Study on the Effects of Defoliation on the Growth of Cotton Plant Using the Functional Structural Model GREENLAB

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Abstract

For the functional structural plant model GREENLAB, parameters for the source and sink relationships can be retrieved through model inversion with plant architectural data as targets. In order to study more precisely the production of source organs, a controlled defoliation experiment was performed on single-stemmed cotton plants. Four regular leaf-pruning treatments were implemented to produce single-stemmed plants that retained a given number of functional leaves (i.e., 6, 9, 12 and 15, respectively) at the top of stem during the whole period of plant development, and compared with control plants (single-stemmed plants retaining all the leaves). Results show that the most productive treatment in terms of fresh above-ground biomass was the treatment with 12 functional leaves retained, which were significantly greater than control plants. The optimized functional parameters of GREENLAB for the source and sink relationships were found to be affected in relation with the number of functional leaves retained on the plants.

Keywords: Cotton (Gossypium hirsutum L.), GREENLAB Model, Plant Architecture, Source and Sink Functions, Pruning, Defoliation.

1. Introduction

In greenhouses and orchards, altering plant structures (e.g. pruning leaves, flowers, buds or branches) is common in attempting to obtain a better harvest. In forestry, regular branch clipping is practiced in order to improve wood quality or to form specific crown shapes. Hence, there are strong needs for mathematical models to explain how the plant responds to structural interventions, as well as to environmental factors. Several process-based crop models have been presented, in particular cotton models such as KUTUN [9], OZCOT [6], GOSSYM [2; 10]. Some attempts have been made to link crop models to structural models, e.g. L-Cotton [5] and COTONS [7] for cotton, and L-PEACH [1] for peach tree. Because these models lack the mechanism to integrate the feedback between plant structural dynamics and plant functioning at organ level, they are unable to simulate the effect of dynamical interventions on plant growth. As a functional structural plant model, the GREENLAB model combines the dynamic simulation of plant architecture, plant biomass production of source organs, and biomass partitioning among the sink organs, resulting resource-dependent growth [12]. The objective of this study is to provide better information on how cotton plants respond to defoliation using the GREENLAB model to deal with structural interventions, in particular the defoliation effects on plant growth.
The subjects in this study are cotton plants that were maintained as having a single stem, through systematic pruning of axillary buds just after their burst. Four regular leaf-pruning treatments were performed so that plants had a given number of leaves retained at the top of the main stem during the whole period of plant development, and compared with the control plants (all main-stem leaves retained on single-stemmed cotton plants). For those leaves that have not fully developed when they are removed from plants, a truncated expansion law has to be used to simulate their growth. As an important issue in biomass partitioning for woody plants, the secondary growth of stems has to be considered for cotton plants. Besides the response of plant morphogenesis with respect to leaf-pruning treatments, we will investigate the GREENLAB functional parameters optimized by the multi-fitting approach on four regular leaf-pruning treatments, compared with control plants, from a statistical point of view.

2. Materials and methods

2.1. Field experiment

A field experiment was conducted at China Agricultural University (39°50′N, 116°25′E) in Beijing, 2003. The cotton (Gossypium hirsutum L. cv. G33B) seeds were sown at a spacing of 0.6 m × 0.6 m. Plants emerged on May 26. Plant growth was not limited by water or nutrition. Weeds were removed by hand to avoid any herbicide effects on plant growth. All the axillary buds were removed at the time of their appearance in the course of plant development so that each plant consisted of a single stem and had purely vegetative growth. The control plants (also single-stemmed) were not subject to main stem leaf removal. Four leaf-pruning treatments were implemented, which differed in the number of leaves that were retained on the top of plants through the growing time after regular defoliation started. Four numbers of leaves (i.e., 6, 9, 12 and 15) were kept for the four treatments, respectively. In the following text, each treatment is identified with T\(x\) where \(x\) is the number of leaves retained by the treated plants.

Leaf removal began when plants had developed 11, 12, 17 and 20 for the treatment T6, T9, T12, and T15, respectively. It was technically difficult to start pruning exactly according to the number of leaves remained for each treatment. The oldest leaf was removed once a new metamer appeared at the top of each plant. As a result, plants subject to the same treatment were always carrying a fixed number of leaves: 6, 9, 12, or 15, according to the treatment. The aim of the experiment was to have simple plant architectures in order to compare results and test the theoretical model in response to leaf-pruning interventions.

The experiment had five blocks, one for each treatment. Destructive samples were taken weekly. For each treatment five plants were sampled in a random order per sampling date. The root system was not considered. Plant architectures were measured including diameter, length, and fresh weight of leaf petioles; area, and fresh weight of leaf blades; diameter, length and fresh weight of internodes. These measurements were done on all existing organs on the plant samples. The blade area was measured using a LI-COR 3100 leaf area meter (Lincoln, NB, USA). The date of onset of senescence was recorded for each leaf in order to estimate its life span. The experiment ended on 31 August 2003.

For each sampling date, the destructively measured organ fresh weight and dimension data were input in a target file which subsequently served as reference for statistical optimization of the GREENLAB model parameters. The target file structure and optimization procedure were as described in [4; 13].

For each treatment, five plants were randomly chosen for nondestructive observation at the start of experiment, for which the removed leaves were recorded and measured accordingly in the course of experiment. These plants were destructively measured on the last date allowing for establishment of the total biomass when combined with previously collected leaf data. These completed data were used not only for comparisons between treatments, but also for model validation, as they were independent of those to which the GREENLAB model was fitted.

2.2. The GREENLAB model and the version used in the study

The functional structural GREENLAB model has been described in detail [12]; model parameter optimization, stability analysis and field validation for maize crop have been previously presented [4; 8]. We will present here the main principles and specific options used for pruned cotton plants.

2.2.1. Modelling concepts. The GREENLAB model simulates plant morphogenesis and architectural development based on several recurrent mathematical equations describing the source–sink relationships, and on generic metamorphic rules to construct three
dimensional structures according to organ biomass or volume. The simulation time step in the model is the Growth Cycle (GC) that is the phyllochron corresponding to thermal time needed for the apical meristem to generate a new visible metamer (the architectural unit comprising a node, an internode and a leaf). Biomass production is modelled by an empirical nonlinear function of intercepted light by the exposed green leaf area, combined with radiation use efficiency (RUE). Other environmental factors may also be taken into account as modulators of RUE.

All the growing organs are sinks for biomass in the course of their development which can span several GCs. No soil water or nutrition limitations are considered in the model.

Freely grown cotton plants bear branches (vegetative and reproductive axes) resulting in complex architectures. Pruned cotton plants with all the axillary buds removed at appearance produce simpler plant architectures, each metamer of which consists of a few components: a node, an internode, and a leaf (except the first metamer with two cotyledons). Thermal time is computed as sum of mean daily air temperature minus a crop specific base temperature (15.5°C in this study [14]). The thermal time elapsing between the first metamer with two cotyledons). Thermal time is expressed  in GC, generally constrained by genetic components: a node, an internode, and a leaf (except the first metamer with two cotyledons). Thermal time is computed as sum of mean daily air temperature minus a crop specific base temperature (15.5°C in this study [14]). The thermal time elapsing between the appearances of two metamers is determined from field observation. Leaf expansion time and longevity are expressed in GC, generally constrained by genetic factors and environmental conditions.

Fresh biomass acquisition at each GC is computed by the following equation as adopted from [4]:

\[ Q(i) = \frac{E(i) S_p}{R_t R_c} \left( 1 - \exp \left( -R_c \sum_{k=1}^{n_o(i)} \frac{S_o(k)}{S_p} \right) \right) \]  

where \( Q(i) \) is the biomass production during GC(i); \( E(i) \) is the average potential of biomass production during GC(i) that generally depends on environmental factors (e.g. temperature, wind, light) and it is assumed constant through all the growth cycles in this study; \( n_o(i) \) is the number of green leaves during GC(i) which will depends on the leaf-pruning strategy in the treatments; \( S_o(k) \) is the blade area of the kth green leaf; \( R_t \) is an empirical resistance parameter of the plant which also serves as the scaling coefficient so as to produce proper result with given \( E \); \( R_c \) sets the effect of mutual shading of leaves according to Beer–Lambert’s law; \( S_p \) is the ground projection area of the leaves, which takes into account their inclination. As \( S_o \) and \( R_c \) appear reciprocally in pair in the formula, \( R_c \) is set to 1 and the leaf pruning effect on the parameter \( S_o \) will be studied.

Fresh biomass feeds all growing organs (sinks) through a globally shared reserve pool. The amount of biomass partitioned to individual organs is proportional to its relative sink strength that is a function of organ age in terms of GCs, with respect to the type of organ:

\[ D_o(j) = P_o f_o(j) \]  

where the subscript o denotes organ type: b, leaf blade; p, petiole; e, pith (the pith is defined as the internal part of the internode once the secondary growth (rings) is removed); \( D_o \) is the relative sink strength of the organ; \( P_o \) is the coefficient of relative sink strength (for leaf blade \( P_b = 1 \) is set as reference); \( f_o(j) \) is an organ type specific function of sink variation in GC(j), taking the beta-like form:

\[ f_o(j) = \begin{cases} \frac{g_o(j)}{M_o} & (1 \leq j \leq t_o) \\ 0 & (j > t_o) \end{cases} \]

\[ g_o(j) = \left( \frac{j - 0.5}{t_o} \right)^{t_o-1} \left( 1 - \frac{j - 0.5}{t_o} \right)^{t_o-1} \]

\[ M_o = \max_{j} \{ g_o(j) \} \left( j \leq j \leq t_o \right) \]

where \( a_o \) and \( b_o \) are parameters associated with the organ type o. These parameters can be obtained simultaneously by fitting the model to observation data, as well as other parameters (\( R_t \), \( S_p \), and \( P_o \)). The model inversion doesn’t allow computing parameters \( a_o \) and \( b_o \) at the same time, so parameter \( b_o \) is empirically set to 5.0 for all the organ types, and optimization of \( a_o \) is sufficient to generate an efficient function shape to fit the plant architecture. Note the leaves that are removed have expansion durations in relation with the treatment: the fewer leaves retained, the shorter duration. For those that have not yet finished their full expansion, they will follow only part of the full expansion function curve. This part is called truncated expansion law. As the definition, a new normalization constraint \( \max_{j} \{ f_o(j) \} = 1 \) is set to facilitate the comparison between coefficients (\( P_o \)) of relative sink strength, and to improve the parameter stability when organ expansion duration varies.

Since the newly formed ring covers all the existing internodes along the whole stem length, the secondary growth is treated as a compartment. Let \( P_c \) be the coefficient of relative sink strength for each ring, and the relative sink strength of the ring initiated at the end of GC(i) denoted by \( D_c(i) \), is assumed to be proportional to \( n_o(i) \) (the number of green leaves during cycle GC(i)), which is compatible with the “pipe model theory” [15]:

\[ D_c(i) = P_c n_o(i) \]  

Unlike other types of organs, rings are considered to expand only in one GC, so a new ring corresponds to
a new growth cycle.

All organs expand in fresh weight according to type specific functions, regardless of crop developmental stage or resources. Secondary growth is sensitive to the changes in number of leaves that occur following defoliation, and consequently will affect plant growth for the following growth cycles.

The choice of using fresh matter here is because we deal with plant architecture and work on the vegetative part of the plant, assuming that the ratio between fresh matter and dry matter is constant [3].

2.2.2. Blade geometry. We define the specific leaf weight (SLW) as the ratio of blade fresh weight to blade area. For a first approximation, the SLW is considered constant across plant developmental stages and across leaf ranks along the stem, although it varies within a small range [3]. The blade area of a leaf can be computed from its fresh matter content using the following relation:

\[ s_b = q_b / \varepsilon \]  

(5)

where \( s_b \) is the blade area; \( q_b \) is the blade fresh weight; \( \varepsilon \) is the SLW. Petiole sizes are not considered in this study, so the corresponding rules are not presented.

2.2.3. Internode geometry. In the model, piths and rings are identified as two different compartments. The pith grows in length and in diameter during a few cycles. The geometric shape for the pith is a cylinder. For the pith of volume \( V_p \), the corresponding length \( l \) and cross section \( \sigma \) of the pith are then computed according to the relation with two allometric coefficients \( b_p \) and \( a_p \) (cf. [3]):

\[ l = \sqrt{\frac{b_p}{\varepsilon} V_p^{1/b_p}}, \quad \sigma = V_p / l \]  

(6)

At each cycle, a new ring is added to the internode so its diameter grows at each time. As the distribution of the fresh matter is proved to be uniform [3] along a stem with length \( h \) and volume \( V_c \), the cross section area of the ring, \( s_r \), is uniform along the stem:

\[ s_r = V_c / h \]  

(7)

But its contribution to the increase of the radius for each internode depends on the radius before the ring was added, as shown by the following formula:

\[ r_i = \sqrt{r_{i-1}^2 + s_r / \pi} \]  

(8)

Where \( r_i \) is the radius at GC(i) while \( r_{i-1} \) is the radius at GC(i-1) for the internode.

2.2.4. Summary of crop parameters used in the model. Nine crop parameters (called hidden parameters) that are not accessible by direct measurement are optimized by fitting procedures. Four coefficients of relative sink strength correspond to four organ types (i.e., \( P_b, P_p, P_e, \) and \( P_c \) for leaf blade, petiole, pith, and ring, respectively); three beta function parameters are used to define the relative sink strength variation while aging for expanding organs (i.e., \( \alpha_b, \alpha_p, \) and \( \alpha_e \) for leaf blade, petiole and pith, respectively); two parameters (i.e., \( R_t \) and \( S_t \)) for biomass acquisition related to internal plant resistance to transpiration and Beer–Lambert’s law. The allometric parameters including \( \varepsilon \) (SLW), \( b_p \) and \( a_p \) (two shape coefficients of pith), as well as seed fresh weight, organ expansion time and leaf longevity were directly measured and input in the model.

2.3. Statistical analysis

To examine the effects of different leaf-pruning treatments on cotton plant growth and functional parameters of the GRENLAB model, we performed one-way analysis of variance (ANOVA) with leaf-pruning treatments and control plants as variables. Multiple comparisons of the levels of leaf-pruning treatments were performed using Tukey “Honestly Significantly Different” (HSD) test procedure. The statistical analyses were performed using the Statistics Toolbox Version 5.2 in MATLAB R2006a produced by The MathWorks, Inc.

3. Results and discussion

3.1. Field observations

No effect of leaf-pruning was found on the number of metamers developed at the end of experiment (one-way ANOVA, \( P = 0.21 \)), indicating that the cotton plant phyllochron did not significantly differ between treatments. The mean number of metamers developed by the plant was 36.5 ± 0.5 (mean ± s.e., \( n = 30 \)). The mean metamer production rate per thermal time that was calculated through linear regression on pooled data (0.0353 ± 0.0003°Cd⁻¹, mean ± s.e.) was used in the simulation (Figure 1).
Number of metamers developed

Thermal time (°Cd after emergence)

Figure 1. Number of metamers of cotton plant developed as a function of thermal time (base temperature at 15.5°C). Treatment is denoted by Tx (x = 6, 9, 12, 15) where x is the number of leaves retained on the top of plants; control plants are not subject to leaf removal.

Leaf-pruning treatments had significant effect on plant biomass production and partitioning among compartments (one-way ANOVA, P < 0.0001). Plants treated with 12 leaves retained produced significantly more fresh above-ground biomass than control plants, but not significantly different from T9 or T15 (Figure 2). Plant fresh weight for T6 was significantly lower than the other treatments, and for T15, T9 and control plants the differences were not significant (Figure 2).

Internode fresh weights for T12 and T15 were not significantly different from the control, but greater than T9. The T6 treatment plant had the lowest internode fresh weight (Figure 2).

The blade fresh weight for T12 was significantly greater than control plants, but not significantly different from T15 or T9 treatment. The blade fresh weight for T6 was less than T15, T12, and T9, but not different from the control (Figure 2).

The petiole fresh weight for the control was significantly less than T12, T9 and T6 (Figure 2).

Furthermore, fresh weight distributions along the stem for the top 12 organs clearly showed leaf-pruning effects (Figure 3). Internode (including both pith and secondary growth) had the lowest weight for T6 (Figure 3A): according to the internode diameters (not presented here) the secondary growth looked smaller, and moreover the stem profile was close to a cylinder instead of a cone shape for the other treatments. Both blade and petiole weights were the highest for T9 and T12 (Figure 3B & C). The control plant had the lowest petiole weights, and had also the lowest blade weights for leaves at the most top (Figure 3B).
Figure 3. Measured organ fresh weights for internode (A), blade (B) and petiole (C), respectively, on the top 12 metamers of the plant. Data are means ± s.e. (five replicates for each treatment). Treatment specifications are as in Figure 1.

The allometric relationship computation for pith length and cross section area used data from the top four internodes where the total diameters had weak contribution from the rings [3]. The sample means of $b_e$ increased with increasing the number of functional leaves retained on the plant: the highest value was for the control and T15, and the lowest was for T6 (Table 1). The value of $a_e$ did not differ significantly between defoliation treatments and the control (Table 1). These allometric parameter values cannot be predicted by the model until now.

Table 1. Effects of different defoliation treatments on allometric parameters

<table>
<thead>
<tr>
<th>Treatment</th>
<th>$\varepsilon$ $(10^{-2} \text{ g cm}^{-2})$</th>
<th>$b_e$ $(10^{-2})$</th>
<th>$a_e$ $(10^{-2})$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>3.42 ± 0.03$^a$</td>
<td>13.49 ± 0.44$^a$</td>
<td>-3.54 ± 1.18</td>
</tr>
<tr>
<td>T15</td>
<td>3.33 ± 0.04$^a$</td>
<td>12.28 ± 0.42$^a$</td>
<td>-7.82 ± 1.44</td>
</tr>
<tr>
<td>T12</td>
<td>3.16 ± 0.02$^b$</td>
<td>11.54 ± 0.39$^a$</td>
<td>-4.51 ± 1.35</td>
</tr>
<tr>
<td>T9</td>
<td>3.06 ± 0.01$^b$</td>
<td>11.09 ± 0.11$^c$</td>
<td>-3.86 ± 0.88</td>
</tr>
<tr>
<td>T6</td>
<td>2.73 ± 0.03$^c$</td>
<td>10.43 ± 0.22$^c$</td>
<td>-3.23 ± 2.65</td>
</tr>
<tr>
<td></td>
<td>$P$ &lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Note $\varepsilon$ is the mean specific leaf weight of the plant; $b_e$ and $a_e$ are two coefficients of the allometric relationship between the internode length and the internode section area. Data are means ± s.e. of five repetitions for each treatment. Probability ($P$) values denote significance levels from one-way ANOVA. Different superscript letters denote statistically significant differences between treatments ($P < 0.05$, Tukey HSD test after one-way ANOVA). Treatment specifications are as in Figure 1.

3.2. Analysis of variance on model parameters

Nine functional parameters were estimated through model inversion on five independent plants per treatment; each plant had four developmental stages of data to fit. Each parameter had five repetitions and five blocks [8]. Because sink strengths are relative, the coefficient of relative sink strength for blades ($P_b$) was set to 1 as reference. Functioning time for leaves was set to 20 GCs. Blade and petiole expansion times were set to linearly increase from 6 to 12 GCs from position 1 to position 10 (from first basal internode upwards) and to equal to 12 GCs for positions above 10. In this
case, leaves older than 12 GCs are no more sinks, but remain source organs.

The results of ANOVA on the optimized parameters showed that all functional parameters were found to be significantly affected by leaf-pruning interventions (Table 2). None of the defoliation treatments was significantly different from the control in the values of \( P_e \), whereas \( P_e \) for T15 and T12 were significantly higher than T9 and T6. Values of \( P_e \) increased with the decrease in the number of leaves retained: the lowest was for the control and T15, and the highest was for T6. Values of \( P_e \) were highest for T12 and T9 whereas the lowest was for the control. The range of variation for \( P_e \) remains fairly small among the treatments. Values \( \alpha_i \) for T15 and T12 were higher than the control and T6. No significant differences were found for both \( \alpha_i \) and \( \alpha_g \) among T15, T12, T9 and the control, whereas T6 had a lower \( \alpha_i \) and a higher \( \alpha_g \) than others. Values of \( R_t \) for T9 and T6 were higher than the control, but \( R_t \) not differed significantly between T12, T15 and the control. Values of \( S_e \) increased with the decrease in the number of leaves retained: the lowest was for T15, T12 and the control, the highest was for T6.

### 3.3. Plant growth prediction

We made simulation using the mean parameter values within each treatment to test plant average responses to leaf-pruning. The simulated fresh above-ground biomass had a similar pattern as the independent observation that were not used in model inversion for parameter estimation, although it was over estimated for T12, and lower estimated for T12 and T15 (Figure 4). Qualitatively speaking, the model parameters captured the major effects of leaf pruning; the shift in the simulation is possibly due to the simple averaging of parameters that doesn’t insure an average effect for a nonlinear model. Simulated cotton plant architectures with the GREENLAB model are shown in Figure 5.

### 3.4. Perspectives for model applications

A constant environment factor \( E \) was assumed through the course of plant growth and development for all treatments. As suggested in [8], linking the integral environment factor \( E \) to the potential evapotranspiration at GC duration may result in better reference variables as model inputs.

Because the model parameters were established upon plants having undergone regular defoliation, it is not assured to be true for other pruning scenarios. The underlying processes have to be taken into account for the parameter variations, so that the model can be of practical use for some specific purpose (e.g. plant structure optimization [11]).

### Table 2. Effects of different defoliation treatments on functional parameters optimized through fitting the GREENLAB model to plant architectural data

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Control</th>
<th>T15</th>
<th>T12</th>
<th>T9</th>
<th>T6</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( P_e ) (unitless)</td>
<td>0.184 ± 0.005(^b)</td>
<td>0.197 ± 0.006(^b)</td>
<td>0.197 ± 0.006(^b)</td>
<td>0.154 ± 0.003(^b)</td>
<td>0.165 ± 0.010(^b)</td>
<td>0.0002</td>
</tr>
<tr>
<td>( P_r ) (unitless)</td>
<td>0.348 ± 0.005(^a)</td>
<td>0.330 ± 0.010(^a)</td>
<td>0.363 ± 0.005(^b)</td>
<td>0.450 ± 0.016(^b)</td>
<td>0.762 ± 0.041(^c)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>( P_i ) (unitless)</td>
<td>0.119 ± 0.005(^a)</td>
<td>0.149 ± 0.004(^b)</td>
<td>0.167 ± 0.003(^b)</td>
<td>0.166 ± 0.003(^b)</td>
<td>0.130 ± 0.001(^b)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>( \alpha_c ) (unitless)</td>
<td>2.21 ± 0.16(^a)</td>
<td>3.02 ± 0.14(^b)</td>
<td>2.96 ± 0.25(^b)</td>
<td>2.44 ± 0.13(^b)</td>
<td>1.77 ± 0.04(^a)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>( \alpha_s ) (unitless)</td>
<td>4.11 ± 0.10(^a)</td>
<td>4.61 ± 0.12(^a)</td>
<td>4.38 ± 0.24(^b)</td>
<td>3.93 ± 0.20(^b)</td>
<td>3.30 ± 0.09(^b)</td>
<td>0.0002</td>
</tr>
<tr>
<td>( \alpha_p ) (unitless)</td>
<td>4.43 ± 0.15(^a)</td>
<td>4.51 ± 0.13(^a)</td>
<td>4.01 ± 0.13(^a)</td>
<td>4.39 ± 0.31(^a)</td>
<td>5.53 ± 0.13(^b)</td>
<td>0.0002</td>
</tr>
<tr>
<td>( R_t ) (m(^3) g(^-1))</td>
<td>45.69 ± 1.84(^a)</td>
<td>51.60 ± 1.69(^ab)</td>
<td>50.71 ± 1.72(^ab)</td>
<td>53.95 ± 2.75(^b)</td>
<td>56.56 ± 0.61(^b)</td>
<td>0.0070</td>
</tr>
<tr>
<td>( S_e ) (m(^2))</td>
<td>0.125 ± 0.005(^a)</td>
<td>0.162 ± 0.010(^a)</td>
<td>0.192 ± 0.011(^a)</td>
<td>0.302 ± 0.039(^b)</td>
<td>0.442 ± 0.018(^c)</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Parameter \( P_e, P_r, P_i, \) and \( P_c \) are coefficients of relative sink strength for blade, petiole, pith, and ring, respectively (\( P_b \) is set to 1 as reference); \( \alpha_c, \alpha_s \) and \( \alpha_p \) are beta function parameters for blade, petiole, and pith, respectively; \( R_t \) is coefficient for plant resistance to transpiration; \( S_e \) is light interception parameter for Beer–Lambert’s law. Data are means ± s.e. (five repetitions for each treatment). Probability (\( P \)) values denote significance levels from one-way ANOVA. Different superscript letters denote statistically significant differences between treatments (\( P < 0.05 \), Tukey HSD test after one-way ANOVA). Treatment specifications are as in Figure 1.
3.5. Discussion and Conclusions

Using a functional structural model that bears the inverse model to compute the source and sink relationships from plant architecture appears relevant especially to study the feedback between plant growth and plant architecture. We modified the plants’ structure by removing source organs; this altered both the plant production and the plant demand.

Regular leaf pruning had no effect on the organ production rate per unit thermal time, whereas strong effects were observed on biomass acquisition, plant organ sizes, and organ biomass profiles along the stem. The total fresh above-ground biomass produced by a plant was observed to be a single peak curve with respect to level of defoliation, and the peak appeared at the treatment with 12 leaves retained, which were significantly greater than control plants. The plants with six leaves maintained were the smallest. The biomass production for plants with 15 or nine leaves was not significant different from plants with 12 leaves or from control plants. Similar results have been obtained systematically on cotton plants in other pruning experiments done previously both in France and China, and they were at the origin of this more accurate study.

The fact that the control plant with all the leaves is smaller in terms of fresh biomass than the plant with 12 leaves retained on the stem looks strange, but it is a reliable result obtained several times. One possibility might be that the balance between shoot and root could be modified, but this is insufficient to explain the effect of the number of leaves on the partitioning at shoot level. So another possibility might be that the leaves could remain more sinks than sources, after 12 GC, but according to observations their expansions become negligible beyond this stage. In the simulation, for mature leaves the expansion time was fixed to 12 GC and the functioning time to 20 GC because the leaves don’t show degeneration until this stage. At last, the secondary growth could be the main factor: the greater the sink strength of the ring is, the more it reduces the plant growth. As a sink, the secondary growth competes with other organs by feedback, and consequently the biomass production is reduced in the following growth cycles.

Allometric parameters including SLW and one shape coefficient for internode pith were affected by leaf pruning. This kind of effect is not predictable by the GREENLAB model as it stands, and is a well known major issue in crop modelling. The results of analysis of variance on the functional parameters optimized through model inversion show that all the parameters were affected by leaf-pruning treatments, but from a statistical point of view, two parameters (i.e. $\alpha_b$ and $\alpha_p$) were stable between T15, T12, T9 and the control; four parameters (i.e. $P_e$, $P_p$, $R_1$ and $S_p$) were stable between T15, T12 and the control.

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