4]Greenhouse Horticulture, Wageningen UR, Droevendaalsesteeg 1, 6708 PB Wageningen, the Netherlands and [5]UMR 1345 Institut de Recherche en Horticulture et Semences (IRHS), AGROCAMPUS OUEST Centre d'Angers, 2 rue André le Nôtre, 49045 Angers Cedex 01, France

**correspondence:* chen@gem.uni-hannover.de

Highlights: We identified that in a two meter high greenhouse grown cucumber canopy, photosynthesis is mostly light-limited, and light interception and biochemical capacity are the major factors limiting photosynthesis. The diffusion pathways, stomatal and mesophyll conductance, are minor restrictions.

Keywords: Digitizing, photosynthesis, photosynthetic limitations, FvCB model, *Cucumis sativus*, *GroIMP*

INTRODUCTION

Improving the crop photosynthesis is important for increasing yield. To achieve this goal, methods to identify and to quantify the factors restricting photosynthesis are required. Several approaches to analyse the relative or quantitative magnitude of diffusional (stomatal and mesophyll resistance to CO_2) and non-diffusional (biochemical and light) limitations of photosynthesis are proposed in the literature (Jones, 1985; Wilson *et al.*, 2000; Grassi and Magnani, 2005; Grassi *et al.*, 2009). The method proposed by Grassi and Magnani (2005), by which the restriction of photosynthesis (% of maximum photosynthesis) can be quantitatively partitioned to the stomatal, mesophyll and biochemical components of limitations, is based on the Farquhar von Caemmerer and Berry model (FvCB model, Farquhar *et al.*, 1980) and considered to be a '*more complex*' but '*more realistic*' approach (Grassi *et al.*, 2009). However, Grassi´s approach can only be applied at light-saturated conditions (Rubisco-limited), and plants in nature, especially at canopy level, should be more often grown under non-saturated light conditions (RuBP-limited). Therefore, modification of Grassi´s approach is required if the limitation analysis should be conducted at canopy level. The objective of this work is to quantify the relative importance of the photosynthetic limitations. We used digitized data to reconstruct a static 3D greenhouse cucumber canopy using the interactive modelling platform *GroIMP*. A modified version of the limitation analysis of Grassi and Magnani (2005) was conducted. This modification allows the limitation analysis to be conducted at non-saturated light conditions, which correspond to the plant conditions in greenhouse.

MATERIALS AND METHODS

Reconstructing a 3D cucumber canopy using GroIMP

Whole plant architecture of cucumbers with 21 mature leaves grown in a greenhouse experiment was digitized as described by Wiechers *et al.* (2011b). Each leaf was represented by a predefined set of triangles and it was reconstructed using the commands *FloatList* and *PolygonMesh* in *GroIMP* (Kniemeyer, 2008). For reconstructing the virtual canopy structure, 18 cucumber plants with density 1.33 (plants per m^2) were distributed in 3 rows. Distance between plants in one row and distance between rows were 0.5 m and 1.5 respectively. The corresponding set-up was used in the virtual reconstruction.

Model description and limitation analysis

The light environment was simulated based on the approach of Buck-Sorlin *et al*. (2010) assuming the photosynthetic photon flux density (PPFD) above the virtual canopy is 600 µmol photon $m^{-2}s^{-1}$, diffuse/direct light ratio is 1:4 and sun position is on 1 July at 12:00. For computing the light distribution an advanced GPU-based ray-tracer, integrated into *GroIMP*, was used, with 10 million rays and a recursion depth of 10 reflections (Buck-Sorlin *et al*., 2010). A modified version of limitation analysis according to Grassi and Magnani (2005) was used to identify and quantify the stomatal (S_{Lj}), mesophyll (MC_{Lj}), biochemical (JB_L) and light (JL_L) limitation of to photosynthesis (Chen *et al*., in preparation):

$$\frac{A_{\mathrm{max}}^{\mathrm{ref}}-A}{A_{\mathrm{max}}^{\mathrm{ref}}} \cong S_{\mathrm{Lj}} + MC_{\mathrm{Lj}} + JB_{\mathrm{L}} + JL_{\mathrm{L}} = l_{\mathrm{sj}} \cdot \frac{\mathrm{d}g_{\mathrm{cs}}}{g_{\mathrm{cs}}^{\mathrm{ref}}} + l_{\mathrm{mcj}} \cdot \frac{\mathrm{d}g_{\mathrm{m}}}{g_{\mathrm{m}}^{\mathrm{ref}}} + l_{\mathrm{j}} \cdot \frac{\mathrm{d}J_{\mathrm{b}}}{J_{\mathrm{cmax}}^{\mathrm{ref}}} + l_{\mathrm{j}} \cdot \frac{\mathrm{d}J_{\mathrm{light}}}{J_{\mathrm{cmax}}^{\mathrm{ref}}} \quad (1)$$

where l_{sj}, l_{mcj} and l_j, are the relative limitations of stomatal and mesophyll conductance and the electron transport rate, $g_{\mathrm{cs}}^{\mathrm{ref}}$, $g_{\mathrm{m}}^{\mathrm{ref}}$ and $J_{\mathrm{cmax}}^{\mathrm{ref}}$ are their maximum values. The limitations are expressed in percentages of the potential photosynthesis ($A_{\mathrm{max}}^{\mathrm{ref}}$) . For this analysis, the intercepted light intensity at leaf level and the parameters of FvCB model and stomatal conductance for cucumber (Wiechers *et al.* 2011a) are used. Here, temperature is assumed to be 25°C.

RESULTS AND DISCUSSION

Photosynthesis is RuBP-regeneration limited

If the chloroplastic CO_2 concentration (C_c) was larger than the intersection point of FvCB model (C_{ctr}), photosynthesis was limited by RuBP-regeneration. Under light-saturated conditions, at which $C_c < C_{ctr}$, limitations were from CO_2-diffusion. In cucumber, C_c remained constantly around 200 µmol mol^{-1} (Fig. 1A and 1B) and at 600 PPFD C_{ctr} was below 150 µmol mol^{-1} (Fig. 1C). This indicated that under the simulated conditions the photosynthesis of the whole canopy was light-limited.

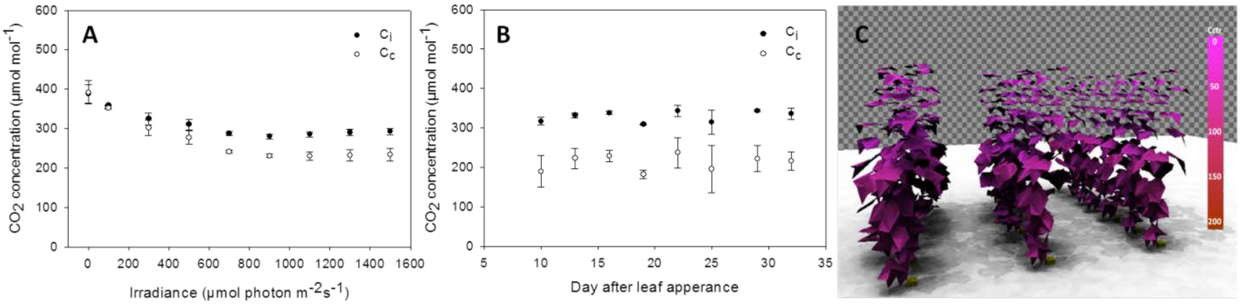

Fig. 1. (A) Influence of irradiance on the intercellular (C_i) and chloroplastic (C_c) CO_2 concentrations of cucumber leaves. (B) Under light saturated condition (1500 PPFD), C_i ranged between 300-320 µmol mol^{-1} and C_c were (n=3). (C) Simulated values of the intersection point of FvCB model (C_{ctr}) in cucumber canopy are between 0-150 µmol mol^{-1}, which is lower than C_i and C_c.

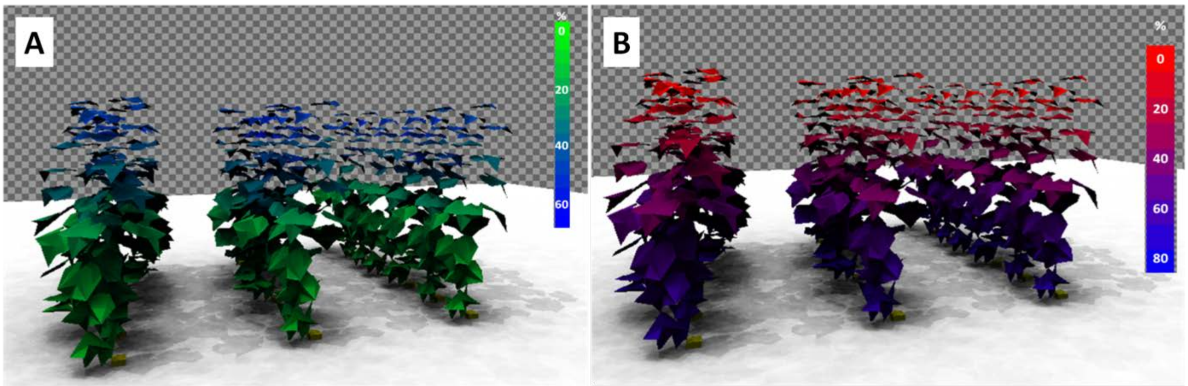

Fig. 2. Visualization of the light limitation (A) and biochemical limitation (B) within a 2 m high cucumber canopy. Light intensity above the canopy is assumed to be 600 µmol photon $m^{-2}s^{-1}$.

Sources of photosynthetic limitation

The sources of photosynthetic limitation changed dramatically with the canopy depth (Fig. 2A, 2B). The CO_2-diffusion pathways only restrict about 3-7 % of photosynthesis (Fig. 3A). The stomatal restriction increased with the leaf rank and mesophyll resistance only reduced less than 2% of the photosynthesis capacity. Light interception and biochemical capacity were the most important factors reducing photosynthesis (Fig. 3B). At the lower canopy, about 68% of photosynthesis was limited by the biochemical capacity and 12% was limited by the light. At the upper canopy, 47% of the photosynthesis was restricted by light, without any biochemical limitation. Interestingly, although older leaves receive less light than the younger leaves, whereas older leaves are less light-limited than the youger leaves. This can be explained by the fact that the decrease in electron transport rate of the older leaves is mainly due to the reduction of biochemical capacity and improving the light interception of the leaves below rank 10 may only increase their photosynthesis rate up to 20%.

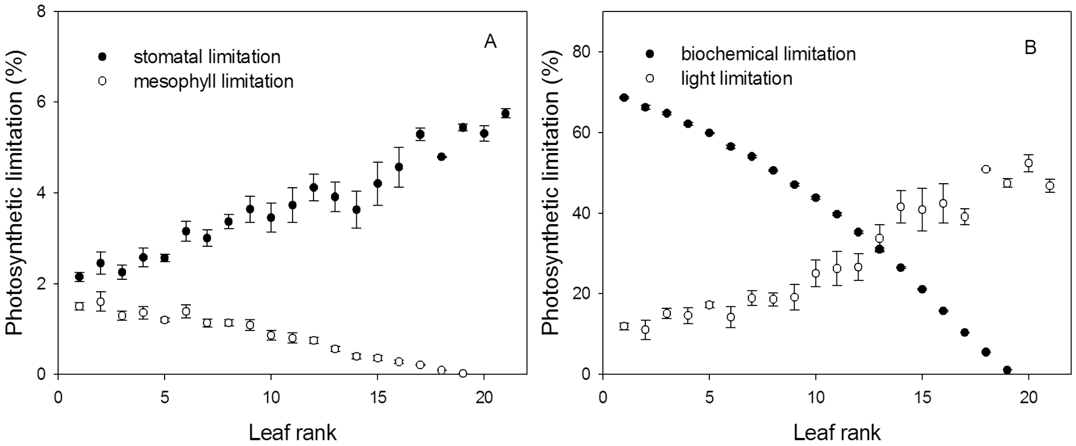

Fig. 3. Photosynthetic limitation. (A) The diffusion pathways of CO_2 restrict 4-6% of photosynthesis. Stomata limitation is 4% higher at upper part (higher leaf rank) than the lower part of the canopy. Above the rank 19, mesophyll limitation drops to zero. (B) Biochemical limitation of older leaves is about 70% and drops to zero at rank 20. Light limitation increases with leaf rank (n = 5).

Here we only demonstrate the simulation assuming that the PPFD above the canopy is 600 μmol photon $m^{-2}s^{-1}$. It will be fruitful to apply this analysis with different light intensities. Further simulations with different canopy structures (e.g. isometric or V-shape training system) and plant densities would also be helpful in discovering the influence of these factors on the photosynthetic limitation. Furthermore, it is known that temperature influences stomatal, mesophyll and electron transport rate. Therefore, a more complex description of the temperature response to these physiological processes would aid in revealing the interaction of temperature and photosynthetic limitation. Using a dynamic structural model (Kahlen and Stützel, 2011; Wiechers *et al.* 2011a) would enable us to explore the effect of developmental stage on photosynthetic limitation at canopy level. These analyses could help greenhouse farmers to determine the strategy for supplemental light.

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