Jonas Coussement

Steps towards a functional-structural plant model of soybean

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Dr. ir. Tom De Swaef
ILVO
Prof. dr. ir. Kathy Steppe
Laboratory of Plant Ecology
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Ghent, June 2014

The promotors,

Prof. dr. ir. Kathy Steppe

Dr. ir. Tom De Swaef

The author,

Jonas Coussement
Preface

The subject of this thesis is situated in the field of functional-structural plant modelling. Although it is a field that has been receiving more and more interest over the past decade, this work is the first of its kind at the university of Ghent. Consequently, the main part of this document revolves around taking the first fundamental steps towards the creation of such a complex model for soybean. In order to make the reader familiar with the concepts of plant modelling and the rationale behind working with soybean, the first part of this thesis provides a concise but thorough introduction to both subjects. The second part of the document focuses on the creation of the model to its current state. It contains the methodology and thought process behind the creation of the model as well as illustrating the current capabilities. Lastly, a short overview is given of the most important processes that still require implementation along with the current approaches of doing so, based on literature.

However, the work presented in this thesis should by no means be accredited to myself alone. When I chose this topic, I already knew it was going to be challenging as I was going to be the only one in the university working on this project. For that reason I would like to thank prof. dr. ir. Kathy Steppe for giving me the opportunity to do so, entrusting me with a project she had been willing to take on for quite a while. When I eventually started this thesis ten months ago, I was still quite oblivious as to how to tackle the tasks that lay before me. Therefore, I would like to express my deep gratitude towards dr. ir. Tom De Swaef as he guided me from start to finish. Even while he was engaged in a multitude of other projects, he always found the time to patiently advise me whenever I found myself out of ideas. From helping me set-up the experiments up to proofreading multiple version of this document, it is safe to say that without him, this work would not have been the quality that it is today. I would also like to thank dr. ir. Peter Lootens for helping me set-up and guiding me through the process of image analysis. His expertise proved very insightful and lead me to pick up a variety of useful methods.

As we used GroIMP as the model basis, I would like to thank Michael Henke for taking the time to personally assist me in tackling a few problems with the platform that I couldn’t manage to solve myself. Also, prof. dr. Winfried Kurth and dr. Katarína Smoleňová for allowing me the chance to participate in the international summer school in Prague on “Modelling of Ecosystems by Tools from Computer Science” and the workshop “Functional-structural plant models in XL” even though I registered last-minute. I would also like to express my appreciation towards the organisation and teachers at the summer school, as it quickly provided me with a strong basis on plant modelling that would otherwise have taken me a long time to acquire by myself.
In a broader perspective, but therefore not less important, I would like to thank all of the friends who influenced my life in a major way over my years as a student. They have been the main reason I’ve enjoyed my life as a student as much as I have. Working alongside my friends in the praesidium of my beloved student union, the VLK, for so long has never been a drag and taught me valuable lessons that I will carry on with me for the rest of my life. My time on erasmus was also too precious not to mention here. It still baffles me how a short period of merely four months can have such an impact on someone, I’ve made friends for life there.

I would also like to express my gratitude towards my parents, Jan Coussement and Lieve Declercq, for allowing me the opportunity to pursue the studies I had chosen, even after a doubtful start. They’ve been a great support along the entire way. Also my brother, Jeroen Coussement, has been a great guide, especially in my early years as a student.

And last but not least, I would like to thank Wanda Pollet, my girlfriend and source of encouragement. She has always been there for me in the past three years and has been the biggest support anyone could ever wish for.

Jonas Coussement
June 2014
Abstract (English)

The purpose of a functional-structural plant model for soybean is the ability to simulate the three-dimensional plant growth based on environmental interaction, eventually becoming a tool to assess the feasibility of cultivating soybean in temperate regions such as Flanders. This thesis aimed to take the first steps towards such a complex model. The plant’s development was monitored by automated, continuous measurements of environmental variables combined with measurements concerning plant organ dimensions at frequent time intervals. The captured morphological data were used to infer growth curves, allometric relations and leaf shape descriptions which were incorporated in the construction of a structural model. This structural model was based on L-system formalism and allowed for comparative evaluations of the effect of light interception on certain scenarios affecting crop morphology. The simulated data on light interception were combined with the acquired environmental measurements to implement and calibrate a basic transpiration model. The result is a structured spatio-temporal model that can serve as a framework for the further development of a more complex functional-structural model for soybean.
Abstract (Nederlands)

De functie van een functioneel-structureel plant model voor soja is het simuleren van de drie-dimensionele plantengroei gebaseerd op de interactie met de omgeving. Hierdoor onstaat uiteindelijk een instrument die de haalbaarheid kan inschatten van het telen van soja in gematigde streken zoals Vlaanderen. Deze thesis was gericht op het nemen van de eerste stappen naar de ontwikkeling van zo een complex model. De ontwikkeling van de plant werd opgevolgd door automatische, voortdurende metingen van omgevingsvariabelen in combinatie met metingen aangaande de dimensies van de plantenorganen op frequente tijdstippen. Deze morfologische data werden gebruikt in het afleiden van de groefuncties, allometrische relaties en beschrijvingen van de bladvorm die in de constructie van het structureel model werden opgenomen. Dit structureel model was gebaseerd op het formalisme van L-systemen en liet toe om vergelijkende simulaties uit te voeren over het effect van een wijzigende gewasmorfologie op de lichtinterceptie. De gesimuleerde waarden van lichtinterceptie werden gecombineerd met de data van de omgevingsvariabelen om een eenvoudig transpiratiemodel te implementeren en te kalibreren. Het resultaat is een gestructureerd spatio-temporeel model dat kan dienen als kader voor de verdere ontwikkeling van een meer complex functioneel-structureel model voor soja.
# Table of Contents

Abstract (English) .................................................................................................................. vii
Abstract (Nederlands) .............................................................................................................. viii
List of abbreviations ................................................................................................................ xi
Introduction .............................................................................................................................. 1

## Part 1: Literature review

<table>
<thead>
<tr>
<th>Chapter 1</th>
<th>Functional-structural plant models ................................................................................. 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Introduction to functional-structural plant models ..................................................... 3</td>
</tr>
<tr>
<td>1.2</td>
<td>L-systems ................................................................................................................... 5</td>
</tr>
<tr>
<td>1.3</td>
<td>Relational growth grammars (RGG) ............................................................................... 8</td>
</tr>
<tr>
<td>1.4</td>
<td>Construction of a structural model .............................................................................. 9</td>
</tr>
<tr>
<td>1.5</td>
<td>The functional counterpart ......................................................................................... 11</td>
</tr>
<tr>
<td>1.6</td>
<td>Available modelling platforms .................................................................................. 12</td>
</tr>
</tbody>
</table>

## Part 2: The functional-structural plant model

<table>
<thead>
<tr>
<th>Chapter 3</th>
<th>Materials and methods ............................................................................................... 17</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.1</td>
<td>Raw data acquisition .................................................................................................. 17</td>
</tr>
<tr>
<td>3.2</td>
<td>Data processing .......................................................................................................... 18</td>
</tr>
<tr>
<td>3.2.1</td>
<td>Internodes ................................................................................................................ 18</td>
</tr>
<tr>
<td>3.2.2</td>
<td>Petioles ..................................................................................................................... 19</td>
</tr>
<tr>
<td>3.2.3</td>
<td>Leaves ....................................................................................................................... 20</td>
</tr>
<tr>
<td>3.3</td>
<td>Description of the modelling environment .................................................................. 21</td>
</tr>
<tr>
<td>3.3.1</td>
<td>The XL-programming language .................................................................................. 21</td>
</tr>
<tr>
<td>3.3.2</td>
<td>The GroIMP modelling platform ................................................................................ 23</td>
</tr>
</tbody>
</table>

## Chapter 4 | Results ......................................................................................................................... 25 |
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>4.1</td>
<td>Morphological differences in changing growing environment ..................................... 25</td>
</tr>
<tr>
<td>4.2</td>
<td>Morphological plant development .............................................................................. 26</td>
</tr>
<tr>
<td>4.2.1</td>
<td>Internode development .............................................................................................. 26</td>
</tr>
</tbody>
</table>
List of Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>FSPM</td>
<td>Functional-Structural Plant Model</td>
<td>1</td>
</tr>
<tr>
<td>PBM</td>
<td>Process-Based Model</td>
<td>3</td>
</tr>
<tr>
<td>RGG</td>
<td>Relational Growth Grammar</td>
<td>8</td>
</tr>
<tr>
<td>GDD</td>
<td>Growing Degree Days</td>
<td>12</td>
</tr>
<tr>
<td>GroIMP</td>
<td>Growth grammar-related Interactive Modelling Platform</td>
<td>12</td>
</tr>
<tr>
<td>PAR</td>
<td>Photosynthetically Active Radiation</td>
<td>17</td>
</tr>
<tr>
<td>XL</td>
<td>eXtended L-system language</td>
<td>21</td>
</tr>
<tr>
<td>R:FR</td>
<td>Red : Far-Red ratio</td>
<td>50</td>
</tr>
<tr>
<td>GREM</td>
<td>Gas and Radiant energy Exchange Model</td>
<td>51</td>
</tr>
</tbody>
</table>
Introduction

Plant models have acquired an important role in understanding plant growth and development in the last decades. Their primary strength is that they allow for the integration of knowledge and for the exploration of plant and plant systems behaviour beyond the conditions that can be covered experimentally. In the last decade however, a new approach emerged as a means to understand the driving physical and biological forces behind a plant’s development. So-called functional-structural plant models (FSPMs) accurately take the plant’s three dimensional architecture into account and allow for the integration of the fundamental plant processes on any chosen spatial scale. During this thesis, we will take the first steps towards the creation of an FSPM of soybean as a means to better understand soybean development in temperate regions. This knowledge can then be used to optimise breeding and crop management of soybean in Flanders.
Chapter 1
Functional-structural plant models

1.1 Introduction to functional-structural plant models

Ever since the start of agriculture, people sought out ways to improve the harvest of the lands they managed. Learning from trial and error, people learned how to best manipulate the environment (Vos et al., 2007). The resulting knowledge could then be applied to predict the effect of a certain factor on a given system (e.g. fertilisation on productivity). Computer modelling allowed for a far larger incorporation of factors in numerical calculations and has become a tool of historically unprecedented power (Vos et al., 2007). Plant models were developed as a key to better understand ecological processes and ecophysiological modelling has become an important field of research during the past decades (Dornbusch et al., 2007). The multitude of modelling approaches allow the arrangement of plant models in a triangle (Figure 1; Kurth, 1994b). Aggregated models at the top of the triangle, consider entire populations from a statistical point of view (i.e. regression analysis). They cannot produce a theoretically justified result, because the response is not based on the underlying theoretical processes within the plant or population (Sievänen et al., 2000). From aggregated models, one can opt for either a functional or a structural resolution. The functional resolution models the biological processes with a more in-depth approach to the functional relations. This results in so-called process models or process-based models (PBMs). The structural
resolution on the other hand, focuses on both the morphological differences in the plant’s structure and its development over time. Although several intermediate models have existed, the structural component remained largely absent from most of the common plant models in the past (Kurth, 1994). Around the mid-1990’s the integration of both types of models became more emphasised (Van Der Heijden et al., 2007).

PBMs focus mainly on the prediction of a single functional parameter, i.e. growth (Vos et al., 2007). Growth is merely a value in this case, absent of any morphological interpretation. Its size is the result of various physiological processes within the PBM, as an attempt to emulate the metabolism of the plant or tree as accurately as possible. The modelling was focused on processes like radiation interception, carbon and nitrogen assimilation and nutrient allocation and transport (Dornbusch et al., 2007). The most important shortcoming of the PBMs is the dependency of some the modelled processes on their spatial position and orientation within the plant and its environment. While not completely unaccounted for, PBMs address the plant’s structure in a simplified manner. With the assumption of horizontal homogeneity, vertical variation is estimated using statistical distributions based on quantities such as leaf area index or overall surface area (Dornbusch et al., 2007). When various position-specific interactions (e.g. collision of branches, accurate light interception by leaves, bending of branches due to gravity) become increasingly important, a 3D architecture is required and PBMs become less applicable (Sievänen et al., 2000).

FSPMs, sometimes also referred to as “virtual plants”, were developed as a combination of these PBMs with morphological models. FSPMs allow insight in the intense interactions between the plant’s morphological structure and the various physical and biological processes driving its development in space and time (Godin & Sinoquet, 2005). Once modelled, these complex interactions allow FSPMs to consider a plant’s response to environmental changes to be not only functional (e.g. photosynthesis, nutrient allocation) but also morphological (e.g. bud dormancy, growth towards light) which in turn causes a feedback loop on the conditions in which the functions operate (e.g. light) (Figure 2; Vos et al., 2010).

![Figure 2: Structure of an FSPM (Kurth, 1994).](image_url)
The first step in the creation of an FSPM is the development of the morphological structure of the plant. This structure can be made at various levels of complexity ranging from coarse descriptions of branching systems to accurate descriptions of each plant organ (e.g. internodes, leaves) (Godin & Sinoquet, 2005). Various studies have concluded that plants consist of a repetitive sequence of units called phytomers, with their evolution following a very specific set of ‘rules’ (reviewed in e.g. Room, Maillette, & Hanan, 1994). Therefore, it has become common practice for FSPMs to divide the plant in a collection of modules or nodes, which evolve on the basis of spatial growth rules (Sievänen et al., 2000). A programming language to translate this natural behaviour of plant growth has been developed by botanist Lindenmayer and has consequently been named after him as Lindenmayer or L-systems (Lindenmayer, 1975).

1.2 L-systems

The general idea behind the L-systems is the description of complex objects by the successive replacement of parts of a less complex initial object (Prusinkiewicz & Lindenmayer, 1990). These replacements are following a strict set of rewriting rules (or production rules). The absolute minimum requirement before rewriting can be applied is to have 2 shapes: one “initiator” and one “generator”. The initiator describes the shape of the initial object, to which rewriting rules will be applied. The generator describes a rewriting rule which will cause a change in shape to at least one part of the initiator (Mandelbrot, 1982). This idea is illustrated in the construction of a Koch snowflake (Figure 3; Koch, 1904). Another example can be provided as an illustration of a plant-like branching structure, generated by a simple rewriting mechanism in Figure 4.

L-systems operate as a rewriting mechanism on character strings (i.e. a word). In each production step, a substring is replaced by other strings following production rules (Kniemeyer, 2008). The production rules are intended to follow the natural behaviour in organisms where production can occur simultaneously in different parts of the organism. Therefore, the production

![First and second generation of the Koch snowflake](image_url)

**Figure 3:** Construction of the Koch snowflake (Prusinkiewicz & Lindenmayer, 1990)
rules in L-systems are all applied in a parallel and simultaneous fashion (in contrast to Chomsky grammars) (Prusinkiewicz & Lindenmayer, 1990; Kniemeyer, 2008). The easiest concept of an L-system is the deterministic and context-free **D0L-system**. Deterministic implies that every character string can result in only one other character string in a production step (and thus excludes randomness). Context-free indicates that the application of a production rule to a substring is not influenced by the substrings in its direct vicinity. A simple illustration of a D0L-system is as follows:

\[
A \rightarrow BA,
\]

\[
B \rightarrow A.
\]

If the initial string consists of simply “A”, subsequent production steps generate:

\[A \Rightarrow BA \Rightarrow ABA \Rightarrow BAABA \Rightarrow ABABAABA \Rightarrow \cdots\]

The application of L-systems to model higher plants requires these strings to have a geometric interpretation. This is done by the so-called “turtle interpretation” (Abelson & DiSessa, 1986). It can be seen as a metaphorical turtle, which possesses a position in a 2 or 3-dimensional space called the “turtle state”. Following a set of “turtle commands”, the position is modified and a graphic interpretation is created. These turtle commands can be simple movement commands (commonly represented as “F”) which cause the turtle to move in the current direction for a set distance, drawing a line as it goes. Other commands can be rotations, movements without drawing or the creation of other primitive shapes like cylinders, rectangles, etc. (Kniemeyer, 2008).

D0L-systems can only result in linear sequences, which are insufficient for modelling plant structures, since these are hardly ever linear. To account for the branching structures present in higher plants, a notation representing the appearance of such a branch is required. The bracket symbols “[” and “]” are commonly used to denote a branch in the turtle geometry. A sequence between these brackets is interpreted as stacked on top of the original sequence. Closing the brackets causes the turtle state to revert back to its original position (Kniemeyer, 2008; Prusinkiewicz & Lindenmayer, 1990). These L-systems are called **bracketed L-systems**. For example Figure 4 can be implemented as:

**Axiom = F**

\[F \rightarrow F/3 \>[L(30)\ F/3] \>[F/3 \>[R(30)\ F/3]]\ F/3\]

\[\text{Figure 4: Koch construction of plant-like branching structure (Prusinkiewicz & Lindenmayer, 1990)}\]
This translates directly into a transformation of a line segment “F” into a line segment of the same length, but having a branch at a 30 degree angle to the left side at one-third of its length, and a branch at a 30 degree angle to the right side at two-thirds of its length, both branches having one-third of the length of the original segment.

In contrast to the deterministic approach described above, in which simulations always generate the exact same result with artificial regularity, stochastic L-systems introduce interspecimen variations. Random effects can be added to both the turtle interpretation and the L-system itself even though the result is different. While introducing random effects in the turtle interpretation will cause only small variations in internode lengths, stem lengths or branching angles, the general topology will remain identical (Prusinkiewicz & Lindenmayer, 1990). Introducing random effects to the L-system means that a production rule has a certain chance to be applied. Thus, the same predecessor can result in a multitude of productions. Stochastic L-systems can be used to model processes for which the underlying physiological processes (which are deterministic) cannot be implemented (Kniemeyer, 2008). This can be for reasons of simplicity, lack of data or lack of knowledge.

The problem with the simple context-free systems described above is the inability to include a flow of information. Interactions between plant parts (e.g. flow of nutrients) can only be modelled if a context is added to the system, resulting in context-sensitive L-systems (Prusinkiewicz & Lindenmayer, 1990).

Another limitation of the previously described L-systems is their modelling power. Though they are able to describe a variety of interesting structures, their power is always limited by the fact that all lengths within the structure must be approximated to multiples of the smallest unit segment (Prusinkiewicz & Lindenmayer, 1990). Taking one step closer to the FSPMs, the problem becomes very apparent when trying to model development over time. The only way to capture continuous development with basic L-systems is the discretisation over time (Prusinkiewicz & Lindenmayer, 1990). This doesn’t only require a large number of symbols and productions, making the system lose its simplicity, it also doesn’t allow for processes like the smooth elongation of an internode to be modelled accurately (Kniemeyer, 2008). Parametric L-systems allow for numbers to be associated with the symbols. This also allows for the introduction of arithmetic expressions and mathematical functions as well as application conditions (e.g. \( F(x) < F(y) \rightarrow F(x \times 1.4) \) increases the length of a certain module by 40% if and only if it is currently shorter than \( F(y) \)) (Kniemeyer, 2008).

To model certain processes that can be described by differential equations, it is easier to incorporate the equations themselves within the L-systems, rather than a discretisation with a numerical solver. The result of so-called differential L-systems is the continuous development over time for a parameter value of a certain module in between the discrete points in time where topological changes (due to production functions) occur (Kniemeyer, 2008).

Several additional L-systems (e.g. table L-systems, environmentally-sensitive L-systems, open L-systems) have been developed for dealing with plant-environment interactions (Lindenmayer & Rozenberg, 1972; Prusinkiewicz et al., 1996; Mech & Prusinkiewicz, 1996). However these were still met with certain limitations caused by the basic structure of L-system formalism. Therefore, the basic data structure of L-systems was changed and environmental interactions (among others) were more easily incorporated in relational growth grammars.
1.3 Relational growth grammars (RGG)

RGGs were developed to overcome several limitations associated with L-systems and their extensions (Kniemeyer & Hemmerling, 2008; Kniemeyer et al., 2007; Kurth, 2007):

- Structures represented by a string of symbols can be useful for the modelling of tree-like structures but they become increasingly difficult when dealing with more complex topologies (e.g. on a cellular level). Additionally, there is no possibility to implement cycles or networks into the model.
- L-system generated structures can only include two direct relations: 'direct successor' and 'branch'. In the case of functional-structural modelling it can prove useful to have more relations at hand.
- Specification of simultaneous development of some structure on several different levels of resolution (i.e. multiscaled modelling) is not supported.
- No support is provided on whole-plant calculations (e.g. total available carbon)
- Strings have to be interpreted geometrically after production following turtle geometry (Abelson & DiSessa, 1986) which requires an extra step of processing.
- From a programming perspective, object-oriented programming is unsupported.

These shortcomings can be overcome by replacing the linear data structure of L-systems by a network of graphs, i.e. nodes connected by edges, whilst retaining the rule-based paradigm (Kniemeyer et al., 2007). This change in fundamental data structure leads to RGGs. This is a natural way to represent trees and networks in a consistent manner (Godin & Caraglio, 1998). The difference in representation with the linear sequences provided in L-systems is illustrated in Figure 5 (Kurth, 2007; Kurth, 2013) while also showing the possibility of different edgetypes. Apart from overcoming the limitations listed above, RGGs allow for the straightforward modelling of internal processes other than just structural components.

Figure 5: A relational growth grammar with L-system rule paradigm; (a) rule; (b) application. The dotted line on the left hand side does not match the rule because the nodes are connected with a different edgetype (Kurth, 2007; Kurth, 2013)
1.4 Construction of a structural model

The construction of a structural model requires information regarding the plant’s topology and geometry of the basic nodes. Topological data is the starting point of a structural model. It provides information about the physical connections between different types of plant components (Vos et al., 2010) and can be considered the framework for internal fluxes of mass, energy and other information (e.g. water transport) (Godin et al., 1999; Sperry et al., 1998). Geometrical data on the other hand, is more relevant to environmental exchange fluxes and resource capture (e.g. light interception) (Godin et al., 1999). It includes the shape, size and spatial orientation of the plant components. Information on the variances of these parameters in a model can also be used to implement some natural variability in the model, though some authors debate the meaningfulness of said results. As the stochastic variability is likely to be caused by correlating parameters still unsupported by the model (Mündermann et al., 2005).

The simulations of a developmental model occur in continuous time, which makes interpolation of experimental data inevitable. Fitting growth curves to the data is a widespread approach to assess this problem in plant modelling (e.g. Xu et al., 2011; Mündermann et al., 2005). The use of allometric relations (i.e. correlation between parameters such as height and width of organs) and the use of growth curves allow for a large reduction in the amount of independent variables in the model (Mündermann et al., 2005). Information about the time at which organs start to develop, the rate and duration at which they do is also required for both above- and below-ground development (Vos et al., 2010). Above-ground development can be related to the relative position within the structure. It has been show that the properties of phytomer components can show a gradient with phytomer ranks (Evers et al., 2005; Evers et al., 2007; Mündermann et al., 2005; Buck-Sorlin et al., 2005; Fournier et al., 1991). This allometric relation allows for another simplification of the model and a reduction in independent variables. The below-ground development requires information about the dynamics of the main root axis, lateral root branching, the type of roots that are formed as well as radial growth and root decay (Pagès et al., 2004) but falls beyond the scope of this thesis. Searching for patterns in the collected data is crucial for understanding the interaction between structure and function (Vos et al., 2010).

The capturing of geometric data is possible with a variety of equipment. The most basic of which involve using rulers and protractors to capture lengths and angles, but more advanced systems allow capturing of data using 3D-digitisers for plant parts or the plants as a whole (Sinoquet et al., 1997; Drouet, 2003; Evers et al., 2005; Dornbusch et al., 2007; Dauzat et al., 2008). These are so-called contact measurements and exist in contrast to non-contact point-cloud measurements (Van Der Heijden et al., 2007). Non-contact methods include laser triangulation (e.g. Kaminuma et al. 2004), automated measurements based on laser interception (Sinoquet & Rivet, 1997), volumetric intersection (de Visser et al., 2007) and stereo vision (Ivanov et al., 1995). All of these non-contact methods can only record the outline of the plant and may not contain enough information in some cases of high plant complexity. If this is the case, X-ray, CT- or MRI scans can be used to fully capture the 3D structure of the plant (Van Der Heijden et al., 2007).

For the description of internodes it suffices to get measurements of length and width at discrete timesteps and finding a logistic or bell-shaped growth function which provides the best datafit (e.g. the sigmoid Boltzmann function) (Vos et al., 2010; Mündermann et al., 2005). If an
allometric relation between length and width can be found, the fitted function will then provide a full description for the internodes shape over time due to their cylindrical nature (Mündermann et al., 2005). Data on leaf width and length can be fitted to a growth curve as well. Leaf shape can be obtained by data from outlines obtained with destructive measurements such as leaf scans (e.g. Evers et al. 2007; Mündermann et al. 2005; De Visser et al. 2007) or straight from positions recorded by a 3D-digitiser (e.g. Vos et al. 2010; Dornbusch et al. 2007). When data is obtained through destructive methods, size data can still be obtained with non-destructive methods, and the obtained shapes can be correlated with the remaining data (Mündermann et al., 2005). Once the shape is obtained, a function can be fitted to describe the contourdata as accurately as possible. A simple \textit{n}th-degree polynomal can be used to fit (Prévot et al., 1991) but meets problems when trying to interpret the parameters in terms of biological characteristics (Dornbusch et al., 2007). Spline curve interpolation (Figure 6; Mündermann et al., 2005) allows for a low interpolation error but is met with the same problem concerning parameter interpretation. Alternatively, functions can be derived where all parameters have a direct morphological interpretation. Dornbusch et al. (2007) proposed the following equation for maize leaves:

\[ b(s = s_i) = b_{\text{max}} \frac{b(a + s)(1 - s)^b}{(1 + a)b^{b+1}} \text{ with } (0 \leq s \leq 1) \]  

Here \( b_{\text{max}} \) represents the maximum leaf width, \( a \) and \( b \) are curvature parameters. The function describes the normalised leaf width in function to the normalised leaf length \( s \). Evers et al. (2006) proposed following function for spring wheat leaf blades:

\[ W_{\text{norm}} = \left( \frac{-L_{\text{norm}}(L_{\text{norm}} - 2L_m)}{L_m^2} \right)^c \text{ with } (0 \leq c \leq 1) \]

\( L_{\text{norm}} \) represents the normalised distance of the base to the leaf tip, \( L_m \) is the normalised position of the maximum width of the leaf blade and \( c \) is a curvature coefficient. In both cases, the remaining parameters allow a direct interpretation in terms of leaf shape traits.

![Figure 6: Spline curve interpolation to capture the leaf shape in Arabidopsis (Mündermann et al., 2005)](image-url)
The construction of a developmental model in terms of RGGs is relatively straightforward. The geometrical data contains all required information to model a collection of graphs (e.g. “Leaf”, “Internode”) that accurately represent the morphology of their real-life counterparts. The collected information regarding topology, time of appearance and plant and graph development over time can then be combined in the construction of production rules. The result is a plant model that develops according to L-system formalism and describes the plants morphological development over time.

1.5 The functional counterpart

The plant’s modelled architecture provides a framework into which interactions and processes can be simulated. Using RGGs as fundamental data structure allows for the flux of information between plant organs and their environment that is required to accurately model functional-structural relations (Buck-Sorlin et al., 2008). The origin of this information remains highly relevant to the ultimate success of FSPMs since they aim to show properties similar to real plants and behave in a similar fashion to allow for virtual experiments to be made (Godin & Sinoquet, 2005). Where field experiments flourish in their capability to make direct measurements, they are often constrained by time, cost and feasibility issues. Virtual experiments can become superior in the cases where these constraints become overwhelming or where direct measurements are simply impossible to make. One example is the accurate model estimations on light sharing at intra-canopy scale of trees, where direct measurements with light sensors scattered in the canopy cannot be made (Allen et al., 2005). Therefore it is important to the relevance of FSPMs that the underlying mechanisms and interactions are fully understood and can be modelled to provide the required information and influence on growth dynamics. Some of these key processes include: photosynthesis and light extinction, water and heat balance and carbohydrate source-sink interactions (Van Der Heijden et al., 2007). Whenever possible, the confidence of the eventual modelling results should then be validated with field or lab experiments (Godin & Sinoquet, 2005).

Based on the plant’s architecture, modelling light interception still requires the reflection, absorption and transmission characteristics of the different plant parts. These characteristics can be obtained by the use of spectrophotometry (Van Der Heijden et al., 2007) and will not only influence fundamental processes like photosynthesis and transpiration but also determine the rate of light extinction below the canopy. Implementation of process-models for photosynthesis, transpiration, growth and respiration can be done with approaches designed for process-based modelling (Vos & Heuvelink, 2006; Vos et al., 2010) as their accuracy will automatically improve due to the finer spatial scale into which the processes are modelled (e.g. photosynthesis calculations on the scale of a single leaf, rather than the entire crop).

When recording the geometrical and topological data during the plant’s development for the creation of an FSPM, a detailed and continuous description of the experimental environment conditions is mandatory (Van Der Heijden et al., 2007; De Reffye & Hu, 2003). This is a requirement in order to synchronise the interactions between function and structure. The type of measurements required (e.g. light conditions, development of relative humidity) depends on the functional
processes (e.g. photosynthesis, transpiration) that will be implemented, which in turn depend on the aim of the model (Tardieu, 2010; Van Der Heijden et al., 2007). Since crop growth is often expressed in terms of growing degree-days (GDD) (e.g. soybean: Kumar et al., 2008; Nafziger, 2013; Jégo et al., 2010) which are dependent upon temperature conditions during development, the logging of temperature conditions near the crop canopy is a basic requirement.

Increasing the number of process-models (and their complexity) in the model can improve the model accuracy but is met with certain disadvantages: i) more measurements must be made due to a rising number of parameters (Van Der Heijden et al., 2007; De Reffye & Hu, 2003), ii) the measurements are more complicated to conduct due to the required precision (De Reffye & Hu, 2003), iii) increased difficulty of calibration may require new techniques that go beyond standard parameter fitting (Buck-Sorlin et al., 2008; DeJong et al., 2011). Consequently, the model complexity should be based on the model goals (Tardieu, 2010; Van Der Heijden et al., 2007).

1.6 Available modelling platforms

The modelling of an FSPM requires a platform that ideally integrates the following functions (Vos et al., 2010): i) availability of suitable templates to model plant organs and the structural development of the plant; ii) accurately simulating light conditions and light absorption based on the light characteristics of the elemental structures. Ideally, simulating different wavelengths should also be possible; iii) allow calculations of process-models on the scale of the elemental structures (e.g. leaf photosynthesis) as well as whole plant calculations (e.g. total plant transpiration); iv) allow the simulation of mass-transfer throughout the plant structure (e.g. carbon allocation, water transport); v) the ability to generate advanced visual output.

Several platforms are have been developed for FSPM. L-Studio is the most universally used platform (Pradal et al., 2008; Vos et al., 2010). Programming in L-studio is based on L-system formalism using the modelling language L+C (Prusinkiewicz et al., 2007). VLab is another platform designed by the same group of L-studio but specifically for Linux systems (Federl & Prusinkiewicz, 1999). GroIMP (Growth Grammar-related Interactive Modelling Platform) makes use of XL which is a programming language based on RGGs specifically made to model FSPMs (Kniemeyer et al., 2007). Modelling of FSPMs is also possible in other platforms, even though they are not all specifically designed for plant modelling. The FSPM GreenLab (Yan et al., 2004) can be implemented in Matlab (Kang et al., 2008) or Scilab (its open source equivalent). The applications of GreenLab have also been translated to the language C++ in the software Digiplante (Christophe et al., 2008; Mathieu et al., 2009). However, the reusability of the code of existing FSPMs would benefit future research, which is hindered by the usage of this large variety of programming languages (Buck-Sorlin et al., 2008; Pradal et al., 2008; Vos et al., 2010). To resolve this issue, OpenAlea is an open-source platform that is being developed as an attempt to homogenise FSPM development to encourage interaction, reusability and comparison between models of different authors (Pradal et al., 2008).
Chapter 2
Soybean

2.1 General growth dynamics and morphology

Soybean (*Glycine max* (L.) Merrill) is native to eastern Asia. It has an optimum growing temperature between 20°C and 30°C and grows significantly slower beyond those boundaries (Rüdelsheim & Smets, 2012). It is a legume that fixes nitrogen via symbiosis with *Bradyrhizobium japonicum* causing formation of nodules in the roots. The development of soybean can be described by a universal system, independent of genotype or environment (Table 1). Introduced by Fehr et al. (1971), this system is now universally accepted and used because of its standardised descriptions and objective nature (e.g. Bastidas et al., 2008; Lion, 2007; Liu et al., 2006; Nafziger, 2013). The objectiveness of the system lies in the fact that vegetative stages and reproductive stages are described separately and independently. While flowering is initiated by environmental conditions, mainly day and night length, the exact environmental factors that trigger flowering depends on the genotype (Hamner, 1969). Therefore, flowering can occur at a variety of vegetative stages, from as early as 4 nodes, or as late as 18 nodes on the main stem (Fehr et al., 1971). The vegetative stages are preceded by V and are determined by counting the number of nodes on the main stem (starting with the unifoliate node) that have or have had a completely unrolled leaf. A leaf is counted as

<table>
<thead>
<tr>
<th>Stage n°</th>
<th>Vegetative stage descriptions.</th>
</tr>
</thead>
<tbody>
<tr>
<td>V1</td>
<td>Completely unrolled leaf at the first unifoliate node.</td>
</tr>
<tr>
<td>V2</td>
<td>Completely unrolled leaf at the first node above the unifoliate node.</td>
</tr>
<tr>
<td>V3</td>
<td>Three nodes on the main stem beginning with the unifoliate node.</td>
</tr>
<tr>
<td>Vn</td>
<td>n nodes on the main stem beginning with the unifoliate node.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Stage n°</th>
<th>Reproductive stage descriptions</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1</td>
<td>One flower at any node.</td>
</tr>
<tr>
<td>R2</td>
<td>Flower at node immediately below the uppermost node with a completely unrolled leaf.</td>
</tr>
<tr>
<td>R3</td>
<td>Pod (0.5 cm long) at one of the four uppermost nodes with completely unrolled leaf.</td>
</tr>
<tr>
<td>R4</td>
<td>Pod (2 cm long) at one of the four uppermost nodes with completely unrolled leaf.</td>
</tr>
<tr>
<td>R5</td>
<td>Beans begin to develop (can be felt by squeezing) at one of the four uppermost nodes.</td>
</tr>
<tr>
<td>R6</td>
<td>Pod containing full size green beans at one of the four uppermost nodes.</td>
</tr>
<tr>
<td>R7</td>
<td>Pods yellowing; 50% of the leaves yellow. Physiological maturity</td>
</tr>
<tr>
<td>R8</td>
<td>95% of the pods brown. Harvest maturity.</td>
</tr>
</tbody>
</table>
completely unrolled when the leaf in the node directly above it has developed sufficiently so that the leaf edges no longer touch. The unifoliate node is the first node above the seedlings’ hypocotyl and is characterised by the development of two unifoliate leaflets at a position directly opposite from one another (Figure 7). From the second node onwards, the developing leaves are trifoliate with one leaf per node in alternate positions. The reproductive stages are marked with R and are described in Table 1. Figure 7 provides an example of a V3 soybean plant. Even though there are five nodes present (i.e. one unifoliate and four trifoliate), only three are counted as fully developed due to the leaf edges of the fourth trifoliate leaf still touching.

2.2 Effects of external changes on growth dynamics and morphology

The planting date of soybean can have a strong influence on the soybean morphology. Early sowing leads to a larger total amount of nodes but also results in shorter internodes at nodes 3 to 9 (Bastidas et al., 2008). Soybean requires about six weeks of warm weather for sufficient development before flowering is induced (Nafziger, 2013). Sowing too late induces early flowering and significantly reduces yield (Bastidas et al., 2008; Nafziger, 2013). Because flowering is induced by photoperiodism (see 2.1), the combination of a region’s length of day and temperature will determine the optimal sowing date and the optimal variety to achieve the highest yield (Rüdelsheim & Smets, 2012). The presence of external light sources such as street lights, can greatly delay flowering (Nafziger, 2013). Light enrichment in the late vegetative stages or reproductive stages results in a significant increase in seed yield, differing depending on the time of light enrichment (Mathew et al., 1995).

Figure 7: A soybean plant at stage V3. The cotyledons are followed by the unifoliate leaves, after which only trifoliate nodes develop. Note that the edges of the fourth trifoliate leaf (at the fifth node) are still touching. Consequently, the fourth node is not counted as having a completely unrolled leaf (Nafziger, 2013).
2.3 Issues of tropical soybean production

International demand for soybean has been rapidly increasing over the past decades and soybean cultivation is expected to expand even further in the coming decades (Smaling et al., 2008). In terms of both volume and value, soybean is currently the most important agricultural crop in the world (Bertheau & Davison, 2011). The reason is that soybean is not only a major booming oil crop, it also offers a protein-rich meal as a by-product (Smaling et al., 2008). Increasing global demands have been an incentive for extensive soybean cultivation in tropical areas, mainly in South-America (e.g. Brazil, Argentina, Paraguay, Bolivia), where the land is cheaper (Fearnside, 2001; Bertheau & Davison, 2011). Brazil is currently one of the world leaders in soybean production with a planted area of approximately 23 million hectares (up from 1 million in 1970), making them second only to the United States (Garrett et al., 2013). This has lead to a large-scale increase of land conversion and deforestation in Brazil (Fearnside, 2001; Smaling et al., 2008). A combination of environmental issues (e.g. Amazon deforestation, GHG emissions and ecological footprint of long distance import, use of genetically modified varieties and excessive pesticide in exporting countries), economical issues (e.g. the development of market niches, the increase of American soybean export to China inducing tension on the prices, the absence of alternative protein-rich crops in Europe in combination with the continuous rises in nitrogen fertilizer prices) and social issues (e.g. willingness to reduce the dependence on import) has been an important stimulus for many European countries to promote local soybean cultivation (Fearnside, 2001; Smaling et al., 2008; Van Waes et al., 2013; Bertheau & Davison, 2011).

2.4 Rationale behind the development of a soybean FSPM

As soybean cultivation is still at its earliest stages in Flanders, further research should show whether Flanders can maintain a sustainable production of soybean. Since the Flemish situation is characterised by lower temperatures and a shorter growing season compared to (sub-)tropical regions, focus should especially be put on the early ripening genotypes (Van Waes et al., 2013). However, the successful introduction of soybean will require a more thorough understanding of the crop-environment interactions.

Our goal in the development of a soybean FSPM is to create a useful tool that describes the plant’s development as realistically as possible while incorporating progressively more internal plant processes at increasingly detailed levels of representation. Such a tool could then be used to indentify the crucial traits related to crop yield (Model & Pine, 2013) in temperate regions like Flanders and consequently guide the current soybean breeding programs towards optimisation. It would also allow for the optimisation of the management regime in silico (e.g. Fournier et al., 2007; Vos et al., 2010; Buck-Sorlin et al., 2005) and could evaluate the feasibility of growing soybean in Flanders. Such simulations could be a cost-effective and fast alternative to expensive and time-consuming experiments (Vos et al., 2010; Godin & Sinoquet, 2005).
One could argue the added value of developing such a complex soybean FSPM for yield optimisation when several soybean crop models have already been developed (e.g. Jones et al., 1989; Jégo et al., 2010; Mohanty et al., 2012). However, in the one-dimension approach used in crop models, plants are not described individually thus limiting the amount of impact factors that can be simulated. Whereas photosynthesis in an FSPM-based crop simulation is based on the individual plant characteristics (e.g. leaf orientation and water-status (gravitropy), leaf chlorophyll content, plant topography), crop models merely base their estimates of light interception on canopy depth, using light-response curves or a radiation use efficiency factor (Evers et al., 2010). This limits the use of crop models for predictions in which individual plant structure is a determinant factor. Therefore, this thesis aimed to take the first steps in the creation of a complex FSPM for soybean.
Chapter 3
Materials and methods

3.1 Raw data acquisition

Soybean (Glycine max (L.) Merrill) seeds of three varieties (Kent, Fiskeby V and GL Hermine) were sown in 5 liter pots at a rate of three seeds per pot on 2 August 2013, and grown in the greenhouse at the ILVO site (50°59'33.3"N 3°47'04.9"E). Because the ‘Kent’ variety was chosen for accurate development observations, 100 pots were sown. The other two varieties were grown for comparison reasons for which 20 pots per variety sufficed. On germination, the seedlings were thinned to one per pot while optimising size and age uniformity. One month after germination, the plants were loosely attached to sticks to prevent lodging.

Six plants of the ‘Kent’ variety were manually measured two to three times per week to record internode length, petiole length and leaf length and width. After the measurements, all six plants were photographed from the side at every 60 degree angle with a digital camera (type D60, Nikon, Tokyo, Japan).

Air temperature and relative humidity were automatically registered with an integrated relative humidity sensor (Type HIH-3605-A, Honeywell, Morristown, NJ, USA), inserted in an aspirated radiation shield. Incoming Photosynthetically Active Radiation (PAR) was recorded with a quantum sensor (Li-190S, Li-COR, Lincoln, NE, USA) placed above the canopy. Transpiration data was automatically assessed by continuously monitoring the weight of twelve plants with a digital weighing scale (Type WLC 12/90/30/C1/R, Henk Maas, Netherlands). All sensor and weighing scale data were logged with a custom-made datalogger at 10-s intervals and stored 5-min averages. To obtain leaf shapes, three plants of the ‘Kent’ variety and one of each other variety were selected and dissected every week.

During development, the greenhouse-grown plants showed extensive internode elongation resulting in a plant habitus substantially differing from field-grown soybean plants. Therefore we conducted a second experiment. Plants were sown in 96 pots and thinned after germination as before. Germination and full plant development occurred in the phytotron under fully controlled circumstances (i.e. constant daily pattern: $T_{\text{min}} = 15^\circ\text{C}$; $T_{\text{max}} = 27^\circ\text{C}$; Daylength = 16h; $\text{PAR}_{\text{max}} = 800 \mu\text{mol PAR m}^{-2}\text{s}^{-1}$; $\text{RH}_{\text{min}} = 35\%$; $\text{RH}_{\text{max}} = 80\%$). Data on transpiration, relative humidity, incoming PAR, temperature, photosynthesis, leafshape and other geometric dimensions were obtained as in the
greenhouse experiment. We chose to focus model calibration on data from the phytotron-grown plants. Data from the greenhouse could then still be used for comparison.

### 3.2 Data processing

To capture the acquired morphological and physiological data in the plant model, these data need to be described by mathematical equations. For the morphological part of the model, we represented the soybean plant as a succession of phytomers exhibiting similar properties, preceded by the hypocotyl and its two cotyledons (Figure 8). The first phytomer in soybean plants is unique, as it is characterised by two unifoliate leaves with an opposite arrangement. From the second phytomer onwards, a single trifoliate leaf arises, forming an alternate pattern. The continuously acquired temperature data in the phytotron were used to calculate the total growing degree days (GDD) at each time a measurement was made. To determine the GDD, the soybean plants were assumed to have a base temperature of 10°C (Kumar et al., 2008).

![Figure 8: Deterministic schematic build-up of the soybean model from two angles. Phytomers are labelled from 0 to 7. P₀ represents the hypocotyl and cotyledons and P₁ the unifoliate phytomer. P₂ to P₇ represent the trifoliate phytomers.](image)

#### 3.2.1 Internodes

Due to the lack of variation in internode width during growth, it was assumed constant. Consequently, internode growth and scaling were based solely on internode length. The sigmoid Boltzmann function (Eq 3.) was fitted to the data to represent growth in continuous time for each internode rank independently:

\[
L(t) = \frac{L_{\text{max}}}{1 + e^{-\alpha(t-t_{\text{half}})}}
\]
where \( L(t) \) represents length [mm] at age \( t \) [GDD], \( L_{\text{max}} \) is the maximal and final internode length [mm], \( t_{\text{half}} \) represents the time at which the internode reached half of its maximal length [GDD] and \( \alpha \) is the specific growth rate [dimensionless]. To estimate the phyllochron (i.e. time interval between the development of successive phytomers), the time at which the internodes reached a size of 1 mm was calculated from the fitted growth curves and averaged (Figure 9).

![Graphs showing internode length development over GDD](image)

Figure 9: The phyllochron is determined by averaging the time of appearance of consecutive internodes. The time of appearance was calculated based on (a) the sigmoid growing curves as the time at which the internode reached a length of 1 mm. (b) is a zoomed image of (a) focussing closer on the phyllochron.

### 3.2.2 Petioles

Similar to the internode dimensions, the width of the petioles was assumed constant and the length development was fitted to the sigmoid Boltzmann function (Eq. 3). In case of the trifoliolate leaves, only the development of the main petiole was fitted (Figure 10 b). The smaller petiole sections to which the centre and side leaflets are connected (Figure 10 c, d) were assumed to be a constant proportion of the main petiole. An allometric relation between petiole length and leaf rank was used.

![Components of the trifoliolate leaf petioles](image)

Figure 10: Components of the trifoliolate leaf petioles: (a) raw image, (b) main petiole, (c) centre petiole, (d) side petioles
3.2.3 Leaves

Leaflet shapes were assessed by means of image analysis. A simplified scheme of the entire process is shown in Figure 11. Using Adobe® Photoshop® CS4 Extended, the trifoliate leaf scans were manually separated in their three single leaflets and rotated to align the central vein of each leaf with the x-axis. Then, discrete datapoints describing the leaflet shape were retrieved with an automated script in WiT®. The script ran the following processes: i) read image; ii) remove background by setting a threshold value based on the green values of the scan; iii) convert to binary image; iv) remove noise by eroding and dilating; v) project image on x-axis; vi) find the maximum width (from both ends if multiple maxima); vii) split data on the average position of the max width (see step vi); viii) write two separate .csv files containing the width of the leaflet and position on the central vein from petiole to the maximum width, and from maximum width to leaf tip respectively.

Fitting of leaflet shape curves was done with a script in Matlab®. The proposed function in Evers et al. (2006) (Eq. 2) was designed for wheat leaves and while the function in Dornbusch et al. (2007) (Eq. 1) was designed to allow a more general leaf shape description, it was created using barley leaves as a standard. They both proved useless for soybean leaves. Consequently, a fourth degree polynomial was fitted on the normalised leaf shape as suggested in Prévot et al. (1991). Leaflet shape was assumed constant with age but dependent on leaf rank. In the case of trifoliate leaves, the centre and side leaflet’s shapes was also considered different. The polynomial was forced through three points during the fit, i.e. (0,0), (xAtMaxWidth, 1) and (1,0) to guarantee that the maximal leaf dimensions were not exceeded by the polynomial’s shape. The resulting function is of the form:

\[ W_{\text{norm}}(L_{\text{norm}}) = a_1 L_{\text{norm}}^1 + a_2 L_{\text{norm}}^2 + a_3 L_{\text{norm}}^3 + a_4 L_{\text{norm}}^4 \]  

(4)

Figure 11: Simplified scheme of the process of acquiring the leaflet shape functions
\( W_{\text{norm}} \) and \( L_{\text{norm}} \) represent the normalised leaf width and length respectively, with \( 0 \leq W_{\text{norm}}, L_{\text{norm}} \leq 1 \). The parameters \( a_1, a_2, a_3 \) and \( a_4 \) are determined by the best possible fit.

Leaflet length and width data were obtained from a combination of non-destructive measurements on four phytotron-grown plants and the destructive measurements from the leaf scans from which the shape was obtained. The length-to-width ratio was assumed constant with age but dependent upon rank. The development of the leaflet length was again fitted to the sigmoid Boltzmann function (Eq. 3) and the width development was taken from the constant length-to-width ratio. Maximum leaflet length was considered dependent upon the rank and the position of the leaflet (i.e. centre or side leaflet) in trifoliate leaves resulting in two allometric relationships. These relationships describe the change in maximal length of the leaf considering its rank for the centre leaflet and for the side leaflets separately. Leaf area calculations were also based on image analysis. Using the leaflet data upon which the shape curve was fitted, the total area of each leaflet was calculated in Matlab®.

### 3.3 Description of the modelling environment

#### 3.3.1 The XL-programming language

A developmental model for soybean, based on the measurements presented above, was written in the RGG (see section 1.3) based language XL (Kniemeyer et al., 2007). eXtended L-system language (XL) is defined as an extension of Java (Figure 12) which provides the language with well-established concepts of structured, modular and object-oriented programming (The XL-programming language, 2006). Another added benefit of being an extension of Java is that all existing Java libraries are immediately accessible. Therefore, the XL-language requires some familiarity with the Java programming language. XL provides support for the basic turtle commands to establish geometrical forms. Some basic relevant commands are:

- \( \text{M}(x) \) Move forward without drawing for a length \( x \);
- \( \text{F}(x,y) \) Move forward while drawing a line of length \( x \) and diameter \( y \);
- \( \text{RL}(x) \) Rotation by \( x \) degrees around the “Left” axis (y-axis);
- \( \text{RU}(x), \text{RH}(x) \) Analogue rotations around the “Up” (x-axis) and “Head” axis (z-axis);

![Figure 12: The basic structure of XL (Kurth, 2013).](Image)
- RV(x) Rotation towards the ground (gravitropism) with strength x;
- Sphere(x) Draw a sphere with radius x with its centre at current position;
- Cylinder(x,y) Draw a cylinder of length x and diameter y (same result as F(x,y));
- Box(x,y,z) Draw a box of length x, width y and height z.

As an alternative to working with the basic movement and structural commands, modules can be defined to allocate a geometric interpretation to a string. These modules are the basic structure of building a model in XL since they are not limited to holding geometrical parameters. As an example the following module transforms the string “Internode(x,y,z)” into a cylinder of length x and fixed diameter of 2 mm while holding the values age (y) and rank(z).

```java
module Internode(supertype, length, double age, int rank) extends Cylinder(length, 0.002);
```

The values for age and rank can be used for model calculations (e.g. calculating the current length depending on the age), contextual or conditional productions (e.g. in soybean an internode of rank one produces unifoliate leaves while other ranks produce trifoliate leaves) or identification purposes.

A production rule implemented in the XL-language is traditionally split in a left-hand and a right-hand side. Left-hand sides are queries, which define the graph and its context as well as the condition at which it must be rewritten. The right hand side is the actual production rule (Kniemeyer, 2008). An overview and the syntax are given in Figure 13. In order to make production rules readable by any XL-compiler (e.g. GroIMP) the rules should be stated within the construction of a “public void run” form and the initial statement within “protected void init”. The production of a simple Koch snowflake (Figure 3) can be done accordingly:

```java
protected void init() {
    Axiom ==> F(1) RU(120) F(1) RU(120) F(1);
}

public void run() {
    F(x) ==> F(x/3) RU(-60) F(x/3) RU(120) F(x/3) RU(-60) F(x/3);
}
```

![Figure 13: Syntax of an XL rule. The effect of this rule is to transform any L in the right positional context C (and only when E is evaluated as true) into R whilst executing P (Kurth, 2007).](image)
Context is given between (* ... *) in XL and provides a way to create a context sensitive transformation. Conditions can be defined after defining the context. Conditions should be put between brackets. The following production rule:

\[(A \, B(x) \, C) \, (x < 5) \implies D\]

will transform B(x) into D, only if B(x) is a successor of A and a predecessor of C and x < 5.

Rules can be used to transform and create graphs. Queries are used to search within an existing graph for a certain feature. They are specified with a pattern and find all matches of that pattern within the graph (Kniemeyer, 2008). Queries can contain conditions based on attributes and edgetypes and are written between (* ... *) similar to context sensitive rules. They can be used to make model calculations in which not all elements should be counted. Some examples are:

\[
\begin{align*}
(*) \text{ Internode} (*) \\
\text{count}((*) \text{ Internode} (*) ) \\
\text{sum}( (+i: \text{ Internode} (*) )[\text{length}]) \\
\text{sum}( (+i: \text{ Internode}, (i, \text{age} \leq 10) *)[\text{length}])
\end{align*}
\]

The first statement is a query in which all “Internode” classes are selected. The second statement will return the number of “Internode” classes found and the third returns a value equal to the summed length of all “Internode” classes. The fourth statement is similar to the third, but adds the condition that a class “Internode” should only be selected if its age is less than 10.

### 3.3.2 The GroIMP modelling platform

GroIMP is an integrated platform that combines modelling, visualisation and interaction. It is designed for the purpose of functional-structural plant modelling and provides several features that make it very suitable program for doing so (Kniemeyer et al., 2007; Kniemeyer, 2008):

- The programming language of XL is fully integrated.
- A full set of 3D-geometric classes is provided. This includes the basic turtle commands, basic shapes (e.g. spheres, boxes, cones, frustrums), height fields and spline surfaces (NURBS, Piegl & Tiller, 1997).
- Several light models are readily implemented.
- The model outcome can be readily visualised within GroIMP using OpenGL.
- After visualisation, interaction with the model is possible by selecting, deleting or modifying elements.
- GroIMP is open-source software. It is freely available at [http://www.grogra.de/](http://www.grogra.de/)
- A 2D representation of the basic data structure (i.e. RGG) is possible.
Chapter 4  
Results

4.1 Morphological differences in changing growing environment

Clear differences in soybean plant morphology were observed between field-grown and greenhouse-grown plants (Figure 14). Greenhouse-grown plants showed extensive internode elongation which resulted in lodging. All three observed genotypes were affected by this behaviour. This extensive elongation was not observed in field-grown soybean (from other ILVO field trials) causing them to be less prone to lodging. The difference in internode length between the soybean plants grown in the phytotron and the greenhouse are given in Table 2. The internodes at lower ranks were significantly shorter when compared to the greenhouse grown plants (p < 0.001 for the lowest two ranks, p < 0.05 for rank three). At higher ranks, the internode ranks no longer differed significantly.

Figure 14: Differences in internode elongation between (a) phytotron-grown and (b) greenhouse-grown plants. The plants are shown at the same scale.
Table 2: Differences in maximal internode length (in mm) in phytotron and greenhouse-grown plants.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Phytotron Average</th>
<th>Phytotron STD</th>
<th>Greenhouse Average</th>
<th>Greenhouse STD</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>44.25</td>
<td>9.60</td>
<td>73.67</td>
<td>7.81</td>
</tr>
<tr>
<td>2</td>
<td>28.75</td>
<td>5.97</td>
<td>64.67</td>
<td>3.45</td>
</tr>
<tr>
<td>3</td>
<td>37.75</td>
<td>5.19</td>
<td>44.50</td>
<td>5.40</td>
</tr>
<tr>
<td>4</td>
<td>37.75</td>
<td>5.00</td>
<td>40.83</td>
<td>6.68</td>
</tr>
<tr>
<td>5</td>
<td>40.25</td>
<td>6.18</td>
<td>46.50</td>
<td>7.15</td>
</tr>
<tr>
<td>6</td>
<td>52.00</td>
<td>21.95</td>
<td>28.83</td>
<td>29.85</td>
</tr>
<tr>
<td>7</td>
<td>34.25</td>
<td>20.43</td>
<td>12.00</td>
<td>29.04</td>
</tr>
</tbody>
</table>

4.2 Morphological plant development

4.2.1 Internode development

A phyllochron of 37 GDD was found as the constant rate of phytomer appearance in the vegetative state. Fitted sigmoid growth curves (Eq. 3) described the internodes length data reasonably well (especially the middle ranks (3-5)) and provided rank-dependent parameter values (Table 3). These parameters thus describe growth in continuous time from the moment the internode is formed. Because no significant trend was found in the maximal length ($L_{max}$) or relative growth rate ($\alpha$) they were assumed constant (Figure 15 b,c). A clear rank-dependent trend was found for the time when the internode reached half of its maximal length ($t_{half}$) (Figure 15 a). The linear regression for $t_{half}$ has an $R^2$ of 0.83 and up to 0.99 when the values of internodes six and seven are considered to be outliers (which can be justified due to the low $R^2$ of the sigmoid fit).

Table 3: Sigmoid parameters for internode growth.

<table>
<thead>
<tr>
<th>Internode rank</th>
<th>$t_{half}$</th>
<th>$L_{max}$</th>
<th>$\alpha$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>43.95</td>
<td>43.98</td>
<td>0.061</td>
<td>0.81</td>
</tr>
<tr>
<td>2</td>
<td>59.69</td>
<td>28.60</td>
<td>0.053</td>
<td>0.84</td>
</tr>
<tr>
<td>3</td>
<td>67.47</td>
<td>37.75</td>
<td>0.060</td>
<td>0.94</td>
</tr>
<tr>
<td>4</td>
<td>77.95</td>
<td>38.09</td>
<td>0.037</td>
<td>0.95</td>
</tr>
<tr>
<td>5</td>
<td>89.29</td>
<td>40.24</td>
<td>0.033</td>
<td>0.92</td>
</tr>
<tr>
<td>6</td>
<td>120.35</td>
<td>52.00</td>
<td>0.046</td>
<td>0.72</td>
</tr>
<tr>
<td>7</td>
<td>95.35</td>
<td>34.27</td>
<td>0.047</td>
<td>0.56</td>
</tr>
</tbody>
</table>
4.2.2 Petiole development

As mentioned in section 3.2.3, only the development of the main petiole in trifoliate leaves (Figure 10 b) was fitted to a sigmoid growth curve (Eq.3). For the sake of simplicity, the centre and side parts of the petiole (Figure 10 c, d) were assumed to be a constant proportion of the main petiole, estimated at 25% and 7% respectively based on observations. The sigmoid function parameters for the main petiole are given in Table 4 together with the R² provided by the sigmoid fits. The fits are generally high (>0.90) but deteriorate at higher ranks. Because the first petiole’s development was not monitored accurately (as it had almost reached its maximal size at the moment of first data collection) a sigmoid function could not be fitted. The parameters t_{half} and alpha are therefore considered as extrapolations of the other petiole’s rank-dependent fit. L_{max} is the only parameter that can be determined from the first petiole’s data. The three parameters are plotted as a function of their respective ranks in Figure 16. A linear trend can be found in the development of t_{half} (R² = 0.98). The development of L_{max} is clearly rank-dependent for the petioles, since a second degree polynomial trend was found (R² = 0.99). The α value of petiole rank seven was exceptionally high (Table 4) and was treated as an outlier (and is not shown in Figure 16 c). No trend was found for the remaining values so α was assumed independent of rank and its average value was used.

Table 4: Sigmoid parameters for petiole growth.

<table>
<thead>
<tr>
<th>Internode rank</th>
<th>t_{half}</th>
<th>L_{max}</th>
<th>α</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-</td>
<td>10.07</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>83.68</td>
<td>31.54</td>
<td>0.036</td>
<td>0.96</td>
</tr>
<tr>
<td>3</td>
<td>101.26</td>
<td>41.25</td>
<td>0.028</td>
<td>0.97</td>
</tr>
<tr>
<td>4</td>
<td>122.89</td>
<td>44.53</td>
<td>0.023</td>
<td>0.95</td>
</tr>
<tr>
<td>5</td>
<td>137.84</td>
<td>44.99</td>
<td>0.032</td>
<td>0.95</td>
</tr>
<tr>
<td>6</td>
<td>167.56</td>
<td>36.12</td>
<td>0.026</td>
<td>0.89</td>
</tr>
<tr>
<td>7</td>
<td>169.34</td>
<td>18.00</td>
<td>0.413</td>
<td>0.57</td>
</tr>
</tbody>
</table>
4.2.3 Leaf development

4.2.3.1 Length and width development

Rank-dependent leaf length development was split in two separate rank-dependent fits, one for the centre leaflet and one for the side leaflets. The unifoliolate leaf was treated as a normal trifoliate centre leaflet since its parameters correspond well with the centre leaflet’s rank-dependent development (Figure 17). The centre and side leaflet’s sigmoid parameters and their $R^2$ are given in Table 5. A good fit was found with the exception of the higher leaf ranks. The parameters for the centre and side leaflets are plotted in Figure 17 and Figure 18 respectively and demonstrate several rank-dependent trends. $t_{\text{half}}$ strongly followed a linear trend for both the centre ($R^2 = 0.96$) and side ($R^2 = 0.86$) leaflets with ranks six and seven showing a slight deviation from the lower ranks. The rank-dependent development of $L_{\text{max}}$ showed a second degree polynomial trend ($R^2 = 0.97$ for the centre leaflet; $R^2 = 0.98$ for the side leaflets). The development of $\alpha$ was more difficult to assess. The centre leaflet showed a negative trend when considering the heavily divergent value from rank seven to be an outlier. A linear negative fit was used and results in an $R^2$ of 0.91 for the centre leaflet. Even though the data for the side leaflet were limited (since rank seven is an outlier), $\alpha$ still showed a similar negative trend and was therefore considered to be equal to the centre leaflets. In botanical terms, this means that the assumption was made that side and centre leaflets grow at the same rate.

Table 5: Sigmoid parameters for centre (left) and side (right) leaf development

<table>
<thead>
<tr>
<th>Leaf rank</th>
<th>Centre leaflet</th>
<th>Side leaflet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$t_{\text{half}}$</td>
<td>$L_{\text{max}}$</td>
</tr>
<tr>
<td>1</td>
<td>73.61</td>
<td>57.31</td>
</tr>
<tr>
<td>2</td>
<td>91.12</td>
<td>79.89</td>
</tr>
<tr>
<td>3</td>
<td>108.21</td>
<td>99.64</td>
</tr>
<tr>
<td>4</td>
<td>122.51</td>
<td>112.16</td>
</tr>
<tr>
<td>5</td>
<td>139.81</td>
<td>98.85</td>
</tr>
<tr>
<td>6</td>
<td>190.15</td>
<td>91.34</td>
</tr>
<tr>
<td>7</td>
<td>204.64</td>
<td>64.91</td>
</tr>
</tbody>
</table>
The development of leaflet width was observed as a function of leaflet length. During development a constant length-to-width ratio of every leaflet was found. The average values of this ratio and their standard deviations are given in Table 6. The resulting constant ratio showed a clear rank-dependent trend as depicted in Figure 19. The trend followed a second degree polynomial shape and was fitted with an $R^2$ of 0.97 for the unifoliate leaf and the centre leaflets of the trifoliate leaves and an $R^2$ of 0.98 for the side leaflets of the trifoliate leaves.

![Figure 17](image1.png)

**Figure 17:** Influence of leaf rank on sigmoid growth parameters for centre leaflet length development. (a) $t_{\text{half}}$, (b) $L_{\text{max}}$, (c) $\alpha$.

![Figure 18](image2.png)

**Figure 18:** Influence of leaf rank on sigmoid growth parameters for side leaf length development. (a) $t_{\text{half}}$, (b) $L_{\text{max}}$, (c) $\alpha$.

The development of leaflet width was observed as a function of leaflet length. During development a constant length-to-width ratio of every leaflet was found. The average values of this ratio and their standard deviations are given in Table 6. The resulting constant ratio showed a clear rank-dependent trend as depicted in Figure 19. The trend followed a second degree polynomial shape and was fitted with an $R^2$ of 0.97 for the unifoliate leaf and the centre leaflets of the trifoliate leaves and an $R^2$ of 0.98 for the side leaflets of the trifoliate leaves.

<table>
<thead>
<tr>
<th>Leaf rank</th>
<th>Centre leaflet</th>
<th>Side leaflet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average</td>
<td>STD</td>
</tr>
<tr>
<td>1</td>
<td>1.16</td>
<td>0.10</td>
</tr>
<tr>
<td>2</td>
<td>1.81</td>
<td>0.15</td>
</tr>
<tr>
<td>3</td>
<td>2.39</td>
<td>0.15</td>
</tr>
<tr>
<td>4</td>
<td>2.46</td>
<td>0.07</td>
</tr>
<tr>
<td>5</td>
<td>2.61</td>
<td>0.24</td>
</tr>
<tr>
<td>6</td>
<td>2.49</td>
<td>0.41</td>
</tr>
<tr>
<td>7</td>
<td>2.54</td>
<td>0.32</td>
</tr>
</tbody>
</table>

Table 6: Length-to-width ratio averaged for ever leaf rank and every stage of development alongside their standard deviations.
4.2.3.2 Shape development

Leaflet shape was fitted for every centre and side leaflet separately. The four parameters from Eq. 4 and the $R^2$ describing the fit of the fourth degree polynomial on the normalised leaflet shape are given in Table 7 for the centre and side leaflets. The unifoliate leaf was again considered as a centre leaflet with leaf rank one. All fits were considered good ($R^2 > 0.92$) though it must be noted that the fit showed a small bias at the leaf basis and tip. The parameters are depicted in function of the leaf rank in Figure 20. The resulting graphs show that the parameters were not only rank independent, but also that there was little variation in the normalised shapes even between the unifoliate leave and the trifoliate leaflets. This means that the differences in shape were determined almost entirely by the changing leaflet length-to-width ratio. This is illustrated in Figure 21 where a unifoliate leaf and a trifoliate centre leaflet scan are compared to their respective modelled counterparts. Though shape differences are apparent, the modelled leaflets were calculated using the same normalised leaflet function.

Table 7: Parameters for the fourth degree polynomial fit on the leaf shape and the respective $R^2$ for the centre and side leaflets.

<table>
<thead>
<tr>
<th>Leafrank</th>
<th>Centre leaf</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Side leaf</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a4</td>
<td>a3</td>
<td>a2</td>
<td>a1</td>
<td>$R^2$</td>
<td>a4</td>
<td>a3</td>
<td>a2</td>
<td>a1</td>
<td>$R^2$</td>
<td></td>
<td>a4</td>
<td>a3</td>
<td>a2</td>
<td>a1</td>
</tr>
<tr>
<td>1</td>
<td>-16.20</td>
<td>35.21</td>
<td>-28.14</td>
<td>9.13</td>
<td>0.99</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>-12.19</td>
<td>26.58</td>
<td>-22.38</td>
<td>7.99</td>
<td>0.94</td>
<td>-14.93</td>
<td>32.82</td>
<td>-26.72</td>
<td>8.84</td>
<td>0.97</td>
<td></td>
<td>-14.63</td>
<td>32.49</td>
<td>-26.69</td>
<td>8.91</td>
</tr>
<tr>
<td>3</td>
<td>-14.78</td>
<td>33.23</td>
<td>-27.45</td>
<td>9.00</td>
<td>0.94</td>
<td>-14.64</td>
<td>32.49</td>
<td>-26.69</td>
<td>8.91</td>
<td>0.97</td>
<td></td>
<td>-16.09</td>
<td>35.68</td>
<td>-28.82</td>
<td>8.84</td>
</tr>
<tr>
<td>4</td>
<td>-14.19</td>
<td>32.72</td>
<td>-27.57</td>
<td>9.04</td>
<td>0.93</td>
<td>-16.09</td>
<td>35.68</td>
<td>-28.82</td>
<td>8.84</td>
<td>0.98</td>
<td></td>
<td>-14.81</td>
<td>33.74</td>
<td>-28.05</td>
<td>9.11</td>
</tr>
<tr>
<td>5</td>
<td>-13.56</td>
<td>31.58</td>
<td>-26.97</td>
<td>8.95</td>
<td>0.97</td>
<td>-14.81</td>
<td>33.74</td>
<td>-28.05</td>
<td>9.11</td>
<td>0.97</td>
<td></td>
<td>-14.55</td>
<td>33.75</td>
<td>-28.41</td>
<td>9.23</td>
</tr>
<tr>
<td>6</td>
<td>-14.03</td>
<td>32.88</td>
<td>-28.00</td>
<td>9.15</td>
<td>0.98</td>
<td>-14.55</td>
<td>33.75</td>
<td>-28.41</td>
<td>9.23</td>
<td>0.96</td>
<td></td>
<td>-13.21</td>
<td>31.26</td>
<td>-27.06</td>
<td>9.12</td>
</tr>
<tr>
<td>7</td>
<td>-13.44</td>
<td>31.77</td>
<td>-27.38</td>
<td>9.04</td>
<td>0.99</td>
<td>-13.21</td>
<td>31.26</td>
<td>-27.06</td>
<td>9.12</td>
<td>0.97</td>
<td></td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 20: The rank independency of the polynomial parameters for the (a) centre and (b) side leaflets.

Figure 21: Comparison of leaflet scans with their respective model simulations. (a) The unifoliate leaf was fitted with the same normalised leaflet shape function as (b) the centre leaflet of rank three. The differences in final shape were obtained through the difference in length-to-width ratio.

4.2.3.3 Area development

The assumption of constant normalised leaflet shape directly led to the assumption of a constant normalised area as well. The normalised leaflet area factor equals the area described by the leaflet shape and holds a value between 0 and 1. It was found to be 0.72 with a standard deviation of 0.03 based on all leaflet scan data again showing strong similarity between all leaflets. As all leaflets were described by the same function, it can be useful to compare the result of the normalised leaflet area factor based on image analysis to the estimate based on the polynomial shape fit. This factor estimate was calculated by integrating the leaflet shape polynomial and is equal to 0.698. Therefore the bias caused by the polynomial fit did not have a strong influence on the simulated leaflet area. The total area can then be found by multiplying the normalised leaflet area constant with its length and width. Because width was described as a constant ratio of the current length, the leaflet area $A$ [m$^2$] can be calculated as follows:

$$A = A_{\text{norm}} \times \frac{L^2}{R}$$

(5)

where $A_{\text{norm}}$ is the normalised leaflet area constant [dimensionless], $L$ the current leaflet length [m] and $R$ the constant length-to-width ratio [dimensionless].
4.3 Model implementation

Using GroIMP, the model was implemented using L-systems as a basis for the architectural development. Plant organs were defined as separate modules that carried a number of predefined parameters required for the correct topological, geometrical and functional development of the model. Temperature, relative humidity and PAR data were read into GroIMP as separate data files. The sigmoid Boltzmann (Eq. 3) functions describing the continuous growth of internodes, petioles and leaves were also defined as separate functions. Three different light models (i.e. diffuse, direct and single light) were also readily implemented and can be selected whichever preferred.

4.3.1 Defining plant modules

As presented in Figure 8, the soybean model was constructed as a series of repeating phytomers. These phytomers are composed of plant organs that can differ from one another due to the parameters and/or variables they contain. In order to use them in the plant model, they need to be predefined. The model starts from within an “Apex” module, which has no geometrical interpretation. It carries a variety of parameters to allow further construction into the correct modules. The “Apex” was defined to carry: i) an integer rank which increases by 1 every time a new phytomer is formed, ii) a double phyllo which carries the time of appearance of the next phytomer in function of GDD, iii) a plant specific integer id, unique for all plants when simulating multiple individuals and iv) a border integer. The border value is a plant-specific number that counts the minimum amount of plants between the plant itself and the crop edge. For single plant modelling the value of this integer is irrelevant.

The module “Internode” was defined as a cylinder. The “Cylinder” class in GroIMP was predefined to carry the doubles length and radius and therefore these variables needn’t be specified. Any other variable or parameter that the module needs to hold was initiated here. The “Internode” carries a double for the age of the plant in GDD. This is because the “Internode” grows in function of its own age. The parameter PlantAgeAtFormation is simply assigned a value equal to the total amount of GDD passed at the moment of the initiation of the module. It has no further use but can be helpful to monitor the accuracy of the model construction.

As we found leaflet shape to be identical, the unifoliate leaves and the trifoliate leaflets were defined by the same module. They include values describing their differences in dimensions and position. The “Leaf” module contains the same parameters as the “Internode” with the addition of: i) ai, a double describing the amount of light captured by the leaf (see section 4.4); ii) transp, a double that holds the amount of transpiration in the leaf (see section 4.3.5); iii) leaflet, an integer describing the position of a leaflet in trifoliate leaves (i.e. centre or side leaflet, modules C1 and C2 in Figure 23); iv) area, a double holding the current area of the leaflet; v) Lmax, a double describing the maximal length the leaflet can obtain; vi) length and width, the current dimension of the leaflet. The leaflet shape was implemented using “Meshes”. A polygon mesh is a collection of triangles describing a surface. The connection points of these meshes are defined as vertices. They hold the coordinates of every point that has to be connected in the meshes. A constant integer was defined as the amount of points at each side of the leaf. Using this integer the distance between leaflet petiole and leaflet tip
can be cut in to equal parts. The leaflet shape function (Eq. 4) can then be of used to describe the width of the leaflet at said points. Every vertex has three values, one x, one y and one z coordinate. As the leaflet shape function was fitted on normalised data, the found x coordinates were multiplied by the current leaflet length, and the y coordinates with half the current leaflet width. Once the outer vertices were found for both leaflet sides, a centre vertex was defined as having half of the leaflet length, and y and z coordinate equal to zero. Once all the vertices are found, they are stored as indices describing the corners of each triangle. A list of indices holds the reference to every three vertices that define a mesh (Figure 22). Once all the indices are stored, the polygons can be constructed. Leaf bending along the z-axis was not yet implemented as we did not capture data for this particular feature.

Two different petiole modules are constructed as “LeafShoot” and “LeafShoot2”. “Leafshoot” carries the information on the leaf petiole on the unifoliolate leaf, and the main part of the trifoliolate leaf petioles (Figure 10 b; Figure 23 A). It was constructed like the “Internode” module and carries the same variables and parameters. “Leafshoot2” is used for the three smaller petioles branching from the main petiole in trifoliolate leaves (Figure 10 c, d; Figure 23 B1, B2). The module carries one additional parameter position. It holds a value of one or two depending on which leaflet is attached (Figure 23).

<table>
<thead>
<tr>
<th>Vertices</th>
<th>Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>(x₁,y₁,z₁)</td>
<td>(1,9,2)</td>
</tr>
<tr>
<td>(x₂,y₂,z₂)</td>
<td>(2,9,3)</td>
</tr>
<tr>
<td>(x₃,y₃,z₃)</td>
<td>(3,9,4)</td>
</tr>
<tr>
<td>(x₄,y₄,z₄)</td>
<td>(4,9,5)</td>
</tr>
<tr>
<td>(x₅,y₅,z₅)</td>
<td>(1,9,6)</td>
</tr>
<tr>
<td>(x₆,y₆,z₆)</td>
<td>(6,9,7)</td>
</tr>
<tr>
<td>(x₇,y₇,z₇)</td>
<td>(7,9,8)</td>
</tr>
<tr>
<td>(x₈,y₈,z₈)</td>
<td>(8,9,5)</td>
</tr>
<tr>
<td>(x₉,y₉,z₉)</td>
<td>-</td>
</tr>
</tbody>
</table>

Figure 22: Vertex and index list in defining the leaflet surface.

Figure 23: Soybean leaf construction in GroIMP, using the following modules: A) LeafShoot; B1) LeafShoot2, position 1; B2) LeafShoot2, position 2; C1) Leaf, position 1; C2) Leaf, position 2
4.3.2 Reading datasets into GroIMP

The model uses 3 datasets coming from the environmental data of the phytotron. The constant observations of temperature, relative humidity and incoming radiation (measured in PAR) were be used to calculate leaf transpiration and the strength of the light model in a later step. We used the excel data import based on the example code by Michael Henke on grogra.de. The code is based on single column imports without a header in the .xls format (excel 97-2003 workbook) and doesn’t work with .xlsx formats.

4.3.3 Model initialisation

Several constants were declared prior to model initialisation. These constants include the phyllochron, the optical properties of the leaf (i.e. absorption, transmittance and reflectance of PAR, Red and Far-Red light), several parameters for the light model (e.g. the height of the light source for the single light model, the latitude for the direct light model, see 4.3.7), the number of plant rows and plants per row and their planting distance. Any dataset used in the model was also initialised. A lightshader was also declared to relate the leaf color to the leaf light constants and the intercepted irradiance.

The initialisation contains two main parts: one that concerns general parameters and datasets and one for the geometrical initialisation. The former was defined within braces and sets the current step to zero, clears the current datasets still logged in the model memory, initialises the charts of any dataset plot and loads and fills the datasets being read. The geometrical initialisation was defined as a production step which originates from the “Axiom”. This results in the selection of the used light model, the placing of apex modules where plant development originates and the tiles (which represent the ground). The amount and position of these “Apex” modules was done according to the constants declared earlier. The “Apex” modules were rotated randomly between -90° and 90° around the head axis to prevent unnatural sowing regularity. They recieved a rank of zero and a phyllochron of zero as well (they are initiated instantly). Their border value is calculated as defined in 4.3.1. The light source is added at the very end of the initialisation. More details are given in 4.3.7. An example setup for simulating 25 plants was given in Figure 24.

Figure 24: Initial model setup for simulating 5 rows of 5 plants with a planting distance of 0.25 m. The height of the light source was lowered and the “Apex” modules are represented as green spheres for visualisation purposes.
4.3.4 Phytomer development

All plants develop from a single “Apex” module initiated in the previous step. The development is driven completely by L-system geometry and the organs receive a size of zero at formation. Instead, the plant is constructed based on a “run” and an “AbsorbAndGrow” function. The “run” function increases the actual development timestep by one. At the start this will invoke the formation of the hypocotyl and the cotyledons along with a new “apex” module that holds the constant phyllochron value. Every time the function “run” is called, this apex phyllochron value will count downwards and the light source power will change according to the PAR data. As the phyllochron is based on GDD and the timesteps of development in the “run” function are based on either hourly or daily steps, the phyllochron is counted downwards based on data concerning the GDD. For instance this means that for timesteps of one day, one timestep will count the phyllochron downwards by the GDD measured in that day (i.e. \( a[\text{phyllo}] = a[\text{phyllo}] - \text{GDD}[\text{step}] \)). If the model should be adapted for hourly growth, a simple change in datasets can be used. Once the phyllochron reaches zero, a new phytomer is formed, along with a new apex module again holding the reset phyllochron value. This means that the size of one timestep is determined by the speed at which the phyllochron is counted downwards as the size of the phyllochron itself depends on the observational plant development. The “AbsorbAndGrow” function calculates plant organ aging, light interception, elongation and transpiration from functions defined in 4.3.5 and will be discussed in 4.3.6.

Every time the apex phyllochron reaches zero, the apex rank will determine which phytomer will be formed and the new apex module will receive a rank increased with one. At rank zero this will cause the formation of the hypocotyl, at rank one this will result in the formation of the first internode with two parallel unifoliate leaves and at rank two or higher, the normal trifoliate phytomers will be formed. The hypocotyl is treated as a normal internode with rank zero and for model simplicity, the cotyledons are treated as static rectangles. As internode and petiole width development was so limited, it was not tracked. Consequently all formed internodes are set to have a fixed width of 3 mm and petioles a width of 1 mm. When modules are initiated, all parameters defined in the module initialisation must be declared. The entire development is deterministic, with the exception of a few angles: i) a 30° angle variation (uniform between -30° and +30°) around the longitudinal axis is introduced on the internodes, ii) a 10° angle variation (uniform between -10° and +10°) is allowed around the perpendicular axis of the internodes, iii) a uniform variation between 0° and 30° on the unifoliate leaf orientation and iv) a uniform variation between 20° and 40° in the side leaflets of the trifoliate leaves. These variations, made to introduce some basic stochasticity without drastically changing the model, are not based on stochastical data as none was collected.

4.3.5 Plant organ calculations

Once every plant organ was initiated at the correct time and in the correct topography, growth functions were applied. Every organ was produced without a geometrical length but in every “growth” step, its age and length should increase. The increment in length is based on the organ’s age and can be called as the result of the sigmoid Boltzmann function (Eq. 3) discussed in 3.2.1. Each of these functions carries the sigmoid parameters found in the previous step. They require the input of the current organ age and its rank in case one or more of the parameters were rank-dependent.
During development, these functions can be called and their current length will be returned on the scale of Lmax (i.e. if Lmax is defined in meters, the function will return a length in meters).

Light absorption and transpiration are calculated for each leaflet separately. Light absorption is determined by the light model used and the current plant topology, leaflet geometry and leaflet orientation towards the light source. The strength of the light source was based on the collected PAR data in the phytotron. The data was rescaled from quantum flux [µmol m⁻² s⁻¹] at sensor level to irradiance [Watt m⁻²] at the light source level. To account for the difference in height between the light source and the PAR sensor, a diminishing factor was used based on the height of the light source to ensure the irradiance levels provided by the light source are representative for the phytotron. The function for calculating the total amount of radiation absorbed is readily available in GroIMP. Since the value returned by this function already incorporates the size and orientation of the leaflet its value can be used directly in the transpiration calculations. We calculated the transpiration based on the Penman-Monteith equation (Allen et al., 2006). The equation differs slightly if the calculations are made in daily (Eq. 6) or in hourly (Eq. 7) timesteps especially in the units through which the variables are expressed.

\[
ET_0 = \frac{0.408\Delta(R_n - G) + \gamma\left(\frac{900}{T + 273}\right)u_2(e_s - e_a)}{\Delta + \gamma(1 + 0.34u_2)} \quad \text{(6)}
\]

\[
ET_0 = \frac{0.408\Delta(R_n - G) + \gamma\left(\frac{37}{T_{he} + 273}\right)u_2(e_s - e_a)}{\Delta + \gamma(1 + 0.34u_2)} \quad \text{(7)}
\]

where

- \(ET_0\) reference evapotranspiration [mm day⁻¹] [mm hour⁻¹]
- \(R_n\) net radiation [MJ m⁻² day⁻¹] [MJ m⁻² h⁻¹]
- \(G\) soil heat flux density [MJ m⁻² day⁻¹] [MJ m⁻² h⁻¹]
- \(T\) mean air temperature at 2 m height [°C] [°C]
- \(u_2\) average wind speed at 2 m height [m s⁻¹] [m s⁻¹]
- \(e_s\) saturation vapour pressure [kPa] [kPa]
- \(e_a\) actual vapour pressure [kPa] [kPa]
- \(e_s - e_a\) saturation vapour pressure deficit [kPa] [kPa]
- \(\Delta\) slope vapour pressure curve [kPa °C⁻¹] [kPa °C⁻¹]
- \(\gamma\) psychrometric constant [kPa °C⁻¹] [kPa °C⁻¹]

It should be noted that this formula was used to estimate transpiration instead of evapotranspiration. As the model will be used for estimations on leaflet scale of plants grown in a phytotron, soil heat flux density is assumed negligible. The mean daily temperature was calculated from the phytotron data. The saturation vapour pressure is dependent upon temperature [°C] and was calculated by Eq. 8.

\[
e^0(T) = 0.6108 e^{\frac{17.27 T}{T + 237.3}} \quad \text{(8)}
\]
The slope vapour pressure curve was determined by:

\[ \Delta = \frac{4098 \, e^0(T)}{(T + 237.3)^2} \]  

(9)

Lastly, the actual vapour pressure was calculated with:

\[ e_a = e^0(T) \frac{RH}{100} \]  

(10)

with RH the relative humidity [%] taken from the phytotron data. The resulting transpiration estimate was then converted from millimetres to grams per day and rescaled to fit the acquired transpiration data from the phytotron with a proportionality factor.

The implementation of the transpiration model requires inputs of total amount of radiation absorbed by the leaflet and the current timestep. The timestep is merely used in the identification of the current temperature and relative humidity based on the data. The function returns the average amount of transpiration [g h\(^{-1}\)] for the any leaflet during the current timestep.

4.3.6 Plant growth

In the next step, the plant organ calculations were implemented in the model. The current length of internodes, leaflets and petioles is calculated as well as leaf absorption and transpiration. To calculate elongation and transpiration, the functions from 4.3.5 are called. Absorption is calculated with “getAbsorbedPower3d().integrate();”. Lastly the graphs initiated in 4.3.3 are updated with the calculated border effect (the average plant light absorption for every plant with the same border value) and leaf light absorption, transpiration and area per leaf rank.

4.3.7 Light models

A selection of light models can be used to model plant growth. We implemented three different models and made them all readily available in the model: i) a single light source, ii) direct light and iii) diffuse light. The single light source can be seen as a spotlight, producing light from a single point. To calculate the power of this spotlight, we used a calibration based on the collected PAR data. As PAR data was collected at the plant height, the power was set as such that the light intensity at plant model height corresponded with the captured data. This means that the height of the light source was used as a means to account for light dispersal over said distance. The direct light uses information on the latitude of the growing position of the plant and the current day of the year to calculate the power and direction of the light for each timestep. The diffuse light model calculates the amount of radiation for a certain day based once again on latitude and day of the year but discards the directional aspect. The diffuse and direct light models were taken from de Visser & Buck-sorlin (2011).

The single light source was implemented with the declaration of light modules. The module requires the input of the timestep, the intensity at plant level and the height of the light source. The
timestep is only used in the model to find the current radiation intensity according to the collected data. The found intensity is then used in this module and multiplied by the second degree of the height of the light source to account for light dispersal.

Prior to model initialisation, the light model needs to be declared as such,

```java
LightModel lm = new LightModel(100000, 5);
```

if any of the three light models will be used. This declaration holds the amount of random rays (100,000 in this case) for the model and the recursion depth (the number of reflections, 5 in this case). If these parameters are not declared (i.e. LightModel( )); a default light model of 30,000 rays and a recursion depth of 10 will be used. In the case multiple light sources are used, the amount of rays will be split according to their respective power. For example if two light sources are present, one with a power of 100W and another with 10W, and a total number of 11,000 rays then the first light source would create 10,000 rays and the second 1,000.

Lastly, the light source must be placed above the scene. This is done in the model initialisation (4.3.3). The placing of the light source can be done by using the operator “==:^”, this operator indicates that the production after the statement originates from the root node (i.e. the original position of the axiom) of the current graph.

4.3.8 Running the model

Finally, all previous steps are combined in the final function “Grow”. This function is what actually drives the model and consists of three steps. First the model phytomer development is calculated (i.e. “run( )”, defined in 4.3.4). Secondly the random rays from the light model are computed (i.e. “lm.compute( )”, the amount of rays depends on what is declared in the light model (see 4.3.7) and has a very strong influence on the calculation time of every step). Lastly the growth, absorption and transpiration calculations are made (i.e. “absorbAndGrow()”, as defined in 4.3.6

4.4 Functional plant development

4.4.1 Transpiration simulations

The environmental data (i.e. PAR, Temperature, Relative humidity) used in the model were based on data from the phytotron. The daily fluctuations are shown in Figure 25. The noticeable rise in temperature from day 29 until day 37 and the rise in irradiance in days 35, 36 and 37 were caused by a malfunction of the phytotron control system. These changes were paired with a decline in relative humidity. The hourly transpiration simulations (see section 4.3.5) resulting from a single plant simulation were used to determine a proportionality factor as a scaling factor for Eq. 7 to the acquired transpiration data. However the data were strongly influenced by soil evaporation which we didn’t account for. Therefore we decided to scale the transpiration data of the last three weeks of
the experiment on the simulation results. As vegetative plant development was nearing its final stages at this point in time, the influence of soil evaporation was considered minimal. During the hours of darkness, the transpiration measurements can be directly related to the wind speed dependent factor in the numerator of Eq. 7. Optimisation of the simulation based on dark transpiration resulted in an average windspeed of 0.06 m/s. The proportionality factor was then found to be 4.5 (Figure 26).

**Figure 25:** Daily fluctuations in the environmental parameters.

**Figure 26:** Comparison of simulated plant transpiration and measured plant transpiration for a single fully grown soybean plant.

### 4.4.2 Light interception during development

The light interception of a leaf changes when a leaf directly above it is being developed. Considering the schematic build-up we presented in Figure 8, a soybean leaf will receive a decreasing amount of light when the leaf at two ranks higher is under development. Assuming a constant daily average of 400 µmol PAR m\(^{-2}\) s\(^{-1}\) and a deterministic model approach, the leaf light absorption simulation per rank is given in Figure 27. The curves of the early trifoliate ranks clearly
demonstrate this decline in interception when higher ranks are developing. The interception of a leaf is unaffected by the development of the consecutive phytomer due to the alternate phyllotaxis. A single lightmodel with 1,000,000 random rays was used for this simulation. The instability of some of the curves presented in Figure 27 is a result of the randomness in which these rays are distributed, meaning that even a fully grown plant’s leaves will therefore not necessarily receive the same amount of radiation in each timestep.

![Figure 27](image)

Figure 27: Incident radiation per leaf rank during soybean plant development.

### 4.4.3 Influence of planting distance and density on light interception

The current ILVO field-trials are done using a planting distance between rows of 0.25 m and a planting density of 65 plants m$^{-2}$. These settings were used as the reference for a 1 m$^2$ model setup with the same assumptions made in 4.4.2. Using the model simulations, an estimate was made of the differences in light captivity when other planting distances or densities are used. The morphological result of the reference simulation is given in Figure 28. A total of four simulations were made in comparison to the reference simulation (Figure 29, Table 8). An interrow planting distance of 0.20 m (20% decrease; Figure 29 d) and 0.33 m (33% increase; Figure 29 c) was simulated, both using 16 plants per row equal to the reference simulation. The remaining two simulations changed the planting density to 12 plants per row (48 plants m$^{-2}$; 25% decrease; Figure 29 a) and 20 plants per row (80 plants m$^{-2}$; 25% increase; Figure 29 b) respectively.

![Figure 28](image)

Figure 28: Morphological result of 1 m$^2$ of a deterministic soybean crop simulation with an interrow planting distance of 25 m$^2$ and a planting density of 65 plants/m$^2$. 

The cumulative light interception \([W \text{ m}^{-2}]\) and average light interception \([W \text{ plant}^{-1}]\) is plotted in Figure 30 and given in Table 8 for all 5 simulations. Increasing the planting density causes an increase in the cumulative light interception but gives a lower average interception per plant than the reference interception while decreasing the planting density results in the opposite effect. Changing the interrow distance instead of the amount of plants per row has a relatively larger effect on the cumulative light interception while the effect on the average light interception is relatively smaller.

Table 8: The effect of changing the planting density on the cumulative light interception and the light interception efficiency.

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Interrow distance [m]</th>
<th>Plants per row</th>
<th>Planting density [plants m(^{-2})]</th>
<th>Cumulative light interception [W m(^{-2})]</th>
<th>Average light interception [W plant(^{-1})]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reference</td>
<td>0.25</td>
<td>16</td>
<td>64</td>
<td>173.8</td>
<td>2.7156</td>
</tr>
<tr>
<td>a</td>
<td>0.25</td>
<td>12</td>
<td>48</td>
<td>155.9</td>
<td>3.2479</td>
</tr>
<tr>
<td>b</td>
<td>0.25</td>
<td>20</td>
<td>80</td>
<td>189.5</td>
<td>2.3688</td>
</tr>
<tr>
<td>c</td>
<td>0.33</td>
<td>16</td>
<td>48</td>
<td>141.0</td>
<td>2.9375</td>
</tr>
<tr>
<td>d</td>
<td>0.20</td>
<td>16</td>
<td>80</td>
<td>207.2</td>
<td>2.5900</td>
</tr>
</tbody>
</table>

Figure 29: Morphological result of 1 m\(^2\) of a deterministic soybean crop simulation with: (a) 75% plants per row, (b) 125% plants per row, (c) 133% interrow distance and (d) 80% interrow distance compared to the reference setup.
4.4.4 Influence of phyllotaxis on light interception

The soybean varieties we looked at had a phyllotaxis of 180° but the model allowed us to investigate what the effect on light interception could be if a hypothetical genotype was found with a different phyllotaxis. We made the comparison to a phyllotaxis of 137.5° (i.e. the golden angle). The morphological differences viewed from above the deterministic plant simulations are shown in Figure 31. A clear difference is visible in the projected area covered by the plant which translates into less shading on the lower rank’s leaves of the 137.5° simulation (Figure 27 for 180°; Figure 32 for 137.5°) with the exception of the unifoliate leaves, which receive approximately 65% less radiation. During development of a single plant the total light interception is approximately the same until the leaf on phytomer four begins to develop (Figure 33). In the plants with a phyllotaxis of 180° this results in the increased shading of the first trifoliate leaf while the shading is less severe in plants with a 137.5° phyllotaxis. The cumulative crop light interception (Figure 34) was simulated using the same planting setup as the reference in 4.4.3. It revealed a slightly lower crop light interception for the 137.5° phyllotaxis up to day 40 (458 GDD) after germination, after which it started to benefit.
Figure 32: Incident radiation per leaf rank during soybean plant development with a phyllotaxis of 137.5°.

Figure 33: Total plant light interception for a changing phyllotaxis.

Figure 34: Cumulative light interception per square meter for a changing phyllotaxis.

4.4.5 Influence of leaf gravitropy on light interception

No data was collected on the leaf gravitropy of the soybean plants. However, this behavior was observed in all specimens and could strongly influence the light interception of the plants. A rough estimate on light interception was made by incorporating a second degree leaf bending function purely on observational estimates. Figure 35 compares the morphological difference of such a soybean simulation with the reference simulation and a photograph of a phyotron-grown
soybean plant. The model simulation showed a decrease in light simulation on all leaf ranks (Figure 36) resulting in a total reduction of over 20% in plant light interception (Figure 37) when compared to the model that did not incorporate leaf gravitropy (Figure 27). The cumulative crop light interception (Figure 38) was simulated using the same planting setup as the reference in 4.4.3, and showed a similar trend as with the single plant simulation. However, the absolute effect was smaller since incorporating leaf gravitropy only resulted in a 15% reduction of total light interception per square meter. The morphological result of the crop simulation (Figure 39) shows a clear difference in total soil cover when compared to the reference setup (Figure 40).

Figure 35: Comparison of (a) a soybean model simulation without leaf gravitropy, (b) a simulation that incorporates leaf gravitropy and (c) a photograph of a phytotron-grown soybean plant.

Figure 36: Incident radiation per leaf rank during soybean plant development incorporating leaf gravitropy.

Figure 37: Total plant light interception when leaf gravitropy is considered.
Figure 38: Cumulative light interception per square meter when leaf gravitropy is considered.

Figure 39: Morphological result of 1 m² of a deterministic soybean crop simulation with leaf gravitropy.

Figure 40: Top view of the simulation of (a) the reference crop model and (b) the crop model incorporating leaf gravitropy.
Chapter 5
Discussion

5.1 Morphological differences in changing growing environment

We have observed strong differences in the vegetative development of greenhouse-grown plants when compared to phytotron-grown or field-grown plants. The extensive internode elongation which induced lodging in the greenhouse-grown plants was probably due to the lower light availability under greenhouse conditions (Figure 41). This illustrates the strong effect of environmental interaction on the plant’s morphology and demonstrates the importance of conducting experiments under different growing conditions (i.e. field, phytotron and greenhouse conditions) as we strive towards an FSPM that is applicable in every growing environment. The monitoring of development under different conditions could help in the search for correlations and processes that induce the morphological differences.

![Figure 41: Comparison of the maximal daily irradiance in the greenhouse to the phytotron.](image)

5.2 Morphological plant development

We found generally good fits when applying the sigmoid growth curves to the data but saw a recurring trend of lower fits at the lowest and highest ranks. These lower fits were probably caused by the limited amount of data captured. At the lowest rank this data limitation was time-related, as the first moment of data collection occurred when the first internode had already reached two
thirds of its final length. At higher ranks the limitation was caused by the low amount of plants monitored (i.e. four). The data showed an increase of inter-plant variations at higher ranks creating a more difficult fit and a decrease in the amount of available data, as not all plants reached the highest vegetative stages. When working with limited amounts of data it is important to avoid overfitting. Especially when data points at either ends of the S-shaped curve are limited, the parameters should be interpreted with care. An example is the sigmoid α for the petiole development of rank seven. It was found to be over ten times higher than any of the lower ranks as a result of data limitation. A value as such is unusable in the model as it would have caused unrealistic simulation results. They were replaced by values related to the parameter values of the other ranks in the model (of which more data was available) which produced more credibly results.

Relating such phytomer-dependent parameters or variables to the phytomer’s rank is common practice in plant modelling (e.g. Fournier et al., 2007; Mündermann et al., 2005) as it reduces the number of independent variables in the model. We found \( t_{\text{shaf}} \) to have a positive lineair relationship with phytomer rank in all three cases (i.e. internode, petiole and leaf length) along with a negative trend for \( \alpha \) (although this assumption could not be made for the internodes as the data showed too much variability). Botanically this means that with increasing phytomer ranks, the plant organs grew increasingly slower, causing them to have reached half of their maximal size later. This could have been the result of mutual development of multiple phytomers during the development of higher ranks or the induction of the generative phase, causing a larger amount of carbon sinks to have been present. The development of \( L_{\text{max}} \) was rank-independent for the internodes while the petioles and leaves showed a strong second degree trend. In botanical terms this indicates that the maximal length of the internodes was the same throughout the plant while leaf and petiole length reached the largest sizes in the middle phytomers (ranks 3–5; Figure 6).

Another allometric relationship was found for the constant length-to-width ratio of the leaflets. The available data on leaflet length and width were more plentiful, as we combined the non-destructive measurements with the data obtained from the leaflet scans which were acquired by dissecting plants at different developmental stages. The rank-dependent development of the length-to-width ratio showed a strong second degree trend, and differed between the centre and side leaflets (Figure 19). The length-to-width ratio on the lower trifoliate ranks (ranks 2–3) was higher for the centre leaflet when compared to the side leaflet and vice versa for the higher ranks (ranks 4–7), indicating a rank dependent difference in trifoliate leaflet shape proportions.

Leaflet shape was more difficult to assess. We evaluated three different methods for shape description: i) leaf shape functions (Evers et al., 2006; Dornbusch et al., 2007), ii) spline interpolation (Mündermann et al., 2005) and iii) polynomial fitting (Prévot et al., 1991). The leaf shape functions (Eq. 1 & Eq. 2) were designed to describe leaf shapes as accurately as possible while limiting the amount of independent parameters. The main advantage of these functions is that all parameters provided by the function fit, can be directly interpreted in terms of morphological leaf traits (e.g. a curvature parameter) (Fournier et al., 2007; Dornbusch et al., 2007). This is contrasting to the approach of polynomial fitting and spline interpolations where the parameters are difficult to interpret. However, the leaf shape functions proved useless for modelling soybean leaflets as they were both designed for the description of leaves of monocotyledons (i.e. wheat (Evers et al., 2006; Evers et al., 2007) and barley (Dornbusch et al., 2007)). Consequently, they were met with severe biases towards the soybean leaflet shapes. Spline interpolation provided an excellent fit but resulted in an excessive number of independent parameters. This would have resulted in a very realistic,
almost unbiased representation of the leaflet’s shape but could have strongly influenced the predictive nature of the model (i.e. overfitting). Therefore we decided to work with polynomial fitting. Applying an \( n \)-th-degree polynomial to the normalised data shows a small bias at the leaflet base and tip and still results in \( n \) independent parameters per leaflet. We chose to work with a fourth degree polynomial since higher degrees did not provide a significantly better fit and added to the number of independent parameters. Some important assumptions were made before fitting: i) the normalised leaflet shapes are constant during leaflet development; ii) the leaves and leaflets are symmetrical and iii) the side leaflets are identical. This resulted in four independent parameters per leaflet, per rank for a total of 52 parameters. However, the parameters were found to be rank and position (i.e. centre of side leaflet) independent, meaning that the normalised leaflet shapes proved nearly identical in the entire plant. The differences in shapes between centre and side leaflets and the differences across ranks were consequently caused by the difference in length-to-width ratio. This reduced the total amount of independent parameters to describe leaf shapes in the entire model from 52 to 4. It is also an indication that the normalised leaflet shape is mainly determined by genetic regulation (Xu et al., 2011), since it appears to be independent of environmental differences (e.g. lower light interception in lower leaf ranks). Therefore it could be worthwhile to investigate if this behaviour is observed in other soybean cultivars. We compared the average normalised leaflet area through image analysis with the fourth degree polynomial describing the equal shapes. We found that the simulation of the leaves according to the found constant polynomial leads to a small average reduction (i.e. 4\% of the leaf area in the model compared to reality. This reduction in leaf area as well as the geometrical bias will slightly impact the calculated light interception of the model.

5.3 The current model

We have taken the first steps towards the creation of a soybean FSPM with the construction of a three-dimensional developmental model for soybean in GroIMP. Morphological phytomer development was calibrated to experimental data causing the model to realistically simulate and visualise the entire plant’s development. Even though the model already incorporates large amounts of spatio-temporal data (i.e. internode, petiole and leaf sizes and shapes), several morphological traits were implemented on merely observational estimates (i.e. petiole angles, variation in phyllotaxis and internode bending) or were not yet implemented at all (e.g. gravitropy of leaves, petioles and internodes, petiole and internode width development, soybean branching, generative development, below-ground development).

The functional part of the model is still early in development. The model allowed calculations for light interception and transpiration. The calculations of light interception were done in GroIMP based on the plant’s topology and geometry as well as the used light model and are likely to show slight deviations due to the morphological model assumptions and simplifications. Leaf transpiration estimates were made with an evapotranspiration model (Allen et al., 2006) where we only took leaf light interception into account while also assuming the absence of soil heat flux. These simplifications as well as the uncertainty in the transpiration data are reasons why the model transpiration simulations should be interpreted with care.
We acknowledge that the current morphological flaws in the model make it difficult to evaluate the outcome of individual estimates on light interception. However, since the model already gives a realistic representation of general soybean topology, the estimates are definitely valuable for reasons of comparison. This allowed us to evaluate the effect of certain factors (i.e. planting density, phyllotaxis and leaf gravitropy) on the light interception of individual plants and crops.

As expected, we concluded that changing the planting density increased the total light interception of the crop but reduced then individual plant’s interception. This influence was relatively stronger when changing the distance between rows, rather then changing the amount of plants per row. This is the result of the standard planting method, which uses 4 rows of 16 plants per square meter. Changing the interrow distance consequently has a relatively larger impact on the density of the crop cover but is not always desirable in some cases (e.g. biological cultivation; mechanical weeding). Another consideration is that increasing the planting density is linked with a lower red : far red ratio (R:FR) (Holmes & Smith, 1977). This is associated with the induction of competitive behaviour, causing increased elongation, strengthened apical dominance, accelerated flowering and altered resource allocation (Smith, 2000; Franklin & Whitelam, 2005). As these changes often occur at the expense of leaf and storage organ development while also accelerating flowering (Franklin & Whitelam, 2005), this could heavily affect the yield per plant and consequently the entire crop. These morphological and physiological responses to increased planting density are not yet incorporated in the model.

We investigated the possible benefit on light interception if a hypothetical soybean genotype were to be found with a phyllotaxis differing from the standard 180 degrees. The simulation of a soybean crop with a phyllotaxis that equalled the golden angle (137.5 degrees) indicated that the effect is rather limited, with only an 8% increase in light interception when the standard planting densities are used.

When we looked at the effect of leaf gravitropy we noticed a decline in interception. The underlying causes of the appearance of leaf gravitropy could be either of genotypical or turgor-related origin. The simulation showed a reduction of over 20% on the light interception when a single plant is considered. A crop simulation with standard planting densities however, only showed a 15% reduction. This could indicate that the effect of leaf gravitropy decreases with increasing planting densities, as it is progressively compensated by mutual shading in the reference crop. Either way the result is an indication that this phenomenon should be investigated further as it was observed in all three genotypes and has a relative large impact on light interception.

Taking all of these considerations into account, we can conclude that the current model is still in its early stages. The model construction was based on the measured averages of a limited amount of plants, creating a deterministic model of the “average” (phytotron-grown) soybean plant. Furthermore, the current model only incorporates the vegetative stages of development. We had data on the parameter’s distributions (i.e. means and standard errors) at our disposal (albeit a very limited amount), which made it tempting and relatively easy to incorporate stochastic variability in the model. However, the meaningfulness of such simulation results would be debatable as the parameter values are likely to be correlated in reality (Mündermann et al., 2005) and the model does not yet hold the complexity to reflect these correlations. As we eventually aim to integrate many ecophysiological processes as accurately as possible, the model should remain largely deterministic.
(with some variety in initial values to represent genotypical variance) so a group of mutually interacting plants will show variation mainly due to spatial heterogeneity in the environment (Vos et al., 2010).

### 5.4 Future development

Model validity is essential for any FSPM and therefore requires the appropriate degree of complexity. When internal processes are simplified, strong deviations can occur and the model output loses in validity. However, when simplifications are made at a very fine spatial scale, the simulation errors become more negligible at a more integrated level (Tardieu, 2010). Since some degree of simplification is inevitable due to computational, knowledge and measurement constraints, the key question is to find the appropriate level of complexity for a given question (Tardieu, 2010). In our case, the question put in the most simplest of term would be: Is soybean cultivation feasible in Flanders? To answer it, we will need to explore and assess the impact of a variety of options ranging from management regimes to optimal variety breeding. This requires model confidence for both plant structure and function. Whenever possible, it is always advisable to validate the model results with field or lab measurements so the FSPM shows properties and behaves as similar to the real plant as possible (Godin & Sinoquet, 2005). Therefore, it is recommended to monitor the development of soybean under a large variety of environmental conditions ranging from field-trials to greenhouse and phytotron experiments.

In a first step, the plant’s morphological development should be more accurately assessed to create a **valuable reference model**. The model should be scaled to data concerning the development of plant organ sizes, leaflet shapes, phyllotaxis, leaf angles, branching angles and branching patterns, generative stages, gravitropy of plant organs, etc. Aside from creating the “average” model, information of variances is equally important. These variances will play a strong role in assessing the validity of the ecophysiological submodels (i.e. transpiration, photosynthesis and nitrogen uptake) and carbon, water and nitrogen transport processes that need to be implemented.

Light absorption estimates will improve simultaneously with the improvements on the plant’s morphology. The implementation of a **photosynthesis** model can then be done by any of the approaches designed for process-based crop modelling (Vos & Heuvelink, 2006). These include (but are not limited to) biochemical models (Farquhar et al., 1980) or working with light-response curves (Marcelis et al., 1998) at the individual leaf level. These require knowledge of the distribution of nitrogen within the plant, since the photosynthesis parameter values of the plant organs are mainly dependent upon nitrogen content per leaf area (e.g. Yin et al., 2009; Braune et al., 2009; Gonzalez-Real & Baille, 2000). A more complex approach would be to work with a local **gas** (i.e. carbon dioxide and water vapour) and **radiant energy exchange** model (GREM; Müller et al., 2007). A GREM combines the processes of radiative-energy and gas exchange (i.e. photosynthesis, respiration and transpiration) into one. This is achieved by combining a biochemical model for photosynthesis (i.e. Farquhar et al., 1980), a stomatal model (e.g. Ball et al., 1987) and an energy and mass transport sub-model (Müller et al., 2007). The implementation of different models can be interesting to compare the validity of the models and assess the value of working with a more complex model considering
the corresponding disadvantages (see section 1.5, last paragraph). Aside from photosynthesis, growth and respiration are two dominant factors in determining the carbon balance. They can be implemented in a similar way as in process-based models (Vos et al., 2010).

The implementation of a mass-transfer model is not only important for nitrogen allocation but also for carbon (and water transport, see further). While the vertical nitrogen distribution in plants still requires research, since current concepts do not yet allow for a straightforward implementation in FSPMs (Vos et al., 2010), several concepts have been developed for sink-source relations of carbon (e.g. Marcelis & Heuvelink, 2007; Lacointe, 2000; Génard et al., 2008). It must be noted however, that an unambiguous theory on assimilate partitioning is presently still unavailable (Marcelis & Heuvelink, 2007). Consequently, allocation models are mostly empirical. A brief overview of five concepts of carbon allocation modelling (i.e. descriptive allometry, functional equilibrium, canonical modelling, sink regulation and transport-resistance (arranged from least to most complex)) is given in Marcelis & Heuvelink (2007). Sink regulation is a simple concept that is often applied in plant modelling (Kang & de Reffye, 2007; Dingkuhn et al., 2006). The idea is based on the assumption of one common, shared assimilate pool in a plant (Heuvelink, 1995) where dry-matter allocation is primarily determined by the sink strength (Marcelis, 1996). The transport-resistance model is based on Ohm’s law, using concentration gradients and transport resistances (Vos et al., 2010). However, this addition is considered to be an unnecessary complexity in many crop models (Dingkuhn et al., 2006; Marcelis & Heuvelink, 2007).

Current literature on nitrogen uptake and allocation is extremely scarce. Bertheloot et al. (2011) have presented a first mechanistic model for nitrogen economy within a plant (i.e. wheat). They succeeded in accurately assessing the above ground distribution of nitrogen taking the effect of soil nitrogen availability into account. The simulations were based on the turnover characteristics of Rubisco in each organ, stimulated by light interception. Extension of this approach may prove useful as a means to simulate nitrogen distributions in FSPMs (Vos et al., 2010). Soybeans however have the added complexity of rhizobia symbiosis, which strongly influences the nitrogen balance. This can be an important incentive to expand the above ground simulations we have currently done to incorporate root architecture and nodulation. An empirical model for simulating soybean root and nodulation development based on L-systems was presented by Han et al. (2007). Even though their focus lies on the understanding of the underlying control mechanisms of nodulation autoregulation rather than nitrogen uptake and allocation, their morphological model can be considered an interesting framework for our model. Furthermore, models incorporating functional root architecture can play a key role in understanding soil-root interactions under different soils conditions, which can strongly influence design and testing of sustainable cropping systems (Pierret et al., 2007).

Water transport is seldom specified in FSPM literature. Two main approaches exist for simulating xylem water transport: i) Darcy flow combined with water storage and conductivity losses (Hydraulic approach; Fruh & Kurth, 1999; Dauzat et al., 2001; Steppe et al., 2006) or ii) the electrical analogue approach (Steppe et al., 2006; Da Silva et al., 2011) similar to the transport-resistance model for assimilate allocation (Ohm’s law). Either way, modelling water transport requires models or data on leaf transpiration, soil water availability and the xylem circuit itself (Da Silva et al., 2011). Leaf transpiration in our current model has been assessed by a model designed to estimate evapotranspiration (Allen et al., 2006). However, more complex models are available often combining transpiration and sap flow (e.g. transpiration can be used as an input to calculate sap
flow (Steppe et al., 2006) or leaf transpiration can be calculated based on sap flow (which in turn is calculated using the hydraulic architecture of the plant; Dauzat et al., 2001). Alternatively transpiration is included in coupled models that combine photosynthesis models with stomatal models (Müller et al., 2007; Kim & Lieth, 2003). Ideally, one of these coupled models could be implemented as an integration of the photosynthesis and transpiration models. The resulting transpiration along with stem diameter variations can then be used to assess the plant’s sap flow and eventually the turgor pressure at every plant organ (Steppe et al., 2006; De Schepper & Steppe, 2010; De Swaef & Steppe, 2010). The calculated turgor pressure at every organ can then be related to gravitropy of the organs (directly impacting the plant’s morphology) and used to incorporate a turgor-driven growth model, which is currently absent in FSPMs.
Conclusion

We have presented our rationale behind the creation of a soybean FSPM as being a means to assess the feasibility of soybean production in Flanders. Since we will not only strive to optimise the management regime but also work towards identification of the crucial traits that affect soybean yield in temperate regions (as a means to guide the current breeding programs), the one-dimensional approach used in current soybean crop models is inadequate. Hence, this thesis was aimed to take the first steps towards the creation of such a complex FSPM.

We chose to create the FSPM in GroIMP using the XL programming language because it provided the benefit of object-oriented programming. In a first step we constructed a descriptive developmental model for soybean. We have done so by integrating a large amount of experimental data related to the plant’s geometry and topology during growth as well as the timing of organ development in the model. We translated this developmental data at discrete timepoints into a description of continuous development using optimised sigmoid Boltzmann growth curves. The leaflet shapes were described by fitting a fourth degree polynomial on leaf scans. Afterwards, we reduced the amount of independent parameters in the model by finding phytomer-dependent allometric relations in the parameters. An important conclusion was that leaflet shapes appeared to be independent on leaf rank, and that changes in leaflet shape were caused primarily by difference in the length-to-width ratio of the individual leaflets. This indicated a strong genetic regulation on the leaflet shape, especially if this behaviour is observed in other genotypes.

Once the morphological model was implemented, we integrated a basic transpiration model to illustrate the ease of implementing such a process-model once the framework is in place. The model also allowed us to evaluate changes in management regime or plant morphology on light interception, although we acknowledge the uncertainty on these comparisons as the model is still in its very early stages.

The overall result was a structured three-dimensional spatio-temporal model that will serve as a stepping stone for the further construction of a more complex soybean FSPM. The implementation of further ecophysiological processes can now be integrated immediately with a step-by-step approach as the basic plant organs were already modelled. In other words we provided a framework into which the functional part of the model can easily be expanded and the morphological part can be freely adapted and improved.
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