Modeling Temperature-Modulated Stem Growth of Cucumber Plants (*Cucumis sativus* L.)

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Abstract— **Variation in temperature has tremendous effects on plant growth and development. Below optimal conditions, a decrease in temperature can result in both, a reduced organ appearance rate and a reduced organ growth rate. For internode growth, the latter also depends on the light signal, which in turn might be altered by the temperature effect on the canopy. The aim of this work was to analyze the importance of both, temperature and light signals for a precise prediction of stem growth. Therefore, we (i) investigated the temperature effects on the main stem of greenhouse grown cucumber plants and (ii) used an extended functional-structural plant model of cucumber, *L-Cucumber*, to analyze the effects of temperature x light on cucumber stem growth. Data of a greenhouse experiment with 24, 20, 16 day temperature (°C) were used for model parameterization. Organ appearance on temperature sum basis rate was significantly reduced just in case of the lowest temperature condition, whereas average internode lengths decreased with temperature. The simulation scenarios highlighted the role of both characteristics on predicting final internode lengths (FILs) and showed how light and temperature both effect on FILs. However, the presented model concept needs to be properly evaluated. Future research should investigate the timing and duration of the temperature sensitive time window for internode growth.**

Keywords- functional-structural modeling; virtual plant; internode; shoot development

I. INTRODUCTION

Temperature is one factor significantly determining plant growth and development. A reduction in temperature below optimal conditions often results in suboptimal plant growth conditions, e.g. [1]. However, in almost all growth processes, more than one environmental factor is involved and their interactions are complex, see e.g. [2, 3]. If we focus the analysis on stem elongation, we could ask, how does temperature effect on final stem length? I.e., which process is more affected by the temperature conditions, the appearance rate of the internodes or their growth rates, and are they similarly affected by changes in the temperature regime? Internode growth also depends, among other factors e.g. [4, 5], on the light signal. Both, the light-quantity and -quality signal significantly effect on final internode length (FIL) [5,6]. So, if individual FILs were longer under higher temperatures in an environment of naturally varying light

conditions, is this solely an effect of the temperature or also an effect of the possibly altered light conditions during internode growth? Moreover, e.g. ambient CO_2 conditions might interact with the responsiveness of the plants to the light quality signal [4]. Due to the above indicated complexity of interacting effects of various factors, it might be a fruitful approach to try to answer these questions based on a combined experimental and modeling study, e.g. [7]. In a previous study [3], Kahlen and Stützel presented a functional-structural model for cucumber plants grown under optimal temperature conditions which already accurately estimates light-modulated final internode lengths under a variety of light conditions.

This study aimed at analyzing light and temperature effects on cucumber stem growth. Therefore, we (i) conceptualized a model approach capturing the temperature effects on growth and development of the main stem of greenhouse grown cucumber plants and (ii) used an extended functional-structural plant model of cucumber, *L-Cucumber*, to highlight the effects of temperature x light quality on cucumber stem growth.

II. MATERIALS AND METHODS

A. Experiment

The experiment was conducted in six greenhouses at the Leibniz Universität, Hannover, which can be cold down below outside temperature. Cucumber plants (*Cucumis sativus* L. 'Aramon' Rijk Zwaan, De Lier, the Netherlands) were grown hydroponically under typical growth conditions. Temperature x CO_2 conditions were established with twenty plants of each treatment in a single greenhouse. Day temperature was set to 24°C, 20°C and 16°C, each combined with a by 4°C reduced night temperature. CO_2 levels were 300 and 800 µmol mol^{-1}. During the experimental phase both factors were kept constant. Internodes with a length of at least 2 cm are referred to as visible. Appearance rates (AR, d^{-1}), lengths (IL, cm) and numbers of internodes of the main axis were measured weekly.

B. Model approach

In the original *L-Cucumber* [4], organ development is expressed by phyllochrom with a constant value of 17°Cd,

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which was derived from experiments at 24°C/20°C day/night temperature and under non-elevated, constant CO_2 conditions of ca. 370 μmol mol^{-1}. The base temperature was set to 10°C. Thus, here the resulting data for appearance rates were also expressed in terms of temperature sum (AR_{TS}, (°Cd)$^{-1}$). We hypothesized that in the rage of optimal temperature conditions, AR_{TS} would be constant. In the experimental part of this study, day/night temperatures were kept constant, thus it was not possible to derive any characteristics about the temperature-sensitive time window for an individual internode, neither the timing nor the duration of the sensitive phase. Consequently, the model approach presented here does not consider this information. Based on the hypothesis that an increased temperature enhances growth rates the model approach for final internode length (FIL) conceptualized in [3] was extended. The original model parameterization was conducted for 24/20°C day/night temperature. The temperature effect was implemented following a multiplicative approach:

$$FIL_T(T, PAR, RFR) = y(T) \cdot FIL(PAR, R:FR) \quad (1)$$

where the function for FIL equals Eq. (MA2) in [4]. PAR is the mean PAR (μmol m^{-2} s^{-1}) of four days starting six days before the internode has reached its maximum growth rate and RFR is 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. The function y(T) is a cubic function of T, with y(24°C) = 1 and it was fitted to FIL data of the treatments with control CO_2 conditions measured 24 days after treatment start. Due to the same plant developmental status at the beginning of the treatment start, only FIL for ranks above 6 were considered to be sensitive to possible changes in the temperature condition.

We additionally extended *L-Cucumber* by including the possibly temperature-sensitive phyllochrom which equals the ratio of one over organ appearance rate, AR_{TS}. Simulation runs with *L-Cucumber* were done for assessing the role of temperature x light modulated developmental processes on FIL along the main stem. Thus, the same canopy set-up as in the experiment (number of plants, distances between plants, temperature conditions, etc.) was established in the simulations. In all simulation runs, daily PAR data and the day temperatures of the above described experiment were used as model input. The local light quality conditions (R:FR ratios) resulted from the interaction of canopy architecture and optical light properties of the leaves in the virtual canopy (see also [4]).

C. Analysis

To assess the significance of the timing of organ appearance on its length, we systematically analyzed simulations based on the exclusively PAR-sensitive model approach [4] for each temperature treatment using measured appearance rates from the other temperature conditions. Comparisons with measured internode lengths were based on RMSD, accuracy and bias. The significance of the effect of temperature x light on the internode elongation was preliminarily assessed using an extended version of a dynamic model of plant growth, *L-Cucumber*, by Kahlen and Stützel [4].

III. RESULTS

A. Measured temperature effects on appearance rates and stem lengths

The stem length, i.e. the sum of lengths of all visible internodes, increased linearly with both the number of visible internodes at the main stem (Fig. 1a) and the average lengths of these internodes (Fig. 1b).
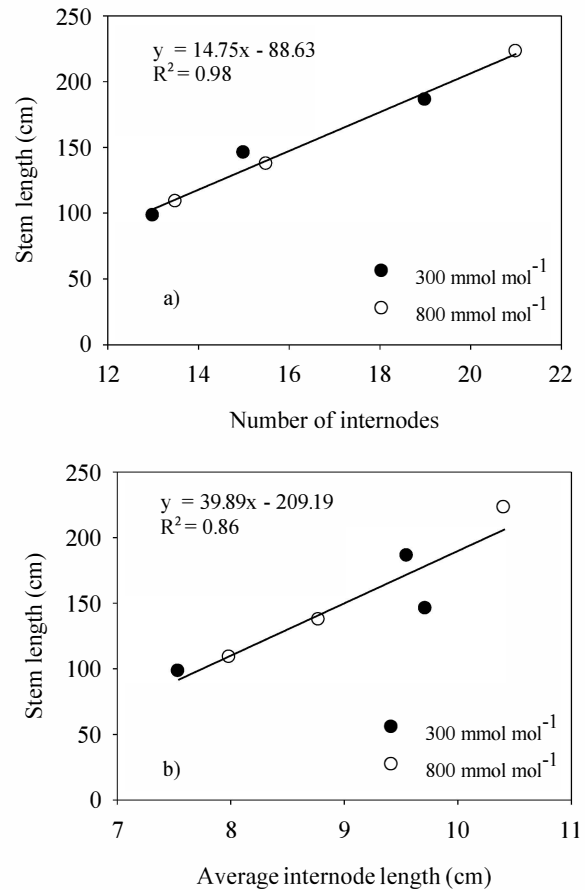

Figure 1. Measured stem length in relation to (a) the number and (b) the average length of visible internodes at the main stem of cucumber plants at 24 days after treatment start. Data of both CO_2 levels are shown. The regression analyses summarise data of both CO_2 treatments .

The number of visible internodes ranged between 13 and 21 and already explained 98% of the variation of stem length, which ranged between 100 cm and 250 cm.. Average internode length varied between 7.5 and 10.4 cm and increased with temperature from 7.8 cm at 16°C to 10.0 cm at 24°C (control CO_2) (Fig. 2a). The regression analysis indicates that the average internode length might already

reach a plateau at 24°C, because the 1st derivative of regression function equals zero at 26°C with an average internode length at 26°C of = 10.1 cm. There was no uniform pattern in the CO_2 effect. Longer internodes (0.9 cm) were observed at 20°C for high CO_2, but shorter in the two other cases (-0.5 and -0.8 cm for lower and higher temperatures). A similar picture emerged if average lengths of fully grown internodes were considered (data not shown). The appearance rate on a day basis also increased with temperature (Fig. 2b). At high temperature, CO_2 additionally seemed to decrease the appearance rate, in detail from 0.63 to 0.54 d^{-1}. The data did not allow us to reveal any kind of saturation pattern. On the temperature sum basis, appearance rates decreased between 16°C and 20°C from 0.07 to 0.06 (°Cd)$^{-1}$, between 20°C and 24°C the rates remained constant, but a lowest rate (0.052 (°Cd)$^{-1}$) was observed at high CO_2.
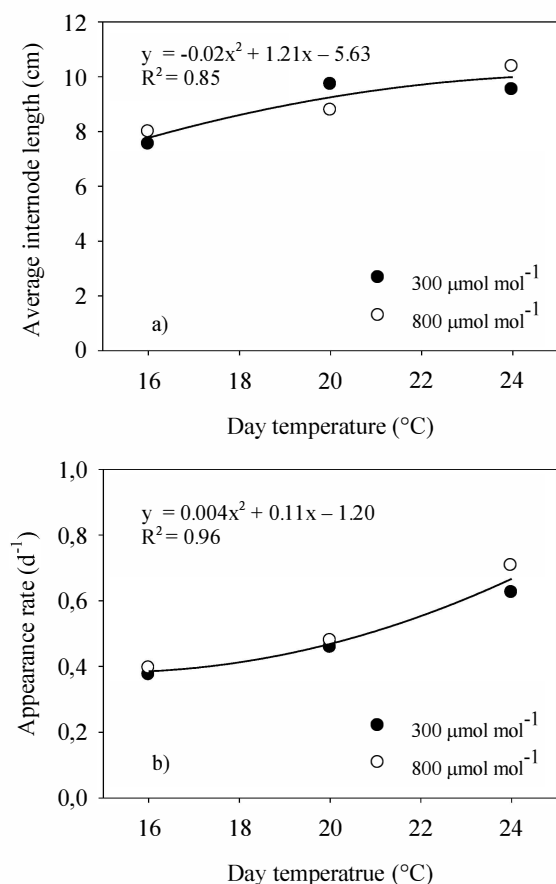
Figure 2. Average lengths of visible internodes (a) and appearance rates per day (b) in relation to the day temperature. Measured data of the main stem of cucumber plants at 24 days after treatment start are shown. The regression analyses summarise data of both CO_2 treatments.

However, CO_2-induced differences in apperance rates and average final internode lengths were relatively small. Thus, the following analyses were conducted with respect to the temperature effects only.

The temperature effect on FILs in Eqn. (1) resulted in

$$y(T) = -0.0031 \cdot (T_{ref} - T)^2 + 1 \qquad (2)$$

with T_{ref} equals the 24°C temperature condition. This forces a 5% reduction in internode length for 20°C and a 15% reduction for 16°C day temperature. The average appearance rate resulted in a phyllochrom of 17°Cd for 24°C and 20°C and equaled 14°Cd for 16°C.

B. Simulated temperature x light effects on internode lengths

For all temperature conditions, the agreement between simulated internode lengths based on the exclusively PAR-sensitive model approach [3] and measured lengths was reduced in case lower or higher appearance rates than data specific ones were used as model input (Tab. 1). Similar agreements were observed for the higher temperature conditions using the associated appearance rate (bold entities in Tab.1). However, the estimates for the low temperature condition were significantly worse. The simulation runs with the extended *L-Cucumber* using temperature corrected phyllochrom values and the adapted day temperature, which is used in the model to calculate organ age, revealed good agreements with measured data for all temperature conditions even though the pattern along the main axes were quite different (Fig. 3). For T_{ref} final internode lengths first increased and then decreased, at 20°C the FILs increased a remained more or less stable, whereas at 16°C they were at a significant lower level and increased at higher ranks. The patterns were observable for simulated and measured FILs.

TABLE I. STATISTICAL ANALYSIS OF AVERAGE FINAL INTERNODE LENGTH BASED ON THE EXCLUSIVELY PAR-SENSITIVE MODEL APPROACH [4] USING THE CALCULATED APPEARANCE RATES (BOLD FROM FIG. 2B) FOR ALL TEMPERATURE CONDITIONS.

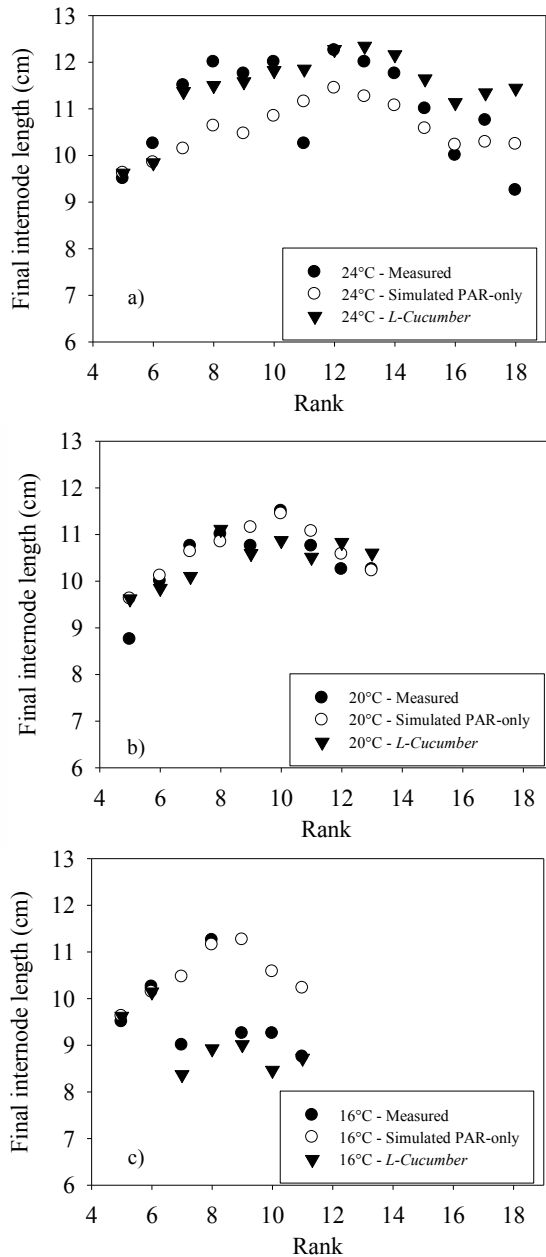| Input		Output		
Day Temperature (°C)	Appearance rate (d^{-1})	RMSD (cm)	Accuracy (%)	Bias (cm)
24	**0.71**	0.67	0.94	0.00
24	0.48	1.35	0.88	0.01
24	0.38	1.20	0.89	0.05
20	0.71	0.82	0.92	0.01
20	**0.48**	0.65	0.94	0.03
20	0.38	1.20	0.89	0.02
16	0.71	1.74	0.82	2.35
16	0.48	1.67	0.83	3.95
16	**0.38**	1.34	0.86	2.17

Figure 3. Final internode length along the main axis of cucumber plants 24 days after treatment start for optimal temperature, 24 °C (a), 20°C (b) and 16°C (c). Simulation runs were based on the exclusively PAR-sensitiv model [4] and on an extended version of *L-Cucumber*, which considered the differences in organ appearance and internode elongation rate due to Eq. (1) and (2).

The model which simply considers light quantity underestimates individual FILs in the high temperature regime (T_{ref}) at higher ranks, but already followed the measured trend in shorter or longer internodes along the main axis (Fig. 3a). In contrast to this pattern, the PAR-only-sensitive FIL predictions were already in line with measured data at 20°C (Fig. 3b), but this model

overestimated measured FILs at 16°C (Fig. 3c). The model which is also sensitive to the light quality resulted in significantly better FIL predictions for T_{ref}, but slightly overestimated FILs at ranks above 15. If the temperature effect on internode elongation is considered, FIL predictions were of high quality for both lower temperature regimes

IV. DISCUSSION

First of all, future work needs to provide a proper evaluation of the model. However, the different internode lengths' patterns resulting from simulation with *L-Cucumber* indicate the importance of considering simultaneously acting factors. Further research should provide sufficient information about the interplay of timing, sensitivity and site of relevant signal perception. In particular, experiments with changing temperature conditions could help to overcome shortcomings of the present study. The elevated ambient CO_2 conditions in our experiment did not allow us to derive any effects of interaction with temperature or light. Cowan and Reekie [4] showed that increased CO_2 resulted in a less homogenous size distribution within plant canopies. Thus, our experimental set up might has been too small and the number of measurement has to be increased significantly. Moreover, there are several implications of system's management in greenhouse cucumber production [e.g., 5] and possibly important interactions with canopy architecture, which could guide directions of future model-assisted research.

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