Modeling of Biomass Acquisition and Partitioning in the Architecture of Sunflower

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Abstract

A mathematical sunflower growth model is presented that simulates interactions between plant structure and function. Dual-scale automaton is used to simulate plant organogenesis from germination to maturity on the basis of organogenetic growth cycles that have constant thermal time. Plant fresh biomass production is computed from transpiration, assuming transpiration efficiency to be constant and atmospheric demand to be the driving force, under non-limiting water supply. The fresh biomass is then distributed among expanding organs according to their relative demand. Demand for organ growth is estimated from kinetics of potential growth rate for each organ type. These are obtained through parameter optimization against an empirical, morphological data sets by running the model in inverted mode. Potential growth rates are then used as estimates of sink strength in the model. These and other "hidden" plant parameters are calibrated using the nonlinear, least squares method. The resulting model accurately simulated the dynamics of plant growth, architecture and geometry, enabling 3D visualization. The potential of the model's underlying concepts to simulate the plant's morphological plasticity in different resource situations is discussed.

Keywords: sunflower, *Helianthis annum* L., simulation, model, architecture, biomass partitioning

1 Introduction

Most quantitative growth models of plants are based on a description of ecophysiological processes, and can be used to compute synthetic and global variables of plant growth such as crop yield from physical variables e.g. temperature, light or morphological descriptors e.g. leaf area index [1, 2, 3]. However, these models rarely treat plant morphology in detail, and their lack of feedback among growth processes, plant architecture and phenology have been identified as a limitation for plant growth prediction. For example, Dingkuhn et al. [4] simulated the hypothetical effects of plant type modifications on yield, such as biomass partitioning among organs and nitrogen distribution among horizontal canopy strata, but these morphological features had to be forced because the model used did not link

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morphogenetic processes to physiological sinks.

On the other hand, computer graphics scientists developed models that represent plants very realistically in 3 dimensions, for example using softwares based on L-systems [5] or automaton [6, 7]. If the objective is to represent plant morphogenesis without a metabolic basis, high degrees of architectural and geometric fit can be achieved, and the resulting 3D representations can be used for different applications such as computing light interception [8, 9]. The lack of environmental control of growth through the plant's physiological apparatus, however, limits the biological and agronomic usefulness of such models.

Recently, new structural-functional plant growth models such as LIGNUM [10], and AMAPHydro [11] were presented to simulate plant morphogenesis on a biomass basis. In these model, plant growth is computed incrementally and the biomass acquired is distributed among organs generated by the architectural model, which is at the same time a phenological model. Final organ size is variable depending on biomass budgets, but constrained by allometric rules.

Such models are based on discrete events and a large number of empirical rules and parameters. In contrast to mathematical models, they require much computational time, particularly for the representation of large and complex structures such as trees. Furthermore, the calibration of a large number of parameters, many of which are not accessible to measurement and thus need to be optimised with genetic algorithms or similar techniques, is likely to leave conceptual or programming errors unnoticed. Mathematical modeling approaches, such as the one proposed here, are "cleaner" and have a surprising capacity to dynamically represent complex systems as long as their behaviour is consistent (underpinning "genetic" properties remain unchanged), but meet limitations where the behaviour of the modeled object itself changes. This study is part of a project that explores the potential of mathematical models to simulate plants with a minimum of discretionary forcing.

The challenge is to efficiently connect two main biological processes in an interactive and dynamic manner: development (including phenology and organogenesis) and growth (including biomass acquisition, conversion and distribution within the architecture). These two groups of processes can be seen as parallel sub-systems implemented incrementally, their interactions constituting part of the phenotype's plasticity. This model being in its early stages of development, we limit such interactions to trophic (assimilation related) effects on organ size and the resulting plasticity of plant geometry. A number of allometric relationships in plant geometry are believed to be robust and are therefore considered constant, enabling the model to remain simple.

The present paper introduces the basic concepts behind the model, then describes the relationship of the rate of organogenesis and of fresh biomass production with environmental conditions, then presents the allometric relationships of sunflower as derived from a field experiment. We discuss procedures for calibration of sink strength and expansion rate parameters, and finally present simulations of biomass partition and the expansion of plant organs using 3D visualization.

2 The Model

2.1 Underlying concepts

The GreenLab model was designed to provide dynamic representations of the morphogenesis and architecture of a plant on the basis of a minimal number of mathematical

equations and metamorphic rules. The model is parameterised by optimisation procedures using a fairly extensive set of botanical and morphological descriptors measured on a sample plant in the course of its development, and subsequently is able to reconstruct identical or divergent phenotypes by implementing the same rules and parameters to the same or different environments. It is thereby capable to simulate some of the phenotypic plasticity of a genotype, as far as these architectural and morphological deformations result from fluctuations in biomass acquisition. The model, however, does not claim to be fully mechanistic with regards to physiological processes and fluxes involved in growth. In fact, it is highly empirical and some of its underlying rules, such as a non-linear relationship between leaf surface and assimilation rate, are rather intuitive. The model explores, and in fact demonstrates as we will present, the possibility to realistically mimic with a small set of mathematical rules not only a complex plant architecture but also its morphogenesis and resource dependent variability.

The model functions parameterised by optimisation are (1) the hypothetical, non-linear relationship between leaf size and assimilation, and (2) functions describing general shape of sink strength kinetics for each type of organ from its initiation to achievement of final size. Model parameters pertaining to botanical structure and metamorphic rules, essentially non mathematical, are calibrated manually.

2.2 Biological assumptions

Modeling of plant growth and architecture relies on biological assumptions borrowed from botany and crop physiology. We distinguish between trophic (growth related) and phenological (development and differentiation related) processes. At the present stage of model development, at which we aim at evaluating the principal concepts, these assumptions are cast in a small number of very basic rules.

2.2.1 Developmental processes

We consider here two aspects of phenology, the temporal and topological organisation. The temporal organisation is based on thermal time by accumulating the daily mean air temperature above a genetic base temperature [12]. No optimal or maximal temperatures [13] are considered at this stage in order to keep the model simple. During each period, or growth cycle (GC), a cohort of organs is produced [14]. For simplicity we assume the thermal time elapsing during a GC to be constant throughout plant development. Maximal organ lifespans are also measured in thermal time. A GC may measure between a few days (case of herbacious plants) and one year (temperate trees). The phytomers produced during one GC are called growth units (GU). The GC also serves as generalised time increment for model execution, which therefore depends on the species and is quite different from that of common crop models (typically, 1-day time increments).

The topological organisation is based on discrete botanical entities (organs) of different type, such as internodes, leaves, flowers and their components, which generally represent metamorphic variations of the basic unit the phytomer. Each phytomer is produced by terminal or axillary meristems, resulting in a tree structure. The organs themselves evolve on their individual, finite, thermal-time axes and are therefore characterised by a certain physiological age (PA), which is an important determinant of their demand for assimilates to grow.

A phytomer consists of an internode and a terminal node bearing leaves (or their various metamorphoses, for example in the case of reproductive organs) and axillary buds

containing a fresh meristem. The parameters characterising a specific phytomer depend on the type of meristem it originated from. Meristem properties depend on the general type (shoot or root, apical or axillary) and position within the plant structure (e.g. ortho- or plagiotropic behaviour). In contrast to apical meristems, which extend existing axes (e.g. branches, tillers, stems), axillary buds create new axes (branching).

Development processes can be restricted to a given organ and will then be governed by its PA. Plant level development processes such as floral induction, however, are systemic and affect many or all shoot meristems, depending on dominance rules. These systemic phenomena require the notion of a chronological age (CA) for the entire plant, even in the case of indeterminate or perennial plants.

2.2.2 Biomass growth

For the current, rather conceptual studies with GREENLAB, we assume dry matter (dm) assimilation to be proportional to transpiration, i.e. water use efficiency (WUE) to be constant [15]. For example, WUE of the C4 crop maize is about 4 mg (dm) g^{-1} (H_2O), and that of the C3 crop potato is about 2 mg g^{-1} if measured over longer periods [16]. WUE is not much affected by crop water deficit but depends on climate, particularly evaporative demand [17]. For the purpose of obtaining a notion of volume and weight of the wet plant biomass, we assume an arbitrary moisture content of 0.8 (water over total weight).

In its conceptual, extremely simple version presented here the model applies an evaporative demand [18] homogeneously to all leaf surfaces, and translates it into a proportional transpiration rate. Two leaf size dependent, empirical attenuation parameters derived from the optimisation procedure during model parameterisation calibrates the relationship between evaporative demand and leaf transpiration, and thus, biomass assimilation. Into this hidden parameters are lumped a number of physiological processes such as differential exposure of leaves (shading) and regulation of stomatal resistance, which at this point are not considered in detail. (Two more detailed model versions are being developed, one that simulates in detail the 3D light distribution in the canopy as a means for weighted implementation of evaporative demand, and another that implements a full carbon and water balance at the plant scale. Only this latter version will simulate a root system and the effects of water deficit.)

The amount of fresh biomass produced during a GC, considered a transitory reserve pool, is entirely converted into new organs which have been initiated according to the automaton-driven phenology model. It is assumed that organs of a given type do not vary in shape nor in the duration and kinetics of the relative sink strength they exert during their growth. However, they may attain variable final sizes, depending on how many sinks have to share the transitory reserve pool. No feedback of biomass acquisition on organogenesis is simulated.

2.3 Modeling

2.3.1 Dual-scale automaton based organogenesis modeling

Dual-scale automaton was used to simulate the topological structure of sunflower [19]. At the cycle level, we use two states to simulate the organogenesis of a sunflower that produces 37 vegetative phytomers. Each state presents a different kind of phytomer corresponding to position on the main axis (Fig.1).

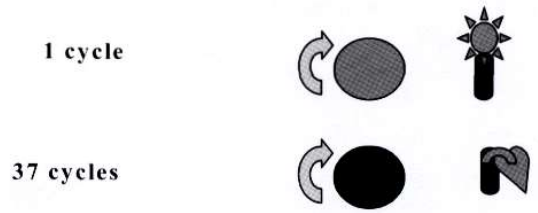

Fig.1 Simulation of sunflower organogenesis by an automaton

2.3.2 Fresh biomass based photosynthesis modeling

Suppose that plant biomass production at GC n is Q_n .Considering the above assumptions, Q_n is the sum of all leaf contributions at GC n except for the biomass of plant at the beginning of the first GC which originates from the seed. Suppose that the biomass produced by each leaf depends only on its surface S according to an empirical function $f(S,r_1,r_2)$. Here r_1 and r_2 are hidden parameters to be computed by optimization [20]. In our model, we approach the effect of the leaf surface on its potential assimilation rate by the equation $f(S,r_1,r_2)=\dfrac{1}{r_1/S+r_2}$ which is an hyperbola in the valid domain for plant growth.

Mono-culm sunflowers create a new metamer during each organogenetic cycle. Supposing the blade area of the leaf appearing at ChA k is S_k , the total biomass Q_n generated by all green leaves at ChA n can be expressed by:

$$Q_n=\sum_{k=1}^{n} f(S_k,r_1,r_2) \tag{1}$$

The expansion time of organ O appearing at ChA i on a plant structure at ChA n is $k = n\text{-}i+1$, and $k = t_o$at the end of finished its growing period t_O (t_O can be measured directly on the plant). The ability of living organ O (blade B, petiole P, internode pith I, internode layer C or inflorescence F) to obtain biomass is denoted as $p_o\varphi_k^o$, p_O being a hidden parameter and φ_k^o a normalized function computed by the optimization. Q_{n-1} is available to satisfy demand for plant growth and is thus distributed among all organs whose growth period falls partly or entirely into the cycle GC n. The biomass increment of organ O at GC n is described as Equation (2):

$$\Delta q_{i,n}^{O}=\frac{p_O\varphi_k^{O}Q_{n-1}}{D_n} \tag{2}$$

The total biomass $q_{i,n}^{O}$ accumulated in this organ is the sum of $\Delta q_{i,n}^{O}$ from GC i to GC n, i.e.:

$$q_{i,n}^{O}=\sum_{j=i}^{n}\Delta q_{i,j}^{O} \tag{3}$$

D_n is the demand from all the living organs for their growth at GC n, as in formula (4):

$$D_n = \sum_{O=B,P,I,C,F} p_O \left(\sum_{k=1}^{t_O} \varphi_k^O \right) \tag{4}$$

During t_O GCs, the biomass demand of organ O varies according function φ_k^o using an extended Beta law:

$$\Phi_k^O = \left(\frac{k+0.5}{t_O} \right)^{a-1} \cdot \left(1 - \left(\frac{k+0.5}{t_O} \right) \right)^{b-1} \cdot \left(\frac{1}{t_O} \right) \tag{5}$$

and

$$\varphi_k^O = \frac{\Phi_k^O}{\sum_{k=0}^{t_{O-1}} \Phi_k^O} \tag{6}$$

Here k takes only integer values, while a and b are real numbers which can be computed by Heuristic methods from the experimental data [20]. The beta function describes the generic kinetics of relative sink strength for an organ type, derived from its observed biomass evolution. It is important to note that a and b parameters are not determined by simple curve fit methodologies, which are unable to distinguish between the inherent function and its deformations caused by changing levels of competition among sinks. Instead, these are taken into account in an optimization process applied to the inverted model.

2.3.3 Geometrical modeling

We consider 4 types of organs: leaf blade, leaf petiole, and internode pith and ring. (The root system is at this stage not taken into account.) For petioles and internodes, shapes change during their growing periods according to allometric rules which are computed from observed data. The model thus estimates organ shape from its size using empirical rules. The primary descriptor of organ size in the model is fresh weight, which equals volume if specific weight of the tissue is considered to be 1. The allometric rules are presented in Section 3.2.

Geometrical modeling of the leaf

Fresh matter is partitioned between leaf blade and petiole according to their relative sink strength, which in turn is estimated from observed geometry. Suppose that the contour of the leaf blade is arbitrary and its thickness ε is constant. The available quantity of fresh matter to build the leaf blade is $q_{i,n}^B$ So the area of the blade surface is:

$$S_{i,n}^B = \frac{q_{i,n}^B}{\varepsilon} \tag{7}$$

We regard the petiole as a perfect cylinder. From the experimental data we established an allometric relation between the length $l_{i,n}^P$ and the area of cross section $S_{i,n}^P$:

$$l_{i,n}^P = K_P (S_{i,n}^P)^{\beta_P} \tag{8}$$

and this leads to formula (9) if the specific weight of the tissue is supposed to be 1:

$$q_{i,n}^P = l_{i,n}^P \cdot S_{i,n}^P \tag{9}$$

The dimensions of the petiole (length and area of cross section) are then:

$$\begin{cases} l_{i,n}^{P} = \sqrt{b_p}.\left(q_{i,n}^{P}\right)^{\frac{1+\alpha_P}{2}} \\ S_{i,n}^{P} = \sqrt{\frac{1}{b_p}}.\left(q_{i,n}^{P}\right)^{\frac{1-\alpha_P}{2}} \end{cases} \quad (10)$$

with b_P and α_P being shape coefficients obtained with equation (11) where β_P and K_P are fitted from experimental data using Equation (8):

$$\begin{cases} \alpha_P = \frac{\beta_P - 1}{\beta_P + 1} \\ b_P = K_P^{\,1-\alpha_P} \end{cases} \quad (11)$$

Geometrical modeling of the internode

For a generic geometrical model of internode, we need to consider two cases: primary growth (the pith) and, in the case of woody plants, secondary growth (rings). The pith grows in length and diameter during the first few GCs, before its length is fixed and further growth occurs only in the form of additional layers of concentric rings, along with lignification. The pith's geometric shape is regarded as cylinder with the same types of parameters b_I and α_I as for the petiole. Length and diameter of the pith with fresh matter $q_{i,n}^{I}$ are calculated accordingly as described. For secondary growth, a new ring is added encircling the pith, thereby increasing the diameter of the internode.

3 Parameters Estimated from Field Experiment

3.1 Methods

A field experiment on sunflower was conducted at China Agricultural University in 2000. A large distance between plants (0.6m) was chosen to minimise competition. Irrigation and nutrients were applied at non-limiting rates. Tillers were pruned upon appearance to obtain a mono-culm architecture. Destructive measurements were conducted on 2 plants every two weeks. The fresh weight of each internode, petiole and blade, the diameter and length of each internode and petiole, and the leaf area of each blade were measured. The fresh weight of the inflorescence was also measured when preseent. Meteorological data were collected at a nearby weather station. The Penman-Monteith equation proposed by FAO was used to compute potential evapotranspiration [18](http://www.fao.org/docrep/x0490e/ x0490e00. htm#contents), and plant transpiration was computed from potential evapotranspiration and plant leaf area index [21].

3.2 Organogenesis and fresh biomass production

The organogenesis of sunflower plants followed the law of sum of temperatures (Fig.2a) and fresh biomass production was proportional to cumulative plant transpiration, except for the

last observation where the production of grains with low water and high lipid content caused deviating results (Fig.2b). These were ignored at this stage, but will be taken into account as the model evolves.

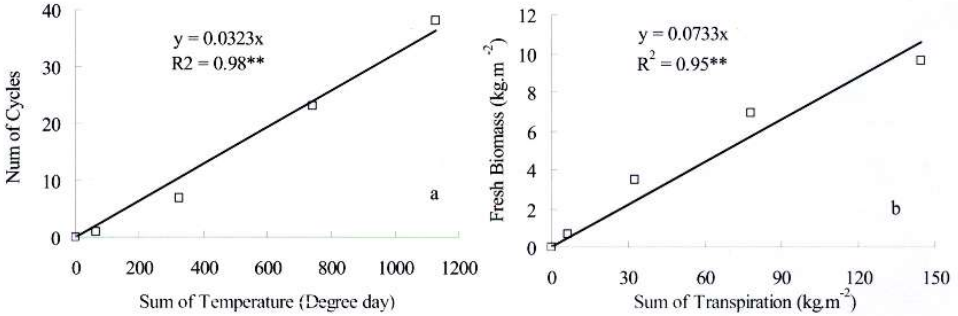

Fig.2 Relationship of plant organogenesis and the sum of temperature (a) and relationship between plant fresh biomass production and the sum of plant transpiration (b)

3.3 Morphological allometries

The specific weight, or density, of organs was calculated from their volumes and weights. From 2 June to 12 August 2000, 12 plants were measured and the mean densities were 0.921 $g.cm^{-3}$ for internodes and 0.976 $g.cm^{-3}$ for petioles (Fig.3a). We considered these values sufficiently close to the density of water, and therefore assumed a constant value of 1.0$g.cm^{-3}$, for all simulations. Volume and fresh weight were therefore considered numerically identical.

A linear relationship was found for the leaf blade between fresh weight and surface area, with an overall coefficient of 0.042 $cm.g^{-2}$ derived from 12 plants and different leaf positions and stages of expansion (Fig.3b). Assuming a density of 1, this allows us to consider a constant thickness for leaf blades.

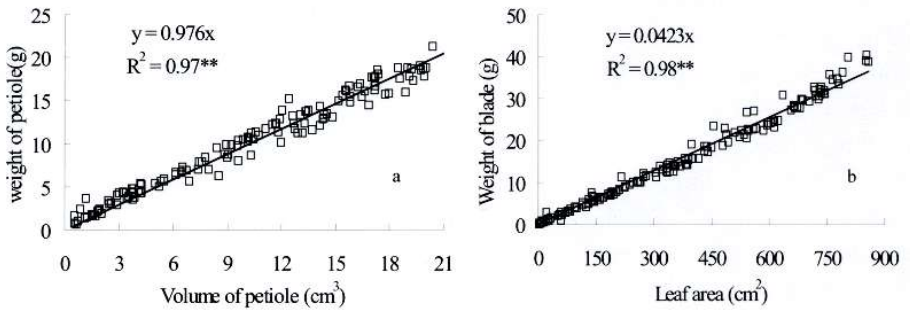

Fig.3 Fresh weight vs. volume for petioles (a) and fresh weight vs area for leaf blades (b)

The allometric relations between petiole length l_p and petiole cross section area S_p can be expressed by Equation (8). With K_p and β_p obtained from direct measurements, b_p and α_p were computed according to Equation (11). Fig.4 shows the dynamics of b_p and

α_P for the petiole, α_P decreasing gradually from -0.30 to -0.45, and b_P increasing from 20 to about 90 and then levelling off.

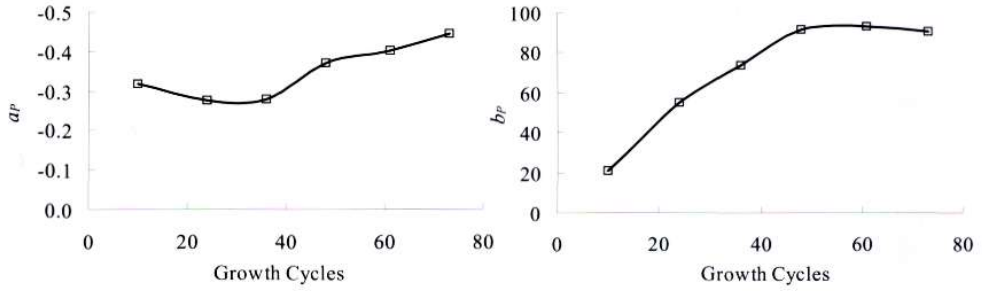

Fig.4 The allometric parameters b_P and α_P of sunflower petioles at different growth stages

The allometric relationship for the pith between its length l_e and cross section area S_e can be determined from the last 3 internodes where the contribution of the ring to the total diameter is still small. The relationship is $l_e = 2.285\,(S_e)^{0.9904}$, this gives b_e = 2.387 and α_e = -0.0526. Unfortunately, total weights of the rings of the internodes that constitute the stem could not be quantified because the internal boundary of the pith was not clearly discernible.

4 Fitting Values for Hidden Parameters

Although some plant parameters, such as those describing allometric rules, can be measured directly, other parameters such as potential organ expansion rates are "hidden" in the cumulative process, and distorted by competition for resources. We need special computational algorithms to calculate their values.

From field measurements on plant architecture, we can organize target files that contain records of organ weight, volume dimensions at different growth stages. The basic assumption is that parameters for a given organ type have constant values across GCs, despite the observed variation in organ size. By running the model in reverse mode and fitting it to observed data, the sink strengths and expansion rates are estimated by using the nonlinear least squares method(CornerFit) [20], resulting in optimized values for parameters.

The sunflower studied here had 37 phytomers, corresponding to 37 GCs. At GC=37 inflorescence appears and the organogenesis ends, but photosynthesis and the organs' expansion continue until GC=63 according to the sum of temperatures. Expansion time for blades, petioles and internodes was estimated to be 15 GCs, and that for the inflorescence 25 GCs. Fig.5 presents a comparison between the observed and fitted data of a sunflower plant having completed 60 GCs. A satisfactory fit was obtained for the internode diameter (Fig.5a), leaf blade surface (Fig.5b), petiole fresh weight (Fig.5c) and fresh weight of the inflorescence (Fig.5d).

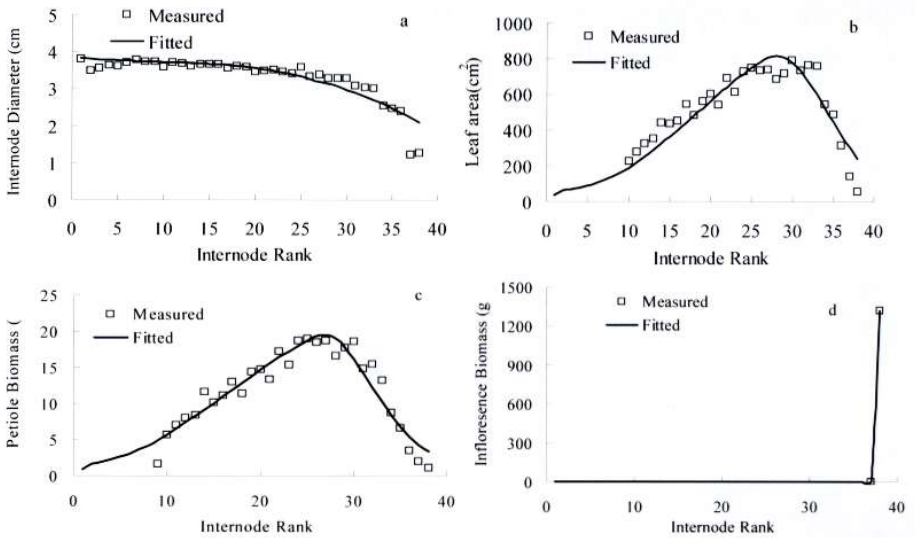

Fig.5 Fitting results on sunflower plants having completed 60 GCs using CornerFit software

Table 1 presents the fitted p (sink strengths) and r_1 and r_2 (function relating relative assimilation rate to leaf size) for sunflower. Values of parameters were stable or shifted slightly, except the sink strength of inflorescence(pf) which was zero during vegetative stages and increased rapidly from 38 GCs onwards, indicating that most of the biomass was then partitioned to the inflorescence. At the same time, r_1 and r_2 changed, possibly indicating effects of terminal (monocarpic) senescence that was not explicitly taken into account in the model.

Table 1 Fitted hidden parameters of sunflower at different growth stages

Stages	23	39	47	60
p_B	1	1	1	1
p_P	0.63	0.75	0.67	0.55
p_I	0.043	0.057	0.073	0.058
p_c	0.043	0.059	0.055	0.046
p_F		10	632	855
r_1	16.82	17.78	28.33	44.25
r_2	0.54	0.32	0.095	0.06

5 Simulated Growth of Sunflower Plant and its Visualization

Fig.6 hows the simulated biomass production and partition ing for the 60 cycles of a sunflower plant. Classical features such as exponential growth during early stages, followed by linear growth and, as leaf production ceases, decreasing growth rates are visible. The biomass partitioned to leaf and internodes increase s each cycle before the inflorescence appearance because total biomass production increase s, and they decrease rapidly after then

because of strong competition from the inflorescence.

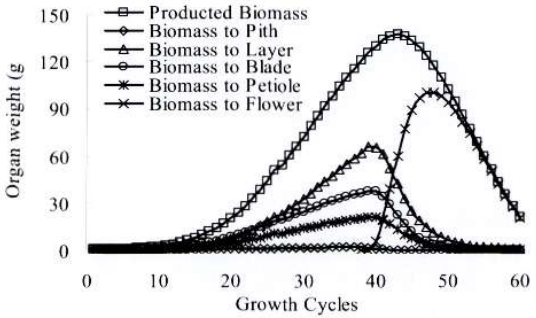

Fig.6 Biomass partition to different organs in each cycle in sunflower

Fig.7 illustrates that although the expansion time of leaf blades on different positions are the same, the slope of expansion curve is different, because the biomass produced and the number of competing sinks varies among different GCs. During the final cycles, no more biomass is partitioned to leaf blades and only very little to the internode pith, due to a dominant inflorescence sink. Consequently, leaf blades stop growing but the diameter of internodes still increase because of the addition of new layers. Also shown in Fig.7 is a 3D representation of sunflower plants at 38 and 60 GCs constructed by the model.

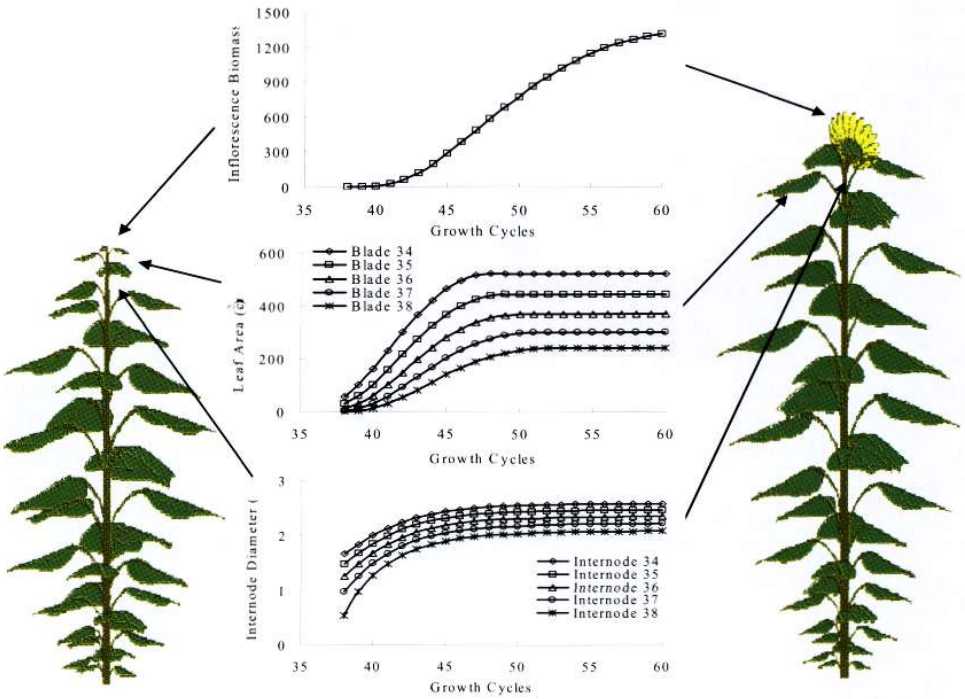

Fig.7 Organ expansion kinetics and 3D visualization of sunflower plants at 38 and 60 GCs

6 Perspectives

The simulations demonstrate the potential of mathematical, architectural models to incorporate some physiological aspects of plant functioning, and go beyond a mere reconstruction of a complex object. In particular, this approach allows the representation of highly variable organ size despite of constant, "genetic" parameters, on the basis of a very simple notion of competition among sinks. The model in its present form, however, over-simplifies a number of processes, such as photosynthesis and assimilate conversion to biomass, and is not able to take into account important resources such as water. The root system is so far not represented, and light harvesting is at this stage insensitive to shading effects within and among plants. Such features will be incorporated as a next step. Conceptually more important than these issues are two mutually related questions: to what extent can mathematical models, in contrast to discrete-event based models, handle plant responses to variable environments? And to what extent can such models, that are demonstrably good at "recreating" an organism using detailed information, be used to extrapolate plant behavior beyond the observed situation ? Research is in progress to answer these questions.

7 Conclusion

In this paper a new sunflower growth model was presented that combines a simple, leaf area and transpiration based calculation of biomass acquisition with dynamic plant architecture, which in turn generates the sinks among which the biomass is distributed. The two basic functions are executed in a parallel fashion using growth cycles as incremental units. A dual-scale automaton is used to simulate phytomer creation at the rhythm of these growth cycles, thus creating sites that are filled with biomass according to their sink strength and available resources. Additional allometric rules are used to achieve representation of plant geometry and morphology. The parameters of this model are simple and small in number, but permit simulation of feedback processes among plant growth, architecture and functioning in an iterative and cyclic way. Satisfactory fittings were obtained by using the least squares method, resulting in accurate representation of growth dynamics, fresh weight distribution and 3D appearance of the plant. Further research and model development is needed, however, to take into account the different dry matter and energy content of vario us tissues, to simulate a root system, and to determine to what extent this modeling approach is able to predict plant growth in environments that differ from data sets used for parameterisation.

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