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SUNLAB: a Functional-Structural Model for Genotypic and Phenotypic Characterization of the Sunflower Crop

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Abstract—A new functional-structural model SUNLAB for the crop sunflower (*Helianthus annuus L.*) is developed. It is dedicated to simulate the organogenesis, morphogenesis, biomass accumulation and biomass partitioning to organs in sunflower growth. It is adapted to model phenotypic response to diverse environment factors including temperature stress and water deficiency, and adapted to different genotypic variants. The model is confronted to experimental data and estimated parameter values of two genotypes “Melody” and “Prodisol” are presented. SUNLAB parameters seem to show genotypic variability, which potentially makes the model an interesting intermediate to discriminate between genotypes. Statistical tests on estimated parameter values suggest that some parameters are common between genotypes and others are genotypic specific. Since SUNLAB simulate individual leaf area and biomass as two state variables, an interesting corollary is that it also simulates dynamically the specific leaf area (SLA) variable. Further studies are performed to evaluate model performances with more genotypes and more discriminating environments to test and expand model’s adaptability and usability.

Keywords—Sunflo; Greenlab; Sunflower; Functional-structural model; Specific Leaf Area; Genotypic variability.

I. INTRODUCTION

As one of the major oilseed crops worldwide, sunflower production has to face the growing social demand in a context of strong ecological and economical constraints: growers are confronted to the challenge of increasing sunflower productivity under changing climatic conditions while maintaining low-input levels and reduced costs. A partial response to this challenge could be found by breeding new genotypes and by identifying the best genotype, among a set of existing ones, for a given location and for given management practices; see for instance [1].

Assessments of genotype performances in *in situ* experimental trials hamper the breeding process by temporal, logistic and economical difficulties. Indeed, genotypes perform differently depending on the environmental conditions (soil, climate, etc) and the management practices (sowing date, nitrogen inputs, irrigation, etc). Therefore a large number of trials are needed to explore a sufficiently diverse set of genotypes x environment x management (GxExM) combinations in order to characterize these complex interactions. An emerging approach to overcome

these difficulties relies on the use of models represented as a set of biophysical functions that determine the plant phenotype in response to environmental inputs. Models can help in breeding strategies and management by dissecting physiological traits into their constitutive components and thus allow shifting from highly integrated traits to more gene-related traits that should reveal more stable under varying environmental conditions [2][3].

Consequently, an important question to examine is how to design models that can be used in that context. The models should simulate the phenotypic traits of interest (e.g. yield) with good robustness and predictive capacity. The models should also present a trade-off between mechanistic aspect and complexity: Chapman et al [4] state that, for such use, a growth model should include ‘principles of responses and feedbacks’ to ‘handle perturbations to any process and self-correct, as do plants under hormonal control when growing in the field’ and to ‘express complex behavior even given simple operational rules at a functional crop physiological level’. Casadebaig et al [5] discuss that question in the case of their model SUNFLO [6]. SUNFLO is a biophysical plant model that describes organogenesis, morphogenesis and metabolism of sunflower (*Helianthus annuus L.*). It has shown good performances to identify, quantify, and model phenotypic variability of sunflower at the individual level in response to the main abiotic stresses occurring at field level but also in the expression of genotypic variability [5]. The authors mixed mechanistic and statistical approaches to deal with highly integrative variables such as harvest index (HI). HI is determined by a simple statistical relationship dependent on covariables previously simulated by the mechanistic part of the crop model throughout the growing season. Although this statistical solution and the large datasets used for its parameterization conferred good robustness to the prediction of HI and thereby crop harvest, feedback effects of biomass partitioning on other processes cannot be taken into account. Moreover, it was shown in [6] that HI is the parameter that contributes the most to the coefficient of variation of the potential yield (14.3%). It was also shown that when ranking the processes in terms of their impact on yield variability, the first one was biomass allocation (before light interception according to plant architecture, plant phenology and far behind photosynthesis). Therefore, LecoEUR et al [6] suggest that a better formalisation of the trophic competition between

organs could be a way to improve our understanding of genotypic variation for biomass harvest index. In order to face this challenge, a new sunflower model, named SUNLAB, was derived from SUNFLO. The representation of plant topological development and allocation process at individual organ scale were inspired by the functional-structural plant model (FSPM) GREENLAB, that has been designed as a “source-sink solver” [7] and is accompanied with the appropriate mathematical tools for its identification [8]. SUNLAB thus inherits the flexible rules of sink competition for biomass partitioning at organ scale (blade, periole, internode and capitulum) from GREENLAB, together with the more detailed representation of ecophysiological processes and environmental stress effects on biomass production and yield from SUNFLO.

This paper will present in detail the mechanisms of SUNLAB, its parameters and identification procedure based on field experimental data. Afterwards, we illustrate the potentials of SUNLAB for genotypic characterization by comparing the parameters obtained for two genotypes, namely “Melody” and “Prodisol”. In the end, we discuss the use of SUNLAB for extracting specific leaf area (SLA, g cm^{-2}), i.e. the ratio of leaf area to dry leaf mass, which is an influent variable often associated with large uncertainty ranges [9].

II. MATERIALS AND METHODS

A. Modeling: SUNLAB modules

SUNLAB consists of five modules: phenology, water budget, organogenesis and morphogenesis, biomass accumulation, and biomass distribution. Phenology, water budget, and biomass accumulation modules are directly inherited from SUNFLO model. Organogenesis and morphogenesis module modifies SUNFLO module by defining each organ’s biomass initialization and termination thermal time. Biomass partition module is a new module. We describe here equations of these modules, briefly for those that have been inherited from SUNFLO - we refer to [5] and [6] for an exhaustive description - and in detail for the new contributions.

1) *Phenology*: Plant phenology is driven by thermal time. Cumulative thermal time since emergence on day d $CTT(d)$ (in $^{\circ}\text{C}\cdot\text{days}$) was calculated in (1) as the sum of the daily mean air temperature $Tm(d)$ ($^{\circ}\text{C}$) above a base temperature Tb of 4.8 $^{\circ}\text{C}$ common to all sunflower genotypes. Four key physiological stages, expressed as genotype dependent thermal dates (in $^{\circ}\text{C}\cdot\text{days}$), were defined: flower bud appearance (Ez), beginning of flowering ($F1$), beginning of grain filling (early maturation, $M0$) and physiological maturity ($M3$) [14]. Crop development can be accelerated by water stress, that causes overheating of the plant through the reduction of transpiration. This was modeled using a multiplicative effect on day d , $FHTR(d)$ with thermal time accumulation. The water stress effect on plant phenology $FHTR(d)$ is calculated as function of the fraction of transpirable soil water $FTSW(d)$ divided by a

genotypic parameter RT of response sensitivity to water deficiency, which is formulated in detail in [5]:

$$CTT(d) = \sum_{k=1}^d ((Tm(k) - Tb) \times (1 + \alpha \times (1 - FHTR(k)))) \cdot (1) \quad (1)$$

where $Tb = 4.8$ $^{\circ}\text{C}$ and $\alpha = 0.1$.

2) *Water budget*: fraction of transpirable soil water $FTSW(d)$ depends on the interaction of root system with the environment including soil features, soil evaporation, precipitations and irrigation. Soil features include horizontally soil particle size texture, humidity capacity, soil density. Plant transpiration decreases the available water in soil. $FTSW(d)$ is used to compute a water stress index and has effects on three processes: leaf expansion, plant transpiration, and biomass production. For example, for biomass production, $FTSW(d)$ acts as a constraint to effective radiation use efficiency $RUE(d)$ (gMJ^{-1}) based on crop’s maximal potential use efficiency $RUEp(d)$ (gMJ^{-1}):

$$RUE(d) = RUEp(d) \times \min\left(1, \frac{FTSW(d)}{RT}\right) \times FT(d) \times PHS \cdot (2) \quad (2)$$

where $FT(d)$ is thermal stress on day d , function of daily mean temperature [6] and PHS is a genotypic parameter giving the ratio of the genotype photosynthesis capacity to that of the reference genotype “Melody”.

3) *Organogenesis and morphogenesis*: The number of blades increases linearly with cumulative thermal time, . The number of emerged leaves on day d , $N(d)$, was thus calculated as:

$$N(d) = R \times CTT(d) + 1 \cdot (3) \quad (3)$$

where R (in leaves / ($^{\circ}\text{C}\cdot\text{days}$)) is the rate of leaf production. Leaf senescence occurs during the period of grain filling between $M0$ and $M3$. Consequently the number of senescent leaves $NS(d)$ was considered to increase in proportion to the time elapsed since $M0$ and was calculated as follows:

$$NS(d) = Ntotal \times \frac{M3 - CTT(d)}{M3 - M1} \cdot (4) \quad (4)$$

where $Ntotal$ is a genotypic parameter equal to the maximal number of leaves.

Since, in sunflower, leaf area distribution along the stem showed a bell-shape, total leaf area $A(d)$ (m^2) per plant, was calculated with a logistic equation:

$$A(d) = \frac{A1}{1 + e^{4 \times A3 \times (A2 - N(d)) / A1}} \cdot (5) \quad (5)$$

where $A1$ (m^2) is the maximal leaf area, $A2$ (m^2) and $A3$ (m^2) are respectively the rank and the area of the largest leaf of the plant. The calculation of senescent leaf area $AS(d)$ (m^2) is determined by a similar logistic equation but replacing $N(d)$ by $NS(d)$. The photosynthetically active leaf area $AA(d)$ (m^2) was estimated as the difference between total leaf area $A(d)$ and senescent leaf area $AS(d)$. Leaf area growth and senescence are affected by water stress and temperature stress coefficients described in detail in [5].

$$AA(d) = \frac{A1}{1 + e^{4 \times A3 \times (A2 - N(d)) / A1}} - \frac{A1}{1 + e^{4 \times A3 \times (A2 - NS(d)) / A1}} \quad (6)$$

From the emergence and senescence blades numbers, the thermal times of initiation $bladeInitTT(i)$ and senescence $bladeSeneTT(i)$ of each blade of rank i can be computed:

$$\begin{aligned} bladeInitTT(i) &= (i - 1) / R \\ bladeSeneTT(i) &= M3 - \frac{i \times (M3 - M1)}{Ntotal} \end{aligned} \quad (7)$$

The petiole i and the internode i from the same metamer of blade i has the same value of initiation thermal time. While petiole i has the same value of senescence time as $bladeSeneTT(i)$, senescence thermal time of internode i is the same as the accumulative thermal time in the end of the plant life. Capitulum initialization thermal time equates $M0$ and it grows until the end. With all the information of initialization thermal time and senescence thermal time of every organ, a general sunflower structure can be constructed. For every organ, besides their appearance and senescence thermal time, their expansion thermal time are also calculated, explained in section C: parameter identification.

4) *Biomass accumulation*: Daily increase in above-ground dry matter $DM(d)$ ($g m^{-2}$) was calculated from Monteith's equation (1977) linking dry matter production to incoming photosynthetically active radiation through two radiation efficiencies as follows

$$DM(d) = RUE(d) \times RIE(d) \times PAR0(d). \quad (8)$$

where $PAR0(d)$ ($MJ m^{-2}$) is the daily incident photosynthetically active radiation. $RUE(d)$ (gMJ^{-1}) is daily radiation use efficiency and $RIE(d)$ is daily radiation interception efficiency, estimated from Beer's law. In order to estimate the total above-ground biomass $CDM(d)$ ($g m^{-2}$) daily biomass production was cumulated from emergence

$$CDM(d) = \sum_{k=1}^d DM(k). \quad (9)$$

5) *Biomass distribution*: As in GREENLAB, the biomass produced by each leaf is distributed to all organs proportionally to their sink strengths and independently of

their position. Blades are sources. Blades, petioles, internodes, and capitulum are sinks. The total above-ground biomass $CDM(d)$ ($g m^{-2}$) is the total biomass of all leaves, petioles, internodes and the capitulum. For each individual organ, the duration of sink activity is equal to the organ expansion duration $epdTT$ ($^{\circ}C$), calculated since its initialization thermal time $initTT$ ($^{\circ}C$). Its sink competition ability $SA(d)$ depends on its type, its time of initiation $initTT$, $epdTT$ and its age. The density function of beta distribution is chosen to model this evolution, with three organ-specific parameters; the organ sink ratio SR and two shape parameters $sinkA$ and $sinkB$:

$$SA(d) = \begin{cases} SR \times \left(\frac{CTT(d) - initTT}{epdTT} \right)^{sinkA-1} \times \left(\frac{1 - CTT(d) + initTT}{epdTT} \right)^{sinkB-1} \\ = \frac{\left(\frac{sinkA-1}{sinkA + sinkB - 2} \right)^{sinkA-1} \times \left(1 - \frac{sinkA-1}{sinkA + sinkB - 2} \right)^{sinkB-1}}{\text{if } initTT \leq CTT(d) \leq initTT + epdTT} \\ = 0 \quad \text{otherwise} \end{cases} \quad (10)$$

On day d , the plant total demand $sumSink(d)$ is computed as the scalar product of the number of appeared organs to their daily sink activity $SA(d)$ corresponding to their expansion status. The part of the dry matter production, $DM(d)$, allocated to a single organ is proportional to its $SA(d)$ divided by $sumSink(d)$. For example the biomass allocated to the leaf at rank i at a day d is:

$$DM(d)_i = DM(d) \times SA(d)_i / sumSink(d). \quad (11)$$

In this way, the daily biomass increments and the cumulated biomass of every single organ can be simulated.

B. Field Experiments and Measurements

Experiments and measurements for designing and constructing modules and parameters directly inherited from SUNFLO are not presented in this paper, as they are described in detail in [6]. Data used for SUNLAB parameters estimation, simulation and application comes from an field experiment conducted in 2001 at SupAgro experimental station at Lavalette ($43^{\circ}36' N$, $3^{\circ}53' E$, altitude 50 m) on a sandy loam soil for five genotypes (Albena, Heliasol, Melody, Mirasol and Prodisol). Sunflowers were sown on 5 May 2001 at a density of about 6 plants m^{-2} and a row spacing of 0.6 m, in a randomized complete block design with four replications. Plots measured 5.5 X 13.0 m. The crop was regularly irrigated to avoid severe water deficits. It was also fertilized and showed no mineral deficiency. So its biomass production could be considered as potential.

During the experiment, meteorological data such as temperatures and radiation were recorded. $FTSW$ representing the available water in the soil was estimated. Organogenesis is described based on the phenomenological stages that are recorded every 2-3 days [6]. Once a week, six plants per genotype were harvested. Individual leaf areas

were estimated from blade lengths and widths. All the above-ground organs (leaves, stem, capitulum and seeds) were collected and then oven-dried at 80°C for 48 h. The dry weights of these organs were measured by compartments. Daily radiation interception efficiency $RIE(d)$ and daily radiation use efficiency $RUE(d)$ are respectively calculated and estimated based on field measurements as in [6].

C. Parameter Identification

Two genotypes “Melody” and “Prodisol” are referred in this paper. They are genotypes characterized by a large study of genetic improvement of sunflower during the last 30 years, and they are two of those most widely grown varieties in France. SUNLAB parameters can be decomposed in two subsets. One subset contains the parameters inherited from SUNFLO which keep the same values in SUNLAB (Table I). The other subset contains 17 additional parameters of SUNLAB which needs parameter estimation. They include 12 parameters that drive the sink competition (SR, sinkA, sinkB for four types of organs), and 5 parameters: $initTTadjust$ (°C), $epdTTA$ (°C), $epdTtB$ (°C), $internodeEpdTT$ (°C), $capitulumEpdTT$ (°C), explained together with the model mechanism defining organs’ biomass expansion.

For organs’ biomass initialization thermal time, according to the experimental criterion: leaves are recorded when lengths of their central vein are bigger than 4cm [10], in SUNFLO blade initialization thermal time $bladeInitTTi$ (°C) is blade appearance thermal time when leaf size could be measured, but then this leaf has already received a small amount of biomass. So in SUNLAB, an adjustment parameter $initTTadjust$ (°C) had to be added to $bladeInitTTi$ (°C) for calculating the initiation thermal time of blade biomass. Petioles and internodes of the same metamers share the same initialization thermal time. Capitulum begins its sink competition at plant age M0.

The biomass expansion duration of blades and petioles can vary with their rank: the variation is linear and depends on two parameters, $epdTtA$ (°C) and $epdTtB$ (°C). For example, blade rank i has expansion duration, expressed in thermal time, $bladeEpdTT(i)$ (°C):

$$bladeEpdTT(i) = bladeSeneTT(i) - (epdTtB - epdTtA \times i). \quad (12)$$

where $bladeSeneTT$ (°C) is the thermal time of leaf beginning of senescence. Internodes and capitulum have respective parameter $internodeEpdTT$ (°C) and $capitulumEpdTT$ (°C) to define its expansion.

Regarding the target data for parameter estimation, only blade areas were measured at organ scale. All other organs were only weighted at compartment scale. In particular, independent blade mass data was not available, while these data are needed for a better estimation of SUNLAB parameters. Therefore, profiles of individual blade mass were estimated as follows: at each date where total blade mass and total blade areas were measured at compartment

level, a virtual SLA value was computed and was used to generate a set of individual blade mass. The model can thus be viewed as a dynamic interpolation solver that generates both blade areas and mass between those fixed measurement dates. This will be detailed in the SLA study.

The non-linear generalized least squares method with Gauss-Newton method for optimization [8] was used for fitting these parameters to field data including total blade biomass, total petiole biomass, total internodes biomass, capitulum biomass and individual blade biomass. The estimation and the simulation for parameter verification were performed with a plant modeling assistant platform PYGMALION developed in Digiplante in Ecole Centrale Paris, France.

III. RESULTS AND ANALYSIS

A. Model Performances for Genotype Melody

Estimated values of SUNLAB subset of parameters for genotype Melody are shown in Table 2. Since the sink competition model is chosen to be proportional (all the daily produced biomass is allocated, no reserves), a reference sink value has to be set: conventionally, the sink of blades $SRblade$ is set to 1.

Simulations of total leaf area, radiation interception efficiency, total dry above-ground biomass, and individual blade area expansion are the same as in SUNFLO. Total blade biomass, individual blade biomasses, total petiole biomass, total internode biomass, and capitulum biomass are simulated by SUNLAB after parameter identification. Their comparisons with experimental data are shown in Fig.1. The simulated and observed values for individual blade areas and masses are displayed for each rank and seven different growth stages. The dynamics of compartment mass variations, as well as individual blade mass profiles, are satisfactorily reproduced by the model.

TABLE I. SUNFLO INHERITED PARAMETER VALUES

Parameters	Values	
	Melody	Prodisol
E1 (°Cd)	540	510
F1 (°Cd)	920	900
M0 (°Cd)	1160	1120
M3 (°Cd)	2060	1840
Nmax (#)	26	25
A1 (cm²)	5671	4575
A2 (#)	15.4	15.9
A3 (cm²)	613	498
k (#)	0.96	0.87

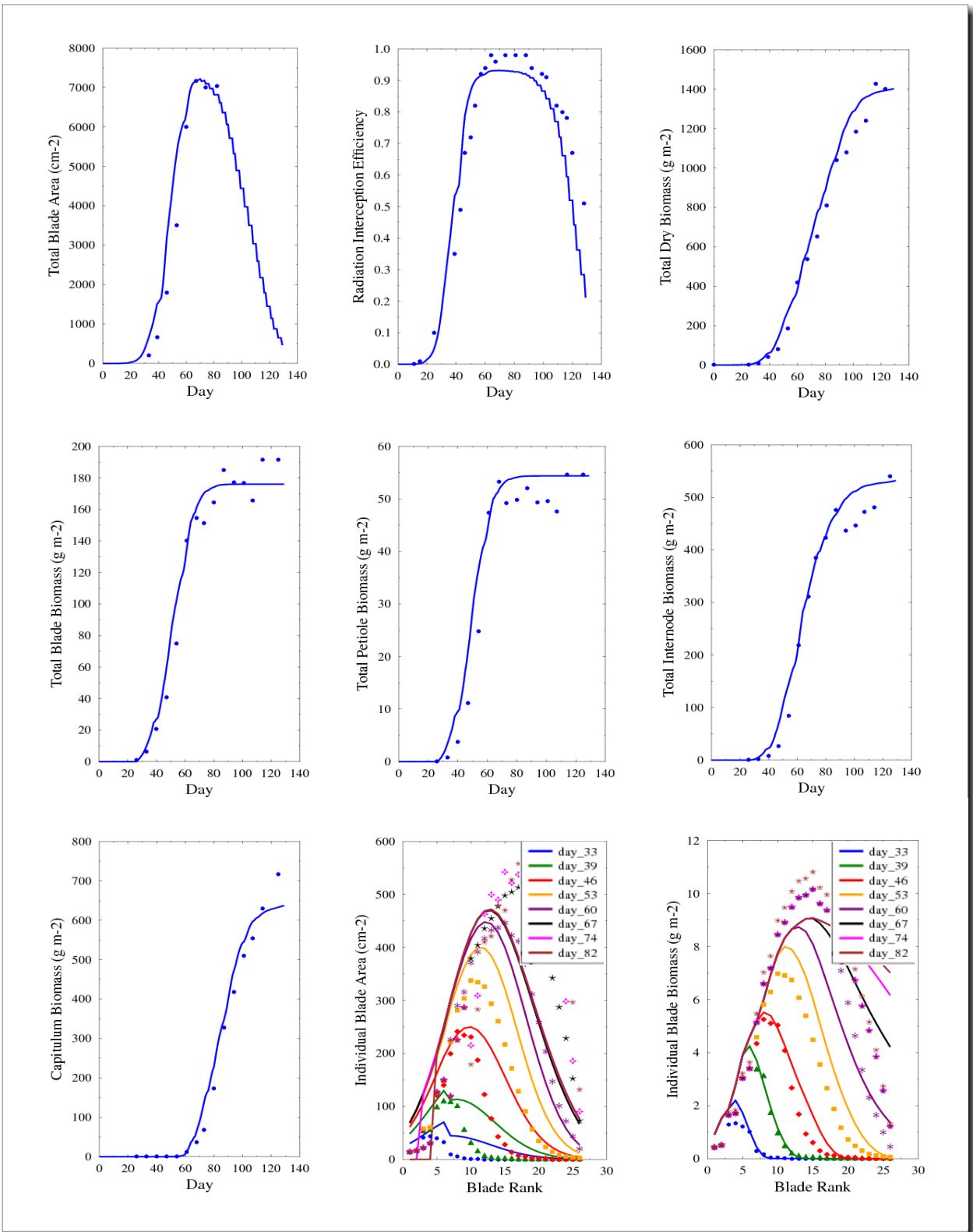


Figure 1. Experimental data (dot) and simulation (line) comparisons for the genotype "Melody". The last two graphs have blade rank for x-axis. Others have crop growth time as x-axis

B. Genotypic Variance in Model Performances

Simulation and field data comparisons of genotype Melody and Prodisol are shown in Fig.2. SUNLAB is able to reproduce the genotypic diversity in biomass partitioning.

In Table 2, significant parameters and their standard errors are compared between the genotype “Melody” and “Prodisol”. With a Student’s t-test, parameters of internode sink ratio SR and the parameter $sinkB$ in the sink variation function of internodes ($SR_{internode}$ and $sinkB_{intern}$) proved significantly difference between the two genotypes, while no clear evidence of genotypic variability was found for other parameters. According to those parameter features, internodes of Prodisol show an earlier peak of biomass

competition but a general low competition capacity than Melody (Fig.2). More rigorous parameter variance analyses and corresponding parameter estimation on more genotypes are to be carried out.

C. Model Application: an Exploratory Study of Specific leaf Area (SLA)

SLA is an important variable in plant growth modeling. For example, it determines blade surface area values based on blade biomass for further simulation loops in GREENLAB [7]. SLA is usually considered constant in those models. In reality SLA varies according to genotypes, leaf ranks and leaf growing periods, as it has been observed for instance for the SLA variations of wheat [9].

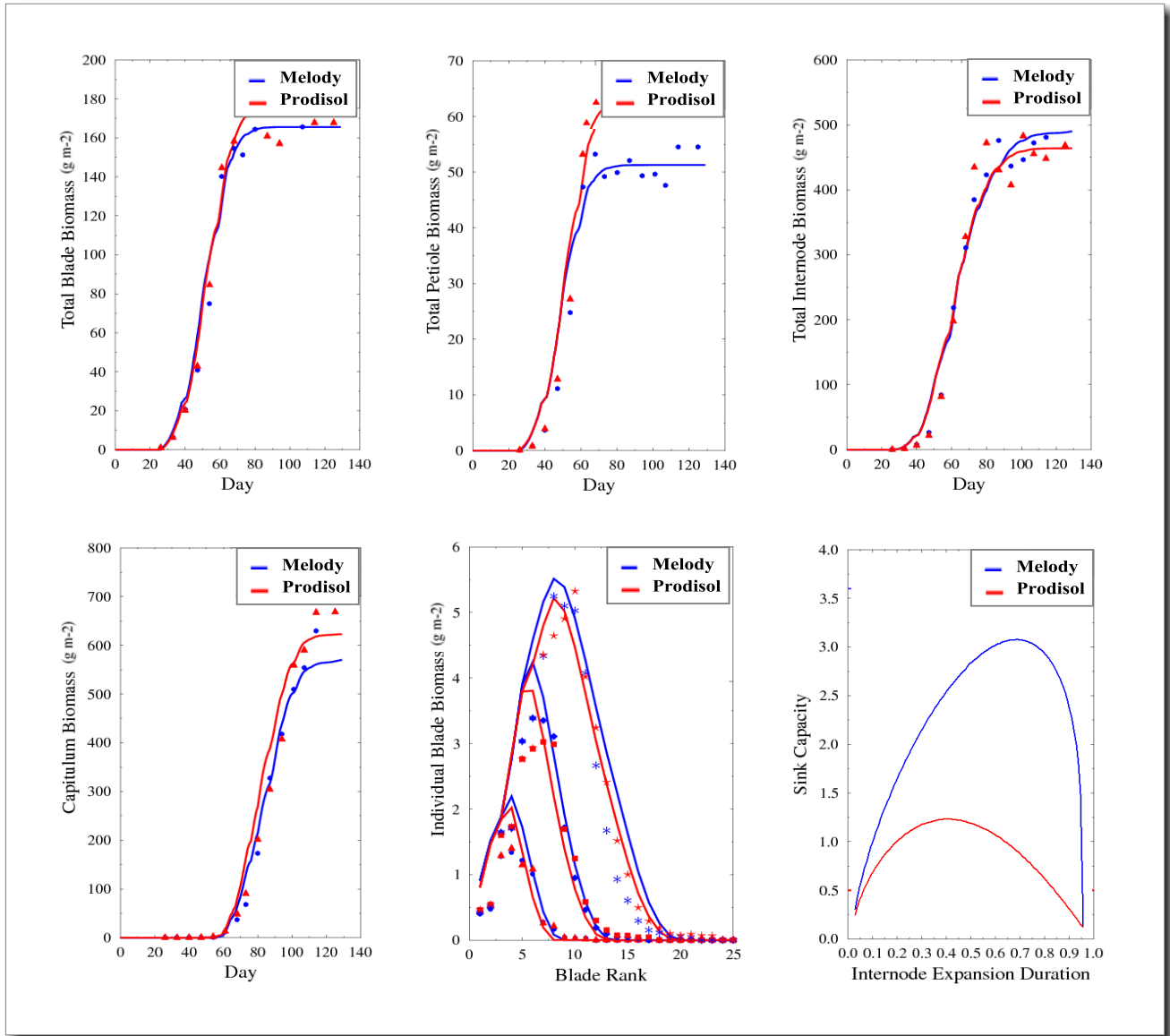


Figure 2. Biomass partitioning comparisons between genotypes “Melody” and “Prodisol”. Experimental data is represented by dot and simulation by line. Last graph displays comparison of sink capacity of internode. Its x axis represents the ratio of internode age to its expansion duration.

TABLE II. SUNFLO INHERITED PARAMETER VALUE SUNLAB PARAMETERS VALUES AND THEIR VARIANCES

Parameters	Parameters values and their standard errors			
	Melody		Prodisol	
	Value	Standard error	Value	Standard error
sinkAblade	2.09	0.27	2.08	0.27
sinkApetiole	1.5	0.85	1.68	0.72
sinkAintern	1.74	0.22	1.73	0.24
sinkAcap	4.67	0.32	4.48	0.31
sinkBblade	3.17	0.46	2.5	0.38
sinkBpetiole	3.46	0.88	2.15	1.04
sinkBintern	1.3	0.08	2.04	0.28
sinkBcap	3	0.41	2.6	0.33
SRpetiole	0.32	0.04	0.33	0.04
SRinternode	3.2	1.67	1.2	0.35
SRcapitulum	360	104	221	58

For sunflowers, the variations of SLA and the factors influencing them are still poorly known. Accurate estimation of SLA is mentioned as a major source of error in models and implies difficulties in obtaining a reliable computation of leaf area index, which is the main component of biomass production modules [11][12]. As SUNLAB simulation outputs include individual blade masses and blade areas, a preliminary study of SLA characteristics based on simulation is carried out. Figure 3.A shows the SLA evolution with time (day 40 to 100) for leaves ranking from 6 to 10. These leaf ranks and time windows were chosen as at that time both their simulated blade biomasses and surfaces were in very good agreement with experimental data. In the selected time period, their SLA curves show a quick increase and afterwards a decline towards a stable value. Figure 3B shows the variation of SLA value among leaves at different positions (ranking 1 to 25) for the two genotypes “Melody” and “Prodisol”. The SLA for each blade in this graph is the value at the time when this blade has its maximum leaf surface and biomass. Blades at the top of the sunflower crop which rank higher in the graph have bigger SLA than those at the bottom. “Melody” blades have slightly bigger SLA than “Prodisol”. Some phenomena coincide with the reported results for SLA of wheat [9]: the genotype with the longer longevity of leaves had smaller SLA, and that SLAs of leaves on top of sunflower crop were bigger. Since the current SUNLAB parameters come from the reconstructed individual blade masses, the simulated SLA results can be improved with better experimental data and corresponding estimations in the future. SUNLAB is a pioneer crop model for detailed study on SLA variable. SUNLAB could assist studying SLA variation response to environment and genotypes. Further studies are planned.

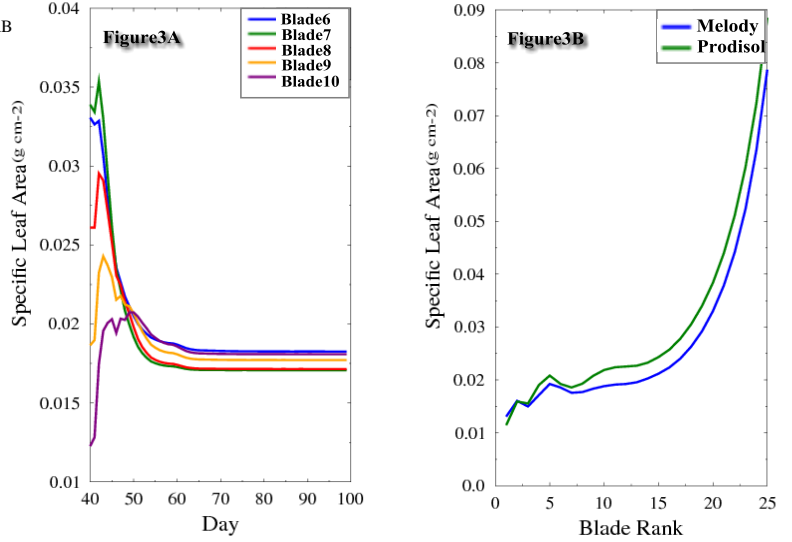


Figure3A: Time evolution of average SLA for “Melody”; Figure3B: SLA for ranked leaves of genotypes “Melody” and “Prodisol”.

IV. DISCUSSION AND CONCLUSION

A functional-structural model, SUNLAB was developed. It describes the sunflower topology and morphogenesis at organ level with blades, petioles, internodes, and capitulum. Coordination of the expansion dynamics of these organs are ruled by their initiation and senescence times, expressed with respect to thermal time. Because of the simple sunflower architecture, organogenesis and morphogenesis modules could be implemented in SUNFLO without adding too many supplementary parameters. Eco-physiological processes work together with plant structural dynamics to affect biomass accumulation and partitioning to organs.

In the present study, we have then evaluated the ability of this newly-developed model to reproduce observed data of sunflower growth. It was applied on data of two different genotypes, Melody and Prodisol. It was observed that Prodisol had a higher capitulum mass accumulation, thus better yield, than Melody after around 80 days (see Fig. 2). Identifying the processes that most contributed to that difference was difficult. Our results suggest several potential factors: Prodisol has slightly larger SLA values, which implies a larger photosynthetically active blade area than Melody for the same leaf biomass. The internode sink variation is different and may also contribute to explain the difference, since less biomass is allocated to the stem compartment of Prodisol. The later peak of internode sink of Melody results in a later internode completion of biomass at the important periods of capitulum biomass accumulation, which may be detrimental to the yield of Melody. Apart from internodes, no significant differences were found for the sink parameters, which suggests that functional balance is similar for the two genotypes and that the difference observed in yield for these two genotypes is also explained by differences in their SUNFLO subset of parameters, such as differences in their phenology.

As a joint concept of SUNFLO and GREENLAB, SUNLAB has better structural features than SUNFLO and it succeeds to deal with the biomass distribution at organ level.

Compared to GREENLAB, SUNLAB inherits the ecophysiological functions of SUNFLO that have been validated in different environmental conditions for 26 genotypes [5][6] and possesses SUNFLO's following merits. Firstly, SUNFLO contains more genotype-specific parameters. It could predict well large phenotypic variability of complex genotypic traits [5]. These genotypic traits, represented as genotypic parameters in the model, have enough genotypic variability to discriminate between genotypes. In the construction process of SUNFLO, the authors used the approach of linking a complex phenotype to a set of accessible genotypic traits. Each genotype is defined by chosen traits which were transcribed into a set of genotype-specific parameters. These genotypic parameters are thus under certain genetic control. With the reason of improving the model parameters update ability for yearly cultivar releases, parameters number is limited while a useful predictive capacity is maintained. Meanwhile, as most SUNFLO parameters could be estimated by direct measures, it allows parameter values to be more representative of crop physiology than those that are estimated indirectly with optimization algorithms [5]. Secondly, SUNFLO and SUNLAB have better ecophysiological functions. GREENLAB over-simplifies a number of processes, such as photosynthesis and assimilate conversion to biomass [13], and it is still in its preliminary stage to include water source influence and root system [14]. In SUNFLO and SUNLAB, the radiation use efficiency is taken into account for photosynthesis. Many environmental stresses to phenotypic plasticity are considered, such as temperature and water. The included root sub-model induces water stress, which affects crop processes such as leaf expansion, plant transpiration, and biomass production. This consideration enriches environment discrimination by taking into account the effects of soil texture, apparent soil density and stone content.

Modeling crop growth and breeding through empirical experimental analysis and direct parameter measurements, such as SUNFLO model, has outstanding ecophysiological advantage such as parameters have good genotypic variability, as explained in the previous paragraph. Alternative modeling methods relying on optimization algorithms are less ecophysiological representative, but they have their advantages of saving cost and producing more information. For example GREENLAB model produces far more details of organs structure and biomass partitioning than SUNFLO. While it is hard to find a balance for a model design, SUNLAB model is an interesting trial. It models ecophysiological functions of photosynthesis and morphogenesis to ensure a more accurate and a better representative of crop physiology for biomass production. But biomass partitioning that was not modeled in SUNFLO cannot be directly measured and can hardly be handled because of the heavy experiments and the difficulty to understand the organs interaction. Then parameter estimation by model inversion from experimental data is necessary, as done in this study for biomass partitioning to all organs. SUNLAB proves that this combination of concepts is

effective because it manages to explain the competition of biomass by simulating organ biomass distribution, while it preserves genotypic discrimination (as shown for the internode sink ratio and the parameter β in the sink variation function of internodes).

SUNLAB could simulate water deficiency effect on the crop sunflower, but in this paper it is only tested with an environmental input data without strong water deficiency. The upcoming research involves model evaluation in strong water deficiency case with many more genotypes.

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