

Modelling temperature-modulated internode elongation in greenhouse grown cucumber canopies

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Highlights: This study highlights the significance of temperature signals for predicting final internode length: Growth and appearance rates need to be adapted to the prevailing temperature conditions. Variations in the light environment additionally alter the pattern of final internode length along the main stem and thus indicate the importance of considering simultaneously acting factors.

Keywords: Temperature, *L-Cucumber*, Arrhenius function, organ growth, light, functional-structural plant model

INTRODUCTION

Plant architecture is significantly influenced by the temperature conditions during plant growth and development (e.g. de Koning 1992, Schouten et al. 2002, Siebert and Ewert 2012). However, in a natural environment, plants are faced with various changing environmental factors acting simultaneously (e.g. Tardieu et al 2012). Models may serve as a tool for a systematic system's analysis (Vos et al. 2010). E.g., concerning the pattern of internode growth along the main stem of greenhouse grown cucumber plants, light-modulated final internode length of each rank can be estimated accurately under a variety of light conditions resulting from independently changing light quality and light quantity signals using the functional-structural model *L-Cucumber* (Kahlen and Stützel 2011a, b). Here, a light response curve for final internode length was parameterized which is valid for temperature conditions optimal for cucumber plant growth. However, even under controlled greenhouse production systems, temperature conditions are rarely constant. High light conditions may increase the temperature inside the greenhouse. In addition, temperatures might be adapted to control plant growth (Kahlen et al. 2012).

A recent study of Kahlen et al. (2012) indicated that temperature conditions during cucumber plant growth affect both, final internode lengths and internode appearance rates. Thus, the light response curve of *L-Cucumber* was extended by a multiplicative factor derived from average internode lengths and the appearance rates were adapted to the measured rates (Kahlen et al. 2012, their Eq. (1) and Fig. 2). Using this adaptations, simulations resulted in accurate final internode lengths on the level of the individual internode and reproduced pattern of FIL along the main stem similar to the measured data. However, the analysis lacked a proper evaluation. Moreover, the derived temperature response curves might have been "experiment"-dependent and lacked universal validity. Interestingly, a recent meta-analysis (Parent and Tardieu 2012) showed that the temperature responses of developmental processes such as organ elongation or the duration of a plant cycle follow an Arrhenius-type response curve after normalization by their rates at 20°C. Maximal normalized developmental rates and their corresponding temperatures vary between species, but not between the above mentioned developmental processes. According to Parent and Tardieu (2012, their Tab. S2) any temperature-modulated elongation rate can be estimated by its value at 20°C multiplied by the value of the species-specific Arrhenius value for the considered temperature, whereas a temperature-modulated duration of a phase at a given T equals its value at 20°C divided by the value for the considered temperature.

The aim of this work was to analyse effects of temperature on internode growth and development of cucumber plants under naturally fluctuating light conditions in a greenhouse production system. We extended the functional-structural plant model of cucumber, *L-Cucumber* (Kahlen and Stützel 2011a) using the proposed approach of Parent and Tardieu (2012) to implement the temperature responsiveness of internode elongation rates and organ appearance rates. For an initial model evaluation, we used data of a greenhouse experiment with three temperature levels.

MODEL

To the knowledge of the authors, at present, there is no cucumber specific parameterisation of the Arrhenius function of the meta-analysis of Parent and Tardieu (2012) available. Thus, we used the average input data of the 17 crop species and *Arabidopsis*, i.e. the activation enthalpy ΔH_A (69350 J mol^{-1}) and the temperature at which the rate is maximum (305 K), to estimate an average temperature response function for all 18 species, $F_{av}(T)$. The model extension of *L-Cucumber* was done by implementing $F_{av}(T)$ into the light response curve for FIL (cm):

$$FIL_T(T, PAR, R:FR) = F_{av}(T) \cdot FIL(PAR, R:FR) \quad (1)$$

where the function for FIL equals Eq. (MA2) in (Kahlen and Stützel 2011a):

$$FIL(PAR, R:FR) = 13.4 - 0.14 \cdot PAR + f(R:FR) \quad (2)$$

and $f(R:FR)$ represents a stepwise linear response of the final internode to local light quality. PAR corresponds to the mean PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) above the canopy of four days starting six days before the internode has reached its maximum growth rate and R:FR equals the mean value of the R:FR ratio at the whole stem at the same timing and the R:FR at the internode at its maximum growth rate. Moreover, the appearance rate was adapted via its reciprocal value, the duration between the appearance of successive organs (d). The duration at 20° was divided by $F_{av}(T)$.

SIMULATIONS

To analyse the interplay of temperature x light on FIL along the main stem simulation runs with the extended *L-Cucumber* model were done. In the virtual scene, a corresponding canopy set-up as in the experiment (number of plants, distances between plants, training and pruning system) was created. As model input the data sets of measured daily PAR data of the above described experiment were used in the simulations. The coupled light model simulated a hemispherical approximation of the sky at the location of the experiments, Hannover, Germany, and was set up for the path of the sun on day 200 of the year. In contrast to these input data, the local light quality conditions (R:FR) emerged from the interaction of canopy architecture and optical light properties of the virtual canopy. For each temperature level of the experiment, individual simulations were run for five slightly different initial leaf orientations with five replications for 24 days. Further details on the virtual canopy can be found in (Kahlen et al. 2012, Kahlen and Stützel 2011a).

RESULTS AND DISCUSSION

Simulations mimicked both, the average numbers and lengths of internodes above rank 8 which reached their final length within the time span of 24 days. Average numbers were ca. 14, 9 and 7 and average lengths were 11.0 cm, 10.5 cm and 9.3 cm for 24°C , 20°C and 16°C , respectively. We excluded internodes below rank 8 from the analysis, because it could be assumed that they were initiated before the different temperature regimes were applied and, so far, it is not clear, during which phase temperature conditions most significantly effect on the internode growth and development. It is also important to reveal the role of temperature on the duration of internode extension. This aspect is missing in this study. A second step of this analysis will include hypotheses on the timing and duration of the temperature signal. However, for the different constant temperature conditions as in our evaluation experiment, simulated data agreed well with measured data and showed similar pattern of FIL along the main stem (Fig. 1).

Even the different patterns in final internode lengths along the main stem observed in our experiment already indicated that for a precise estimation of FIL of cucumber plants grown under different temperature regimes both characteristics, growth and appearance rates, need to be adapted to the actual temperature condition. Altered light conditions during the light-sensitive phase of internode growth might additionally affect on growth and thus result in significantly different internode patterns along the main stem. This can be nicely visualized by simulations with temperature responsiveness of either the internode elongation rate (Fig. 2A) or its appearance rate (Fig. 2B). However, there is still a need for further research to predict FIL under varying temperature and light conditions. It would also be fruitful to analyse the impact of these simultaneously acting factors on time of harvest and yield. Here, the study of Wiechers et al. (2011) could be a good starting point.

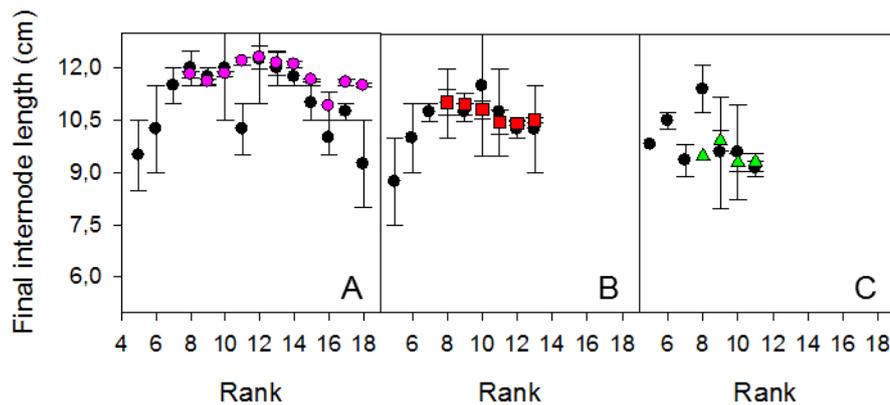


Fig. 1. Final internode length along the main axis of cucumber plants 24 days after treatment start for 24 °C (A), 20°C (B) and 16°C (C) day temperature in the greenhouse. Black circles represent measured data, whereas the coloured symbols represent simulated data for the corresponding temperature conditions.

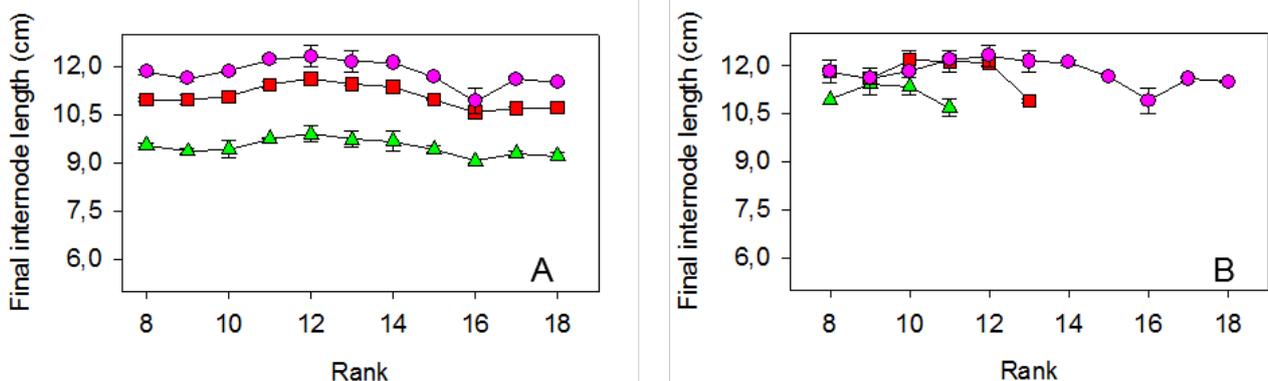


Fig. 2. Simulated final internode length along the main axis of cucumber plants 24 days after treatment start for scenarios of 24°C (pink circles), 20°C (red squares) and 16°C (green triangles) day temperature, where the temperature responsiveness of (A) the elongation rate or (B) the appearance rate were used in the model.

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