Simplification of a light-based model for estimating final internode length in greenhouse cucumber canopies

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INTRODUCTION

Plant height is a major characteristic of crop management and productivity (Liebig and Fricke, 2002; Boonekamp, 2005) as canopy architecture affects the light distribution within the canopy (Wiechers et al., 2011). In greenhouse production systems of cucumber (Cucumis sativus), where plants are vertically trained, the number of internodes and their individual lengths determine crop height. The internode appearance rate is mainly driven by temperature (e.g. for cucumber, Kahlen, 2006; for barley, Repkova et al., 2009), a factor which can be easily controlled in a modern greenhouse production system (Krug, 2002). On the other hand, ontogeny might also induce variation in length from one internode to the other along the main axis (e.g. Fournier and Andrieu, 2000). Moreover, final internode length can be affected by various environmental factors, such as the difference between day and night temperature (Xiong et al., 2002; Patil and Moe, 2009) and the ambient CO₂ level inside the greenhouse (Cowan and Reekie, 2008.). In a greenhouse production system, artificial light of specific wavelengths can be added to influence internode lengths (Shinkle et al., 2004, 2005; Trouwborst et al., 2010). However, under controlled conditions without supplemental light sources, mainly the naturally fluctuating light conditions in the canopy that affect internode elongation in unstressed cucumber plants. Changes in both, light quantity and quality, induce variations in final internode lengths (FILs) (e.g. Vandenbussche et al., 2005; Franklin, 2008; Ballaré, 2009). An increase in photosynthetically active radiation (PAR) above the canopy reduces FILs, whereas a reduction in the red : far-red (R : FR) ratio of the incoming radiation promotes internode elongation (e.g. Ballaré et al., 1990, 1991a, b; Christophe et al., 2006; Kurepin et al., 2007). Little is known about how exactly the internode to internode variation of FILs in a growing canopy is regulated. Recently, a model approach for the estimation of light-modulated internode lengths in such a system, which considers PAR above the canopy and the R : FR ratio at the internodes, was presented to estimate the R : FR contribution to the FIL (Kahlen and Stützel, 2011). This model, in the following referred to as original model, is expressed as

\[ \text{FIL} = 13.40 - 0.014 \cdot \text{PAR}_{4d} + f(R : FR) \]  

where \( \text{PAR}_{4d} \) is the mean PAR (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) of 4 d starting 6 d before the internode has reached its maximum growth rate. According to our observations, maximum growth rate occurs on the day when the internode length is approx. 3 cm. \( R : FR \) is the mean value of the \( R : FR \) ratios perceived by the internode at its maximum growth rate and the whole stem’s \( R : FR \) ratio in the same period as the PAR signal. The term for
the $R:FR$ contribution to FIL is linear with $f(R:FR) = 3.52 + 3.87(R:FR)$ for $0.91 > R:FR > 0.24$, $f(R:FR) = 0$ for $R:FR \geq 0.91$, and $f(R:FR) = 2.6$ for $R:FR \leq 0.24$. For greenhouse conditions, the original model accurately estimates FILs in various cucumber canopies (distribution and plant density) and under different PAR conditions above the canopy (Kahlen and Stützel, 2011), but it needs local $R:FR$ data as input, which therefore have to be measured or accurately estimated. In previous work it has been shown that the virtual plant model L-Cucumber, which is a functional–structural plant model of cucumber growth and development coupled with a light model (QuasiMC of Cieslak et al., 2008), can provide these local $R:FR$ data (Kahlen et al., 2008; Kahlen and Stützel, 2011). But, the current simulation duration is limiting the practical applicability of this virtual plant model. Providing reliable light quality data by L-Cucumber for an accurate estimation of FILs of a tall plant grown within a canopy of 19 plants takes approx. 5 h on a 3.5-GHz computer (see also Cieslak et al., 2008). So, can the practicability of this estimation approach be improved for FILs? There is clear evidence for the role of the $R:FR$ signal for internode elongation (e.g. Franklin and Whitelam, 2005). But for modelling purpose, can it be replaced by some easily measurable canopy property data, such as LAI (m$^2$ leaf area m$^{-2}$ ground)? Thus, the basic idea behind the following work was to shift the input data from the $R:FR$ signal at the possible sites of signal perception to the source of the $R:FR$ signal, which is mainly the leaf canopy with its specific optical properties (Kahlen et al., 2008). Obviously, the larger the leaf area which interacts with the incoming radiation, the lower is the average $R:FR$ ratio below the canopy. It is, however, unclear whether leaf area data reflect $R:FR$ signals at the sites of signal perception, especially for different canopy structures as created by plant distributions and plant densities. Moreover, is the whole plant’s leaf area or only a certain part of it mainly affecting the $R:FR$ signal of interest? If only the leaf area of a small number of leaves had to be known for an accurate estimate of the final length of an internode, measurement effort could be reduced substantially.

The objective of this work was to evaluate the significance of the $R:FR$ signal source, the leaf canopy, for an accurate prediction of internode lengths in growing cucumber canopies. The following hypotheses were tested: (a) LAI data can replace the required $R:FR$ signal data in the original model without reducing prediction quality; (b) there is a minimum of leaf area information required for accurate FIL prediction; and (c) an indirect model simplification, which is based on $R:FR$ ratio estimation using leaf area and plant density data, also reduces the amount of input data.

**MATERIALS AND METHODS**

**Experiments**

For model parameterization and evaluation, the same experimental data sets were used as in the original model work (Kahlen and Stützel, 2011). Here, the focus is only on the light quality-dependent aspects relevant for estimating FILs. Therefore, only the data from expts 2 and 3 in the original paper are considered. This numeration is preserved to facilitate comparability. Both experiments were carried out at the Institute of Biological Production Systems, Leibniz Universität Hannover, Germany (52°23’N, 9°37’E) in experimental greenhouses and had plant distribution and plant density as factors. Cucumis sativus were laid out in a randomized complete block design with three replications in either row or isometric distribution at a density of 1 and 2 plants m$^{-2}$. Distances between rows were 1.86 m in the row canopies, whereas in the sparse isometric canopy, the distance between direct neighbours was 108 cm. Plants were vertically trained and all side shoots were removed. Only the natural PAR conditions were different in both experiments. In expt 2, the daily light quantity mainly decreased with time with a slight increase at the end of the considered time period of approx. 3 weeks, whereas expt 3 was carried out under considerably fluctuating PAR conditions. Since the light quantity above the canopy has a significant effect on FIL, FIL profiles were different (Kahlen and Stützel, 2011; their figs 5A, B and 6). Further information on plant cultivation and management strategies, as well as on measurement details can be found in Kahlen and Stützel (2011).

In all approaches, the sparse isometric canopy, I1 (isometric distribution, 1 plant m$^{-2}$), of expt 2 was used to parameterize the models. The remaining treatments of expt 2, which were I2 (isometric, 2 plants m$^{-2}$), R1 (row, 1 plant m$^{-2}$) and R2 (row, 2 plants m$^{-2}$) and all treatments of expt 3 were used for the evaluation of the models.

**Model simplifications**

Substitution of $f(R:FR)$ by $f(LAI)$ using LAI thresholds of the original model. Initially, the light quality signal data used in the original model to estimate FILs was simply replaced by a function of LAI. In the parameterization treatment (I1 in expt 2), the corresponding measured LAI thresholds of the $R:FR$ response curve $f(R:FR)$ were $LAI_{\text{min}} = 0.3$ m$^2$ m$^{-2}$ for $f(R:FR) = 0$ and $LAI_{\text{max}} = 1.6$ m$^2$ m$^{-2}$ for $f(R:FR) = 2.6$ (Kahlen and Stützel, 2011). Substituting the $R:FR$ threshold data used in the original model by these LAI resulted in the following model functions (for calculation see the Appendix):

$$\text{FIL} = 13.40 - 0.014(\text{PAR}_{\text{ad}}) + f(\text{LAI})$$  \hspace{1cm} (2)

with

$$f(\text{LAI}) = 2(\text{LAI}) - 0.6, \text{ for } LAI_{\text{min}} > LAI > LAI_{\text{max}}$$

$$f(\text{LAI}) = 2.6 \text{ for } LAI \geq LAI_{\text{max}}$$

$$f(\text{LAI}) = 0 \text{ for } LAI \leq LAI_{\text{min}}$$

where $\text{PAR}_{\text{ad}}$ is the mean PAR (μmol m$^{-2}$ s$^{-1}$) of 4 d starting 6 d before the internode has reached its maximum growth rate. LAI data measured on the same day are used as input.

**Substitution of $f(R:FR)$ by $f(LAI)$ for partial LAI values.** Here, the effect of substituting the LAI information used in eqn (2) was evaluated by partial LAIs, i.e. LAIs calculated from
the cumulative leaf areas of $n$ leaves (counted from the top):

$$\text{FIL} = 13.40 - 0.014(\text{PAR}_{4d}) + f_n(LAI_n)$$

with

$$f_n(LAI_n) = a_n(LAI_n) + b_n, \quad \text{for LAI}_{\text{min},n} > \text{LAI}_n > \text{LAI}_{\text{max},n}$$
$$f_n(LAI_n) = 2.6, \quad \text{for LAI}_n \geq \text{LAI}_{\text{max},n}$$
$$f_n(LAI_n) = 0, \quad \text{for LAI}_n \leq \text{LAI}_{\text{min},n}$$

$LAI_n$ is the cumulative leaf area per m$^2$ ground, where leaf area ($>40$ cm$^2$) per m$^2$ ground is accumulated from the top of each plant until a number, $n$, of leaves per plant is reached. This number was stepwise increased by one starting from 5 up to 16. For each $n$, the function $f_n$ was parameterized individually. Measured LAI$_n$ data of 4 successive weeks were used to determine the LAI$_n$ contribution to the FILs at the corresponding ranks. The LAI$_n$ contribution to the FILs at all other intervening ranks was calculated from stepwise linear interpolation. For each $n$, the sum of the squared differences between measured and simulated FILs in the sparse isometric canopy of expt 2 was minimized by allowing the values of LAI$_{\text{min},n}$ and LAI$_{\text{max},n}$ to change. This resulted in $n$-dependent LAI thresholds, slopes and intercepts.

Estimation of the $R:FR$ ratio from leaf area and plant density.

This model uses the same function as the original model. Here, the $R:FR$ signal data is estimated from the two components of LAI, leaf area per plant (LAI, m$^2$) and plant density (PD, plants m$^{-2}$). At first, only LA of the individual plant was used to estimate the $R:FR$ signal. The larger the LA, the more light might interact with the leaf canopy resulting in a decrease in the $R:FR$ ratios. Thus, $R:FR$ ratios were estimated based on leaf areas, $R:FR_L$. Similar to eqn (3), the approach was evaluated for partial leaf area data:

$$R:FR_L = LA_{\text{ref},n}/LA_n$$

$LA_n$ is the cumulative leaf area data per plant, where leaf area is accumulated from the top of each plant until a number, $n$, of leaves is reached. For each $n$, the sum of the squared differences between ‘measured’ $R:FR$ ratios and estimated $R:FR$ ratios in I1 of expt 2 was minimized by allowing the value of LA$_{\text{ref},n}$ (m$^2$), which describes a reference leaf area value, to change. The ‘measured’ $R:FR$ data were obtained from a virtual canopy simulated with L-Cucumber. Specific model simulations were run, where the FIL of each individual inter-node was fixed in advance according to the measured final length in I1 of expt 2. This resulted in realistic canopy characteristics (Kahlen, 2007; Kahlen and Stützel, 2011).

Subsequently, the influence of the plant density was established in two different ways. The first approach just multiplies LA$_n$ with the plant density, which results again in LAI$_n$:

$$R:FR_L = LA_{\text{ref},n}/(LA_nPD) = LA_{\text{ref},n}/LAI_n$$

Alternatively, PD was dissected from the LA influence on light quality signals:

$$R:FR_L = (LA_{\text{ref},n}/LA_n)^{PD}$$

Both approaches for estimating $R:FR$ ratios, eqns (5) and (6), result in PD = 1 in eqn (4), and there is no further need for parameterization.

Assessing prediction quality

The prediction quality of each model was described by the root mean-squared deviation (RMSD) and the systematic prediction error (bias) (e.g. Kobayashi and Salami 2000; Gauch et al., 2003; Kahlen and Stützel, 2007):

$$\text{RMSD} = \sqrt{\frac{1}{n} \sum_{i=1}^{n} (x_i - y_i)^2}$$

$$\text{Bias} = \frac{1}{n} \sum_{i=1}^{n} (x_i - y_i^2) - \frac{1}{n} \sum_{i=1}^{n} y_i^2$$

where $x_i$ and $y_i$ are simulated and measured values, respectively.

RESULTS

Substitution of $f(R:FR)$ by $f(LAI)$ using LAI thresholds of the original model

Simulation. Simulated data using eqn (2) showed an overall agreement with the measured data (exemplarily shown for the row canopies in Fig. 1). In particular in ranks 8–14 (middle section of the plant), they fitted well in both experiments independent of the differences in the pattern of the natural light conditions (for PAR conditions, see Kahlen and Stützel, 2011; their fig. 6A, B). In expt 2, systematic overestimations occurred in all treatments at ranks 5–7 and ranks 15–19 (Fig. 1A, B), whereas in expt 3, the main deviations occurred at one specific rank (10) over all treatments with an overestimation of FILs of at least 1 cm and for the ranks 18–20 with increasing deviations with increasing ranks (Fig. 1C, D). Here, the overestimations were largest in the dense isometric canopy and smallest in the dense row canopy (Table 1). The positive biases reflect systematic overestimations. In particular, simulated FILs for the dense isometric canopies revealed up to 3 times higher deviations than the other canopy compositions.

Substitution of $f(R:FR)$ by $f(LAI)$ for partial LAI values

Parameterization. Leaf area per square metre ground for any considered number of leaves, LAI$_n$, changed with $n$ and time, which is here exemplarily shown for the dense row canopy in expt 2 (Fig. 2). Doubling plant density roughly doubled the corresponding LAI$_n$ in the experiments, but there were no systematic differences between the canopy structures. Small numbers of leaves resulted in more or less constant LAI$_n$ over time, e.g. LAI$_5$. With increasing $n$, the characteristic patterns turned continuously from constant to increasing with time over all measurements (Fig. 2).

The parameterization of $f_n(LAI_n)$ with corresponding LAI$_n$ of the sparse isometric canopy in expt 2 revealed that the LAI thresholds, LAI$_{\text{max},n}$ and LAI$_{\text{min},n}$, behaved differently.
with changing $n$ (Fig. 3A). LAI$_{\text{max},n}$ increased nearly linear, whereas LAI$_{\text{min},n}$ only slightly increased at $n = 5–7$ and remained constant over all following $n$. The maximum LAI$_{\text{max},n}$ was with 2.1 m$^2$ m$^{-2}$ > 7-fold larger than the LAI$_{\text{min},n}$ plateau. Slopes, $a_n$, and intercepts, $b_n$, showed inverse patterns (Fig. 3B). The slope decreased exponentially with $n$ starting at 67.0 for $n = 5$ and reaching a lower plateau of 1.5 cm, whereas the intercept increased from –12.6 to a threshold of –0.4 cm.

Simulation. Both experiments showed similar characteristics for the mean RMSD over all treatments in relation to the considered number of leaves, $n$ (Table 1). The mean RMSDs followed an exponential decay from 1.4 to 0.8 cm in expt 2 and from 1.5 to 1.0 cm in expt 3. The lower threshold was reached at a higher $n$ in expt 2 compared with expt 3. On the level of the individual canopy structure, RMSDs showed similar patterns with increased RMSDs over all $n$ for the dense isometric canopies in both experiments (Fig. 4).

The prediction quality expressed in terms of the biases showed patterns only slightly different from the RMSDs for the individual canopy treatments. The variation is exemplarily shown for the sparse row canopy of both experiments (Fig. 5). The predicted FILs tended to spread up to 1.5 cm higher ranks. Higher $n$ resulted in greater FILs. But the spread was mainly caused by $n < 8$. At lower ranks, there was no such spread, but only if $n$ was larger than 7. Otherwise, both experiments revealed different patterns. Decreasing $n$ resulted in slightly smaller FILs in expt 2, whereas $n = 5$ especially predicted larger FILs at lower ranks in expt 3.

Estimation of the R:FR ratio from LA and PD

Parameterization. Increasing the number of leaves, $n$, considered in eqn (4) and subsequently in eqns (5) and (6), resulted in an increasing trend with a saturation pattern for the estimated reference value of leaf area, LA$_{\text{ref},n}$, which reached a plateau of approx. 0.38 m$^2$ at $n = 14$.

Simulation. Both experiments showed similar characteristics for the mean RMSD over all treatments in relation to the considered number of leaves, $n$, and the model approach for estimating R:FR ratios, eqns (5) and (6), respectively (eqn 6 in Table 1). The mean RMSDs decreased approx.
TABLE 1. Mean RMSDs of the model simplifications for final internode length (FIL, cm) over different canopy architectures established in two experiments as well as and treatment-dependent biases

<table>
<thead>
<tr>
<th>Expt 2</th>
<th>Expt 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>Mean RMSD</td>
</tr>
<tr>
<td>eqn (2)</td>
<td>eqn (3)</td>
</tr>
<tr>
<td>5</td>
<td>0.84 ± 0.25</td>
</tr>
<tr>
<td>6</td>
<td>1.37 ± 0.28</td>
</tr>
<tr>
<td>7</td>
<td>1.25 ± 0.41</td>
</tr>
<tr>
<td>8</td>
<td>1.22 ± 0.45</td>
</tr>
<tr>
<td>9</td>
<td>0.90 ± 0.33</td>
</tr>
<tr>
<td>10</td>
<td>0.86 ± 0.31</td>
</tr>
<tr>
<td>11</td>
<td>0.82 ± 0.29</td>
</tr>
<tr>
<td>12</td>
<td>0.80 ± 0.27</td>
</tr>
<tr>
<td>13</td>
<td>0.78 ± 0.24</td>
</tr>
<tr>
<td>14</td>
<td>0.77 ± 0.21</td>
</tr>
<tr>
<td>15</td>
<td>0.77 ± 0.23</td>
</tr>
<tr>
<td>16</td>
<td>0.77 ± 0.19</td>
</tr>
</tbody>
</table>

The first direct simplification (eqn 2) substitutes \( f(R : FR) \) by \( f(LAI) \) in the original model, whereas the second, eqn (3), uses partial LAI data [cumulative leaf area data m\(^{-2}\) ground, where leaf area (>40 cm\(^2\)) m\(^{-2}\) ground is accumulated from the top of each plant until a number, \( n \), of leaves per plant is reached.

The lower part shows mean RMSDs of FIL predictions based on the original model using estimates for the R : FR signal data, here exemplarily based on eqn (6).

Data for the sparse isometric canopy (I1) in expt 2 are not included in the case of expt 2, because they were used for the parameterization of the original model (Kahlen and Stützel, 2011).

For higher \( n \), the mean RMSDs increased again until reaching a plateau close to the deviations at \( n = 5 \). On the level of the individual canopy treatment, RMSDs showed comparable patterns in both experiments. The minimum mean value of RMSDs was obtained around \( n = 8, 9 \) or 10 (Fig. 6). The biases followed roughly the pattern of the RMSDs for both experiments and R : FR estimation methods, but on a more constant level for lower \( n \) and with a clearly pronounced increase in biases for \( n > 10 \) in all treatments (data not shown).

There was an effect of the number of leaves considered on the pattern of FIL predictions, which is exemplarily shown for the FIL predictions using eqn (6) to estimate R : FR ratios of the sparse row canopy in both experiments (Fig. 7). Increasing \( n \) resulted in a spread of estimated FIL data at the lower ranks (<10) with better fits for \( n > 7 \) in both experiments, but similar predicted values at higher ranks in expt 2 over all \( n \) and overestimated FIL data for higher \( n \) for ranks above 11 in expt 3.
DISCUSSION

In all the models tested, the overall trends in simulated FIL over the ranks were in similar agreement with measured trends (Fig. 1) and comparable to those trends obtained by the original model (Kahlen and Stützel, 2011). This can be attributed to the common sensitivity to PAR of all models. Thus, all approaches might be suitable for simple FIL prediction.

Substitution of \( f(R : FR) \) by \( f(\text{LAI}) \) for partial LAI values

For \( n \geq 11 \), the fits for both experiments were better than in the case of just replacing \( f(R : FR) \) by \( f(\text{LAI}) \) (Table 1). This might be attributed to the additional estimation of the LAI thresholds in case of the partial LAI approaches. The different trends in the LAI thresholds, \( \text{LAI}_{\text{max,n}} \) and \( \text{LAI}_{\text{min,n}} \) (Fig. 3A), can be evaluated with respect to their functionality. \( \text{LAI}_{\text{min,n}} \) corresponds to the minimum \( R : FR \) signal required to trigger an elongation response of an internode, which might explain the constant pattern of \( \text{LAI}_{\text{min,n}} \). Moreover, \( \text{LAI}_{\text{min,n}} \) is slightly lower than \( \text{LAI}_5 \) (Fig. 2), which might highlight the role of the upper five leaves as initial signal source. In contrast, the increasing \( \text{LAI}_{\text{max,n}} \) with \( n \) can be related to the increasing leaf area (per m² ground) from the top of each plant until a number, \( n \), of leaves per plant is reached. Root mean-squared deviations (RMSDs) per canopy treatment (I1, isometric, 1 plant m⁻²; I2, isometric, 2 plants m⁻²; R1, row, 1 plant m⁻²; R2, row, 2 plants m⁻²) for (A) expt 2 and (B) expt 3 for different values of \( n \) are shown.

On the level of the mean RMSD, the prediction quality of the original model is reached at experiment-dependent \( n \) values. This might be explainable by slightly different pattern in the leaf growth in the experiments, which were not accounted for by the virtual experiments for parameterization of the original model and the subsequent simulations.
The biases of FIL estimates for dense canopies were more sensitive to decreasing $n$ than the RMSDs. This explains, why the best fits over all treatments and experiments were obtained with $n = 16$ (Fig. 1).

Estimation of the $R : FR$ ratio from LA and PD

The indirect model simplification concerns how to estimate the $R : FR$ signals. Here, the parameter $L_{Aref,n}$ is used to estimate light-quality data by dividing it by measured cumulative leaf area of a single plant, $L_{An}$, and plant density is considered as factor or exponent (eqns 5 and 6). Both methods resulted in similar mean RMSDs with an $n$-dependent pattern significantly different from the deviations obtained with the simplification which substituted $f(R : FR)$ by $f(L_{An})$ (Fig. 4 vs. Fig. 7). The specific patterns in the biases, which increased for $n > 10$, finally explain why the best fit in both models was obtained at approx. $n = 10$, if considered over all treatments (Fig. 1 for original model with eqn 6).

This simplification resulted in some cases in a higher prediction quality (in terms of the RMSDs) than the original model established by using the virtual plant model, L-Cucumber ($n = 8, 9, 10, 11$ as cut set over both experiments). The main reason might be that the virtual light quality signal depends on many factors, such as (a) measured optical properties, (b) simulated leaf areas and (c) their simulated positioning in 3-D space, and (d) the modelled feedback between light distribution and morphological adaptations (e.g. Chelle et al., 2007; Kahlen et al., 2008; Vos et al., 2010). In the case of the measured LA, all this information is indirectly accounted for, because the actual size of a leaf is already the result of growth and development under the specific environmental conditions.

Fruitfulness of the model simplifications

Both simplification strategies use the leaf area of leaves growing along the vertically trained main stem as model input. Thus, the validity of all models has to be proven in
case any other training system is applied to the plants, e.g. a V-shaped or umbrella system (Liebig and Fricke, 2002). For a V-shaped system, a scaling factor with respect to the deviation angle from vertical might be introduced to overcome possible limitations. Contrastingly in an umbrella system, the LA of the top of the plant is not necessarily the LA of the growing part of the plant and, possibly even more important, these leaves might not significantly contribute to the R : FR signal perceived at the growing internode at all. Therefore, in such complex systems it seems to be favourable to estimate local R : FR conditions using the virtual plant model as established in L-Cucumber (Kahlen and Stützel, 2011). It has already been shown that it is possible to implement various training systems into the virtual cucumber model (Kahlen, 2007). Moreover, recent developments in the field of functional structural plant models (e.g. Fourcaud et al., 2008; Hanan and Prusinkiewicz, 2008; DeJong and Da Silva, 2010), such as models for plant–pest interaction (Mammeri et al., 2010), could be connected to L-Cucumber (e.g. Room et al., 1996; Tardieu, 2010; Vos et al., 2010).

Even though the indirect simplification allowed FILs to be estimated at least as accurately as the original model, it is not possible to draw any conclusion from the source of the R : FR ratio (leaf area) to the possible site of signal perception or on the validation of the underlying time window (approximate week before maximum growth rate). Moreover, it is still unclear which specific leaves might really contribute most to the R : FR signal of interest, e.g. are only those nearly fully grown or those located in the close vicinity generating important parts of the R : FR signal of interest? Nevertheless, the fact that the top ten leaves resulted in the best simulation fits might guide further research in all adjacent research areas, such as systems biology and virtual plant modelling, to allow for scaling up basic research findings to the whole plant and even crop level (see also Granier and Tardieu, 2009). For example, a recent study highlighted the role of cell division on internode length in apple trees (Ripetti et al., 2008). This might be of importance in cucumber, too, as cell number in cucumber leaves is related to final leaf size and cell division is sensitive to PAR conditions (Wilson, 1966) and local light conditions result from effects on crop level, which can be simulated by virtual crops (e.g. Kahlen and Stützel, 2011). Finally, further investigations should consider the general validity of the present findings, because, for example, in ornamental crops such as chrysanthemum plant height is a quality specification (e.g. Carvalho et al., 2002).

Conclusions

This study showed that for an accurate estimation of light-modulated internode lengths, leaf-area data can substitute local light-quality data. In particular, the leaf area of the upper ten leaves seems to be a good estimator for the light quality signal in a vertical training system of cucumber. Thus, this work provides a simple, non-destructive method to predict final internode lengths based on light-quantity and leaf-area data. But, for plant training systems other than vertical training, the model might have to be adapted, whereas in complex architectural systems, the virtual plant model might be superior to the proposed simpler one. All in all, the present findings could guide future research on up-scaling local processes to the level of the whole plant and crop.

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LITERATURE CITED


**APPENDIX**

Substitution of $f(R : FR)$ by $f(LAI)$ using LAI thresholds of the original model:

$$f(LAI) = a + b(LAI)$$

with $f(0.3) = 0$ and $f(1.6) = 2.6$ results in $a = -0.3b$ and $b(1.6 – 0.3) = 2.6$ and thus in $b = 2$ and $a = -0.6$. The plateaux (above and below the thresholds) result from the concept of the original model.