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Rui Qi, Yuntao Ma, Baogang Hu, Philippe de Reffye, Paul-Henry Cournède

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1 Optimization of source-sink dynamics in plant growth for ideotype breeding: a case  
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9 Rui QI <sup>ab\*</sup>, Yuntao MA <sup>bc</sup>, Baogang HU <sup>b</sup>, Philippe de REFFYE <sup>de</sup>, Paul-Henry  
10 COURNÈDE <sup>ad</sup>

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16  
17 <sup>a</sup> Ecole Centrale Paris, Laboratory of Applied Mathematics, 92295 Chatenay-Malabry,  
18 France

19  
20  
21  
22 <sup>b</sup> Institute of Automation, Chinese Academy of Sciences, LIAMA, Beijing 100080,  
23 China

24  
25  
26  
27  
28 <sup>c</sup> China Agricultural University, Key Laboratory of Plant–Soil Interactions, Ministry  
29 of Education, College of Resources and Environment, Beijing 100094, China

30  
31  
32  
33  
34 <sup>d</sup> INRIA saclay Ile-de-France, EPI Digiplant, Parc Orsay Université, 91893 Orsay  
35 cedex, France

36  
37  
38  
39 <sup>e</sup> CIRAD montpellier, AMAP, 34398, France

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45  
46 Corresponding author: Rui QI

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48  
49 Telephone: (+33) 01 41 13 17 89

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51  
52 Email address: [qiruitree@gmail.com](mailto:qiruitree@gmail.com)

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58  
59 Fax: (+33) 01 41 13 17 35

1       1    **Abstract**

2               The objective of this work is to illustrate how a mathematical model of plant  
3               growth could be possible to design ideotypes and thus leads to new breeding strategies  
4               with optimization guidance. As a test case, maize (*Zea mays* L., DEA cultivar), which  
5               is one of the most widely cultivated cereals all over the world, is selected for this  
6               study. The experimental data reported in a previous study are used to estimate  
7               parameters of a plant growth model. As the cob and the compartment of leaves and  
8               stem can be benefited from economically, an optimization problem with single  
9               objective maximization of cob weight and a multi-objective optimization problem are  
10              formulated, respectively. The Particle Swarm Optimization approach is applied to  
11              solve these two optimization problems based on the existing plant growth model,  
12              namely, "GreenLab". The optimized variables are specific parameters of GreenLab  
13              model related to plant genetics, specially the parameters of the cob sink variation  
14              function. The cob position on the stem is an additional factor in the investigation.  
15              Plant growth behavior is analyzed based on the plant growth model through  
16              optimizations. The optimization results revealed the source-sink dynamics. In  
17              comparison with the experimental data reported in a previous study, the numerical  
18              results showed significant yield increasing from both optimization problems. The  
19              work described in this paper confirmed that optimization approaches will be a  
20              promising tool for genetic analysis and management control to improve breeding  
21              strategies and to design an ideotype of high-yield maize, especially in the current  
22              agricultural context and the increasing importance of co-products when designing

1 cultivation practices.

2 **Key words:** *Pareto front*, GreenLab, functional-structural model, *Zea mays.*,  
3 multi-objective optimization

#### 4 **Introduction**

5 In plant breeding, the concept of ideotype is first defined in (Donald, 1968): “a  
6 plant model which is expected to yield a greater quantity or quality of ... useful  
7 product when developed as a cultivar”, “plants with model characteristics known to  
8 influence photosynthesis, growth, and (in cereals) grain yield”. Since then, the design  
9 of ideotype has been a major issue in genetic selection in order to optimize crop yields.

10 There are two main strategies to investigate ideotype breeding: experiment based and  
11 plant model based approaches. Peng *et al.* (2008) presented the research results of  
12 almost 20 years on the ideotype design of rice with the objective of high potential  
13 yield, using an experiment based approach. However, the performance of the  
14 improved plant type, which is obtained after the first five year experiments, is worse  
15 and disappointing. The critical drawback of experiment based approach is that the  
16 time consuming for experiments is long (10 years needed by Dencic (1994) and by  
17 Lauri and Costes (2004)) and it consumes resources that are limited (field, water,  
18 labor) due to the cultivation of thousands of plants (Dencic, 1994). Nowadays, it  
19 becomes widely accepted that plant growth models may provide efficient tools to  
20 study plant growth behavior (Tardieu, 2003; Letort *et al.*, 2008a), since they can not  
21 only complement field experiments, but also save time and resources. Therefore,  
22 researchers dedicated themselves to study ideotype breeding based on plant models

1 (Yin *et al.*, 2003; Cilas *et al.*, 2006). As plant architectural information is more  
2 intuitionistic and is easier to measure, Cilas *et al.* (2006) used an architectural plant  
3 growth model to study the ideotype of *Coffea canephora* for good yield capacity. Like  
4 as, in Peng *et al.* (2008), the architecture traits of the ideotype plant were highlighted.  
5 Yin *et al.* (2003) pointed out that the physiological information of plant growth can  
6 also be used to improve the ideotype breeding efficiency; hence, he used a process  
7 based plant growth model for ideotype breeding. However, note that even though  
8 Cilas *et al.* (2006) and Peng *et al.* (2008) investigated ideotype breeding from the  
9 architectural point of view, and Yin *et al.* (2003) from the physiological point of view,  
10 they all agree that there exist critical relationships between plant architectures and  
11 physiological processes during plant growth, with other researchers like Rasmusson  
12 (1987), Sievänen *et al.* (2000), Luquet *et al.* (2006), and Fourcaud *et al.* (2008). The  
13 design of ideotypes should thus take into account both architectural and physiological  
14 aspects. In parallel, functional-structural plant growth models were developed  
15 (Perttunen *et al.*, 1998; Kurth, 2000; Allen *et al.*, 2005; Cournède *et al.*, 2008),  
16 combining the description of organogenesis, photosynthesis and biomass partitioning.  
17 They can serve as the basis to improve plant breeding.

18 Maize (*Zea mays* L., DEA cultivar) is chosen for ideotype breeding in the present  
19 work, as it is one of the most widely cultivated cereals all over the world. Commonly,  
20 it is used in the human diet in both fresh and processed forms; the grain and  
21 vegetative parts of maize are fed to livestock, and the components of the grain may be  
22 refined for direct consumption (Pratt, 2001). Moreover, the fruit compartment and the

1 vegetative compartment can be used as biofuel of the first and second generations,  
2 respectively, which becomes of important economical interest (Baenziger *et al.*, 2006).  
3 Therefore, the objective of this work is to breed maize first with the potential best cob  
4 yield, and second with high yields of both cob and vegetative compartments. To find  
5 the appropriate ideotype of maize that satisfies the requirement of high yield capacity,  
6 optimization problems with respect to plant physiological processes are formulated  
7 and numerical optimization methods are applied to a functional-structural plant  
8 growth model.

9 There have been a lot of works about optimization on crops based on plant  
10 growth models in the past decades. Most of the corresponding works are related to  
11 optimization of environmental components including water (Ho *et al.*, 2004), soil  
12 (Mustafa, 1989) or temperature (Fink, 1993); others related to optimization of  
13 cultivation modes, such as fertilizer (van Evert *et al.*, 2006), seeding strategy  
14 (Prasanna Kumar *et al.*, 2008) or water supply strategy (Wu *et al.*, 2005). Moreover,  
15 several works focused on optimizing climate conditions especially in greenhouse  
16 (Linker *et al.*, 1998; Dieleman *et al.*, 2006; van Henten *et al.*, 2006). Morimoto *et al.*  
17 (1993) also did optimal control of water supply (Morimoto *et al.*, 1995), humidity  
18 (Morimoto *et al.*, 1997) and temperature control (Morimoto *et al.*, 2003) on plant  
19 growth. But the plant growth model he used is a kind of “black-box”, which is trained  
20 and formed by neural networks, without using physiological mechanisms of plant  
21 growth. The corresponding review about optimization on environmental factors can  
22 be found in (van Straten *et al.*, 2000; King and Sigrimis, 2001; Ferentinos *et al.*, 2006).

1 Technically and generally speaking, all of these optimization works belong to optimal  
2 control. Even though Haverkort and Grashoff (2004) and Herndl *et al.* (2007) used  
3 plant models to find the ideotype of plants with the optimum product with respect to  
4 physiological parameters, the results they found were through trial and error method  
5 based on simulation. None of them did optimization on the parameters that describe  
6 the inner physiological processes of plant growth, the factors related to genetic  
7 parameters or new genotype investigations for a specific species.

8 For this study on ideotype breeding, GreenLab plant growth model is chosen for  
9 the following reasons. First of all, GreenLab is a functional-structural plant growth  
10 model, which can describe the interaction between plant architecture and plant  
11 physiological processes (Mathieu *et al.*, 2008) that is necessary for ideotype breeding.  
12 Second, Preliminary studies have allowed modelling the growth of maize cultivars  
13 with the GreenLab model. Model parameters had already been estimated from  
14 experimental data over different years (Guo *et al.*, 2006; Ma *et al.*, 2007) and over  
15 different density conditions (Ma *et al.*, 2008). The relative stability of model  
16 parameters in a wide range of environmental conditions leads us to consider a  
17 probable link of the model parameters to the genotype of the species. Letort *et al.*  
18 (2008a) explored the possibility to link GreenLab to a genetic model in order to  
19 design new breeding strategies. Third, Carson *et al.* (2006) pointed out that plant  
20 growth is a complex system, which raised a challenge on plant growth models for  
21 parameter estimation and model validation. This challenge must be overcome for  
22 model application. Over decade of GreenLab model development, besides maize, its

1 parameters have been well estimated on tomato (Dong *et al.*, 2008), chrysanthemum  
2 (Kang *et al.*, 2006), wheat (Kang *et al.*, 2008), cucumber (Mathieu *et al.*, 2007),  
3 Chinese pine tree (Guo *et al.*, 2006), Arabidopsis (Letort *et al.*, 2006), and beech tree  
4 (Letort *et al.*, 2008b). GreenLab model was shown to be an efficient tool to describe  
5 source-sink dynamics in plant growth. Fourth, GreenLab model can be considered as  
6 a dynamic system, whose mathematical formulation makes it suitable for solving  
7 optimization problems.

8 As mentioned above, from an economical point of view, there are potential  
9 benefits from both cob weight and the total weight of leaves and stem (to feed animals  
10 as forage, or biofuel). Firstly, an optimization problem with single objective  
11 maximization of cob weight is formulated and investigated, as the most beneficial  
12 component in maize is cob. And then, a multi-objective optimization problem with  
13 two conflict objectives: maximization of cob weight and of the total weight of  
14 vegetative compartment at the same time, is formulated with a constraint of a minimal  
15 tassel weight. The optimization is based on the GreenLab plant growth model, which  
16 is used to simulate the growth behavior of maize and to estimate parameters from  
17 measured data which are the preconditions of applying optimization. It is  
18 acknowledged that cob weight is highly dependent on growth conditions during the  
19 early stages of grain filling and the final cob weight reflects the source-sink ratio of  
20 the entire grain filling period (Borrás *et al.*, 2002); final cob weight of maize depends  
21 on the relationship between cob sink and availability of assimilates resulting from the  
22 biomass production of the plant to fill this sink (Borrás *et al.*, 2003). Therefore, the



1 optimized variables of both problems are specific GreenLab parameters related to  
2 plant genetics: parameters of cob sink variation function. In addition, the impact of  
3 cob position on the cob weight and on the total weight of vegetative compartment is  
4 investigated. A heuristic optimization algorithm, Particle Swarm Optimization (PSO)  
5 was used to solve the problems.

6

## 7 **Materials and method**

### 8 *Description of the GreenLab model*

9 GreenLab is a functional-structural plant growth model combining the  
10 descriptions of plant architecture and physiological processes of plant growth, in  
11 interaction with the environment (light, water, temperature and density). The dynamic  
12 mechanisms to generate plant architecture (organogenesis), plant biomass production  
13 and partitioning to the organs are introduced in details in (de Reffye and Hu, 2003;  
14 Yan *et al.*, 2004; Cournède *et al.*, 2008). Here, only the necessary points to understand  
15 our approach are recalled.

16 In the usual cultivation conditions, maize is a single stem crop. The phytomer  
17 appearance is controlled by the thermal time in GreenLab model for maize. The  
18 model time step, also called growth cycle (GC), is thus equivalent to the thermal time  
19 necessary for a new phytomer to appear. The topology of maize cultivar ND108 is  
20 simplified as follows: first six phytomers with short internodes appear; they are  
21 followed by 15 phytomers with longer internodes; the last one bears the male flower  
22 (tassel). Therefore, the organogenesis terminates at the end of the 21<sup>st</sup> growth cycle,

1 but the plant is still alive until the 33<sup>rd</sup> growth cycle. Even though several phytomers  
 2 may bear female flowers (cobs), Guo *et al.* (2006) chose to gather all the potential cob  
 3 weights on the 15<sup>th</sup> phytomer. This simplification was proved very effective for plant  
 4 modelling and model calibration (Guo *et al.*, 2006).

5 The functional processes of plant growth are described by a source-sink model in  
 6 GreenLab, with a common pool of biomass. GreenLab simulates plant growth from  
 7 the seed stage, hence the initial plant biomass is from seed and the initial organs are  
 8 driven by seed. And then, at the following growth cycle  $n$ , biomass production  $Q_n$  of  
 9 an individual plant is described in Eqn.(1). It depends on the total green leaf surface  
 10 area at the end of the previous growth cycle  $n-1$  ( $S_{n-1}$ ), on environmental factors  
 11 gathered in the function  $E_n$  and on empirical parameters  $\beta$  (linked to energetic  
 12 efficiency) and  $\gamma$  (linked to light interception):

$$\begin{aligned} Q_n &= \beta E_n (1 - \exp(-\gamma S_{n-1})) \\ Q_0 &= Q_{seed} \end{aligned} \quad (1)$$

14 where  $Q_{seed}$  is seed biomass.

15 All living organs (blades, sheaths, internodes, cob and tassel) are sinks among  
 16 which biomass is distributed according to their sink values. The total demand of the  
 17 plant at growth cycle  $n$ , denoted by  $D_n$ , is given by:

$$D_n = \sum_o \sum_{j=1}^{\min(n, t_{x_o})} N_{n-j+1}^o p_o(j) \quad (2)$$

19 where  $p_o(j)$  is the sink of organ  $o$  with age  $j$ ;  $o$  represents blade ( $a$ ), sheath ( $s$ ),  
 20 internode ( $e$ ), female ( $f$ ) and male ( $m$ ) organs;  $t_{x_o}$  is the expansion duration of organ  $o$ ;  
 21  $N_n^o$  is the number of organ  $o$  generated at growth cycle  $n$ .

1 The biomass increment of an organ  $o$  with age  $j$  at growth cycle  $n$  is proportional  
 2 to its sink value  $p_o(j)$  and the ratio of biomass production to the total demand of the  
 3 plant, as detailed in Eqn.(3).

$$\Delta q_o(n, j) = p_o(j) \frac{Q_n}{D_n} \quad (3)$$

5 The accumulated biomass for an organ  $o$  with age  $j$  at growth cycle  $n$  is given by:

$$q_o(n, j) = \sum_{k=1}^j \Delta q_o(n - j + k, k) \quad (4)$$

7 As a consequence, the total green leaf surface area at growth cycle  $n$ , denoted by  
 8  $S_n$ , is

$$S_n = \frac{\sum_{j=1}^{t_a} N_{n-j+1}^a \cdot q_a(n, j)}{slw} \quad (5)$$

10 where  $t_a$  is the blade functioning duration, and  $slw$  is the specific leaf weight.

11 The family of Beta functions was chosen to describe the sink variation during the  
 12 expansion, as in Eqn.(6).

$$f_o(j) = \begin{cases} be_o(j) / M_o & (1 \leq j \leq t_{x_o}) \\ 0 & (j > t_{x_o}) \end{cases}$$

14 with  $be_o(j) = (j - 0.5)^{a_o - 1} \cdot (t_{x_o} - j + 0.5)^{b_o - 1}$  (6)

15 and  $M_o = \max_j (be_o(j), 1 \leq j \leq t_{x_o})$

16 where  $a_o$  and  $b_o$  are the coefficients of the sink variation function.

17 The sink value of an organ with age  $j$ , denoted by  $p_o(j)$ , is  $f_o(j)$  multiplied by the  
 18 sink amplitude (also called sink strength)  $P_o$  as in Eqn.(7). Diverse sink variations can  
 19 be obtained by setting different values of the coefficients:  $a_o$  and  $b_o$  in Eqn.(6). An  
 20 example is given in Figure 1.

$$p_o(j) = P_o f_o(j) \quad (7)$$

### ***Field experiment and field measurements on maize***

Maize cultivar ND108 (*Zea mays* L., DEA cultivar) seed was sown 0.6 m apart in north–south-oriented rows that were 0.6 m apart, at the China Agricultural University (CAU) (39°50'N, 116°25'E). The resulting plant population (28 000 plants ha<sup>-1</sup>) is about half that commonly used by local farmers and was chosen to minimize competition among plants. Plants emerged on the 18th May 2000. Soil, irrigation and fertilizer inputs were managed so as to avoid any mineral and water limitation to plant growth, and plant disease, pest or stress symptoms. Samples were taken destructively on 12 dates. Fresh weights of blades, sheaths, internodes, cob and tassel were measured and recorded individually at each sample date. The number of organs generated at each growth cycle, the functioning duration of blades and the expansion duration of organs, specific leaf weight, can be observed and measured by field experiments. The detailed information about the environmental conditions, sampling strategy and the measured data is given by (Guo *et al.*, 2006).

### ***Parameter estimation of GreenLab***

In GreenLab, the parameters are classified into two categories: measurable parameters, i.e. functioning duration of blades, number of organs emerged at each growth cycle, and hidden parameters which cannot be measured directly in the field, i.e. organ sink. To guarantee that GreenLab can describe the dynamic processes of plant growth well, it is necessary to estimate the hidden parameters through

1 minimizing the difference between the measured data and the corresponding  
2 simulation results of GreenLab.

3 The same set of parameters is estimated simultaneously by fitting with several  
4 plants of a species at different development stages, which is called multi-fitting. In  
5 this paper, the data measured at three stages (8<sup>th</sup> GC corresponding to vegetative stage,  
6 18<sup>th</sup> GC approximately corresponding to flowering stage and 33<sup>rd</sup> GC corresponding  
7 to physiological maturity) are used as target data.

### 8 ***Multi-objective Optimization***

9 In multi-objective optimization problems, several objectives are optimized  
10 (maximization or minimization) simultaneously. The mathematical formulism of a  
11 multi-objective optimization problem is given by:

$$\begin{aligned} & \text{Maximize } (J_1, J_2, \dots, J_m) \\ & \text{s.t. } g_i(x_1, x_2, \dots, x_n) \leq 0, \quad i = 1, 2, \dots, k \\ & \quad h_j(x_1, x_2, \dots, x_n) = 0, \quad j = 1, 2, \dots, l \end{aligned} \quad (8)$$

13 where  $x_i$  is the  $i$ th element of the vector  $\mathbf{X}$  on which we optimize and  $n$  is the  
14 dimension of the problem;  $J_i$  is the  $i$ th objective which is a function of  $\mathbf{X}$  and  $m$  is the  
15 number of objectives;  $g_i$  is the  $i$ th inequality constraint of the problem and  $k$  is the  
16 number of inequality constraints;  $h_j$  is the  $j$ th equality constraint and  $l$  is the number of  
17 equalities.

18 For multi-objective optimization problems, generally, objectives are in conflict  
19 with each other. In comparison with single objective optimization problems for which  
20 we may have results on the existence and unicity of the solution, the situation of  
21 multi-objective problems is more complex, since there is no canonical relationship in

1 the feasible space. Thus, the optimal solutions for multi-objective optimization  
 2 problems is defined such that for these solutions, performance on one objective cannot  
 3 be improved without sacrificing performance on at least another. The solutions  
 4 satisfying this property form the *Pareto front* (Mostaghim and Teich, 2003).

5 For maize, one of our objectives is to maximize cob weight, which is used for  
 6 food or biofuel of the first generation. The formula for calculating the final weight of  
 7 cob when plant age is  $n$  is as follows:

$$J_1 = \sum_{k=1}^{t_{x-f}} p_f(k) \frac{Q_{n-(t_{x-f}-k)}}{D_{n-(t_{x-f}-k)}} \quad (9)$$

9 However, for the cultivar of maize ND108 (*Zea mays* L., DEA cultivar) that we  
 10 considered, leaves and stems are useful for poultry as a kind of forage. Moreover,  
 11 leaves and stem of maize will be also used for biofuel of the second generation,  
 12 whereas cob should be reserved for food. Thus, it is also of economical interest to  
 13 maximize the total weight of leaves and stem. The equation for calculating the final  
 14 weight of leaves and stem is given by:

$$J_2 = \sum_{j=1}^n N_{n-j+1}^a \sum_{k=1}^{\min(j, t_{x-a})} p_a(k) \frac{Q_{n-j+k}}{D_{n-j+k}} + \sum_{j=1}^n N_{n-j+1}^i \sum_{k=1}^{\min(j, t_{x-i})} p_i(j) \frac{Q_{n-j+k}}{D_{n-j+k}} \quad (10)$$

16 In Eqn.(10), the first item corresponds to the total weight of leaves, and the  
 17 second item to the stem weight.

18 A constraint on the tassel weight is also imposed, since cob weight and tassel  
 19 weight are interrelated. Cob weight is controlled by pollen production, while the  
 20 pollen production depends on the tassel size of maize. Uribelarrea *et al.* (2002)  
 21 showed that if the tassel size is reduced, the cob size will be limited. Thus, a

1 constraint that the tassel weight should be beyond a threshold is set. The formula for  
 2 calculating the final weight of tassel when plant age is  $n$  is as follows:

$$g = \sum_{k=1}^{t_{x\_m}} P_m(k) \frac{Q_{n-(t_{x\_m}-k)}}{D_{n-(t_{x\_m}-k)}} \quad (11)$$

4 Finally, the multi-objective optimization for maize is given by:

$$\begin{aligned} & \text{Maximize } (J_1, J_2) \\ & \text{s.t. } g \geq \text{threshold} \end{aligned} \quad (12)$$

6 For potential applications in breeding, the parameters we optimize should be  
 7 linked to plant genetics and therefore should be representative of some physiological  
 8 processes. As it is acknowledged that final cob weight of maize depends on the  
 9 relationship between cob sink and biomass production (Borrás *et al.*, 2002), we  
 10 choose to study the cob sink variation. Thus, the parameters we optimize are the cob  
 11 sink strength  $P_f$  and the two coefficients of the Beta function  $a_f$  and  $b_f$ . The effect of  
 12 cob position on the cob weight and on the total weight of leaves and stem is also  
 13 studied.

### 15 ***Particle Swarm Optimization (PSO)***

16 The optimization problem revealed non convex and multimodal, particularly  
 17 since there is no unique solution for multi-objective problems. Therefore,  
 18 population-based heuristic optimization algorithms, which usually allow obtaining  
 19 quickly a number of acceptable solutions, were used in our study. Compared to the  
 20 other population-based heuristic optimization algorithms, PSO has a high  
 21 convergence rate for a wide range of optimization problems (Kennedy and Eberhart,

2001). Hence, it was chosen to solve our problems.

PSO is proposed by Kennedy and Eberhart (1995), which originally simulates the behaviour of bird flocking. It is also an iterative algorithm, similar to other population-based optimization algorithms. The feasible solutions found at the current iteration are recorded separately in each individual in the population as their current positions. The direction and the distance controlling how the individuals move are determined by their velocities and their experiences during the searching. With the help of social and cognition knowledge of each individual (also called particle), the population (also called swarm) converges to the optimal solution (or position). With the increasing development of PSO in the past decade, there are many variants of PSO in order to improve its performance (convergence rate, convergence accuracy, etc). In this paper, PSO with passive congregation (He *et al.*, 2004) is used to solve the single objective optimization problem, thanks to its generalization capacities and robust performance. The equations used to calculate velocities and the new positions are given by:

$$\begin{aligned} v_{ij}^{k+1} &= \omega^k v_{ij}^k + c_1 r_1 (B_{ij} - x_{ij}^k) + c_2 r_2 (B_{gj} - x_{ij}^k) + c_3 r_3 (B_{rj} - x_{ij}^k) \\ x_{ij}^{k+1} &= x_{ij}^k + v_{ij}^{k+1} \end{aligned} \quad (13)$$

where  $v_{ij}^k$  is the  $j$ th coordinate of the velocity of the  $i$ th particle at iteration  $k$ ;  $B_{ij}$  is the  $j$ th coordinate of the best position recorded by the  $i$ th particle during the previous iterations;  $B_{gj}$  is the  $j$ th coordinate of the position of the global best particle among all the particles in the swarm, which is marked by  $g$ ;  $B_{rj}$  is the  $j$ th coordinate of the best position recorded by a random selected particle  $r$  during the previous iterations;  $x_{ij}^k$  is the  $j$ th coordinate of the current position of particle  $i$  at iteration  $k$ ;  $w^k$  is inertia weight



value at iteration  $k$ , which decreases linearly from the maximal inertia weight to the minimal one;  $c_1$  and  $c_2$  are acceleration coefficients;  $r_1$  and  $r_2$  are uniformly distributed random values between 0 and 1. The second and the third items of Eqn. (13) on the right hand side are considered as cognition knowledge and social knowledge of a particle respectively, and the last item is used to avoid getting trapped into the local optimum.

Many researchers have already applied PSO to solve multi-objective optimization problems (Fieldsend, 2004). The specific algorithm that we used is the mixture of the algorithms proposed by Mostaghim and Teich (2003) and by Tripathi *et al.* (2007). To extend the original PSO to solve multi-objective problem and to find the *Pareto front*, the equations for changing the velocity and position of each particle are improved slightly, as given by Eqn.(14).

$$\begin{aligned} v_{ij}^{k+1} &= \omega^k v_{ij}^k + c_1^k r_1 (B_{ij} - x_{ij}^k) + c_2^k r_2 (B_{l_{ij}} - x_{ij}^k) \\ x_{ij}^{k+1} &= x_{ij}^k + v_{ij}^{k+1} \end{aligned} \quad (14)$$

To make the balance between exploration and exploitation, the acceleration coefficient  $c_1^k$  decreases linearly, and the acceleration coefficient  $c_2^k$  increases linearly. For the problems with constraints, there are two criteria to decide whether the  $j$ th coordinate of the best position of each particle  $B_{ij}$  is updated by the  $j$ th coordinate of the new position  $x_{ij}^{k+1}$ : if  $x_{ij}^{k+1}$  satisfies the constraints while  $B_{ij}$  does not, or if one of the objective function value with respect to  $x_{ij}^{k+1}$  is better than the one with respect to  $B_{ij}$ , no matter whether the constraints are satisfied, replace  $B_{ij}$  with  $x_{ij}^{k+1}$ .

The aim of multi-objective optimization problems is to find all the optimal solutions that form the *Pareto front*. Therefore, to obtain various solutions at a given

1 iteration, the algorithm is changed by replacing the unique global best position with a  
2 local guide best position for each particle, denoted by  $Bl_{ij}$  for the  $j$ th coordinate of  
3 particle  $i$  in Eqn.(14).

4 All the optimal solutions are recorded in an archive with limited size. The Sigma  
5 method (Mostaghim and Teich, 2003) is used to determine the local guide best  
6 position of each particle. The solution in the archive which has the nearest distance  
7 from a given particle is decided to its local guide best position. For more details, we  
8 refer to (Mostaghim and Teich, 2003). When the maximal number of solutions in the  
9 archive is reached, the solutions which have the shortest distance from the other  
10 solutions in the archive will be deleted. If the number of solutions in the archive is  
11 less than its maximal number, new optimal solutions will be added into the archive.

## 13 **Results**

### 14 **Multi-fitting results**

15 The hidden parameters estimated by a generalized non-linear least square method  
16 are different from the ones in Guo *et al.* (2006) and Ma *et al.* (2007), as the sink  
17 variation function (Beta function) in this work is slightly improved as shown in  
18 Eqn.(6). The comparison of the simulation results by GreenLab with the estimated  
19 parameters and the measured data is given in Figure 2. The optimization results in the  
20 following sections are based on the maize modelled by GreenLab with the estimated  
21 parameter values listed in Table 1.

### 22 **Single optimization problem of maximization of cob weight**

1           Fixing cob expansion duration, on one hand, it limits the potential duration of  
2  
3           obtaining biomass for cob. On the other hand, cob potential ability to obtain biomass  
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6           will be missed. To avoid these two drawbacks, in this subsection, we suppose that cob  
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9           expansion duration depends on its position on the stem, to ensure that the cob has  
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11  
12           possibility to obtain biomass until the end of the plant growth. For example, if the cob  
13  
14           appears at the 19<sup>th</sup> growth cycle, its expansion duration is 15 growth cycles with plant  
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16  
17           age 33 growth cycles.

18           The maximal cob weights associated to different cob positions are not  
19  
20           significantly different, as shown in Figure 3(a). The corresponding optimal cob sink  
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23           strength variations are similar as shown in Figure 3(b) marked only with symbols, and  
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26           the estimated one is represented by the curve in “-.-”. Wherever the cob is and  
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29           whatever its expansion duration is, we found that the optimal cob development  
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32           strategies are similar. The optimal cob sink is almost zero at the beginning of cob  
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34  
35           development, in order to reduce the competition for biomass with source organs and  
36  
37           to let leaf surface area increase, and then the sink increases monotonously till the end  
38  
39           of plant growth.

40           Comparing the estimated and optimal cob sink variations with cob particularly  
41  
42           born by the 1<sup>st</sup> phytomer counted from the bottom shown in Figure 3(b), we can  
43  
44  
45           separate the cob development process into 4 stages. During the first stage from the 1<sup>st</sup>  
46  
47  
48           growth cycle to 15<sup>th</sup> growth cycle, the optimal cob sink is a little larger than the  
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51           estimated one, but can be neglected. It has no negative effect on the source organ  
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54           development. In this period, the leaf surface areas for the estimated plant and the  
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1 optimal plant are the same. Consequently, there is no difference among the optimal  
2 cob weights when the cob is born by the 1<sup>st</sup> phytomer to by the 15<sup>th</sup> phytomer;  
3 meanwhile, it leads to a slight difference among the optimal cob weights when the cob  
4 position is higher than the 15<sup>th</sup> phytomer, as shown in Figure 3(a). The second stage is  
5 from the 16<sup>th</sup> growth cycle to the 23<sup>rd</sup> growth cycle. Even though the optimal cob sink  
6 is still a little larger than the estimated one, it does affect the source organ  
7 development. The cob competes for biomass against the source organ and the other  
8 organs. This competition leads to the decrease of the leaf surface area as shown in  
9 Figure 4. During the third stage from the 23<sup>rd</sup> growth cycle to the 31<sup>st</sup> growth cycle,  
10 the optimal cob sink value keeps increasing, but smoothly. On the contrary, for the  
11 observed plant, the cob sink increases significantly, biomass allocation to the cob is  
12 done with detriment to leaves. Hence, the leaf surface area begins to decrease. During  
13 the last stage of plant growth within two growth cycles, the optimal cob sink begins to  
14 increase significantly and quickly. Since the other organ sinks are negligible, all the  
15 biomass is allocated to the cob as shown in Figure 5: the ratio in this period tends to  
16 infinity.

17       The comparison results of the cob sink variation reveal the source-sink dynamics.  
18 The increment of the cob weight is the product of the cob sink value and the ratio of  
19 the plant biomass production, which depends on the leaf surface area, to the plant  
20 demand that is the sum of all the organ sinks, as described in Eqn.(3). Even though the  
21 cob sink value is smaller than the estimated one, the leaf surface area is higher. Due to  
22 the optimal trade-offs between sources and sinks, the cob weight with the optimal

1 parameter values (1032 g) is bigger than the observed one (895 g).

## 2 **Multi-objective optimization problem**

3 Economically speaking, we can benefit both from cob as food for human beings  
4 and as biofuel of the first generation, and from leaves and stem as forage for poultry  
5 and probably as biofuel of the second generation. Therefore, an optimization problem  
6 with two objective functions on maximization of cob weight and total weight of  
7 leaves and stem simultaneously is investigated. The optimal result of this  
8 multi-objective optimization problem, known as *Pareto front*, is shown in Figure 6,  
9 for each cob position. There is no obvious difference among the *Pareto fronts*  
10 associated to each cob position. They are all very similar and can not be distinguished,  
11 as shown in Figure 6. Each *Pareto front* is given by about 500 optimal solutions of  
12 cob sink variation. Hence in Figure 7, we outlined the area covered by all the optimal  
13 solutions of cob sink variation. Particularly, two examples of the optimal cob sink  
14 variation are given, when the cob is born by the 12<sup>th</sup> phytomer with cob weight of 792  
15 g and total weight of leaves and stem of 1695 g, and when the cob is born by the 15<sup>th</sup>  
16 phytomer with cob weight of 503 g and total weight of leaves and stem of 2050 g,  
17 respectively.

18 The *Pareto front* of our multi-objective optimization problem reveals source-sink  
19 dynamics and the necessary balance between both objectives. Maximization of the  
20 total weight of leaves and stem leads to a zero cob sink strength. On the other hand, to  
21 maximize the cob weight, the cob sink value can not be maximal all the way,  
22 otherwise there would not be enough leaf surface area, and the reduced biomass

1 production would decrease the final cob weight. For this reason, the left extremity of  
2 the *Pareto front* corresponds to a zero cob weight whereas the right extremity  
3 corresponds to a strictly positive weight of stem and leaves. For maize cultivar  
4 ND108 (*Zea mays* L., DEA cultivar), the tassel appears and begins to develop at the  
5 21<sup>st</sup> growth cycle, with a very quick expansion (2 growth cycles). From the optimal  
6 results shown in Figure 7, we found that the tassel expansion corresponds to the early  
7 stages when the cob sink begins to increase.

8 In Figure 8, the evolution of the tassel weight corresponding to the points on the  
9 *Pareto front* is illustrated. We see that for a wide range, the tassel weight does not  
10 vary since its expansion corresponds to growth cycles when the cob sink is still very  
11 low. However, we found that for the maximal cob weights (above 900g), the tassel  
12 weight is decreasing. It corresponds to experimental observations of Westgate *et al.*  
13 (2003) who indicated that there is a potential gain of cob yield by decreasing the tassel  
14 weight.

15 The cob weight simulated by GreenLab with the estimated parameter values is  
16 1013 g, whereas the total weight of leaves and stem is 927 g and the tassel weight is  
17 29 g. With the optimal parameter values, the maximal cob weight among the *Pareto*  
18 *front* in Figure 6 is 1032 g, the corresponding total weight of leaves and stem is 955 g  
19 and the tassel weight is 30 g. Comparing the Harvest Index (HI) of the simulated and  
20 the optimal plants, HI of the optimal one is surprisingly a little smaller than the  
21 simulated one, even though both the cob weight and the total weight of leaves and  
22 stem are higher than the simulated one. It revealed the trade-offs between sources and

1 sinks. Post-expansion and fast growing rate as shown in Figure 3(b) and Figure 7 will  
2 not only enhance the cob weight but also the weight of leaves and stem.

#### 3 4 **Discussion**

5 In this paper, we have illustrated how the optimization of the parameters of plant  
6 growth models could be used to design ideotypes for genetic selection. The GreenLab  
7 model was chosen for the simplicity of its parameterization. Moreover, it describes  
8 plant growth, both from ecophysiological and architectural points of view, at the  
9 individual organ scale, which potentially allows distinguishing more easily genetic  
10 and environmental effects. However, we should note that the model can be  
11 extrapolated to stand level by taking into account competition between individuals  
12 (Cournède *et al.*, 2008).

13 Particle Swarm Optimization (PSO), which is a population-based heuristic  
14 optimization algorithm, is used to solve the single and multi-objective optimization  
15 problems. As it does not require the differentiation of the objective functions, and it  
16 returns several solutions at the same time, we can benefit from it to solve non-convex,  
17 single objective or multi-objective optimization problems, with potentially non-unique  
18 solutions. Compared to other population-based heuristic optimization algorithms, such  
19 as Genetic Algorithm, the PSO has a high convergence rate and a better accuracy  
20 (Kennedy and Eberhart, 2001). Even though the optimal solutions found by the PSO  
21 cannot be proven to be global, the results are better than observations and can be used  
22 to practically guide genetic selection.

1           The sink variation function corresponding to the maximal cob weight reveals the  
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4           optimal source-sink dynamics. In order to obtain the maximal yield of cob, the cob  
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6           sink value keeps extremely small: almost zero during the early development stages, so  
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8           that the leaf surface area may increase. When biomass production almost saturates,  
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10           the cob begins absorbing biomass quickly, especially during the last several growth  
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12           cycles where nearly all the available biomass is allocated to the cob and the cob  
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14           becomes the strongest competitor for biomass against the other organs. This  
15  
16           phenomenon can be derived from the monotonously increasing cob sink variation as  
17  
18           illustrated in Figure 3(b) for the single objective optimization of maximization of cob  
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20           weight and in Figure 7 for the optimal solutions of the multi-objective optimization  
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22           problem. This optimal cob development strategy is in agreement with Weiner (1988)  
23  
24           and Vega *et al.* (2000): there is a threshold size for plants to produce flowers and fruits,  
25  
26           the plant will grow as much as it can until its biomass reaches a threshold, and then  
27  
28           the biomass may be distributed to fruits and flowers.

29           The interaction between cob and tassel is also deduced from the single and  
30  
31           multi-objective optimization problems. The optimal solutions of cob sink variation  
32  
33           revealed that the cob growth requires pollen which is provided by tassel. To get better  
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35           cob weight, cob begins to absorb biomass mainly from the 20<sup>th</sup> growth cycle, while  
36  
37           the tassel appears and absorbs biomass at the 21<sup>st</sup> growth cycle, and stops growing one  
38  
39           growth cycle later, i.e. at the 22<sup>nd</sup> growth cycle. Considering this strong interaction  
40  
41           between cob and tassel (Borrás *et al.*, 2002; Uribe Larrea *et al.*, 2002), tassel weight is  
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43           integrated into our multi-objective optimization problem as a constraint. A threshold is  
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1 set for tassel weight (not less than 10 g). In contrary to optimal solutions of general  
2 optimization problems with constraints that are on the boundary of the feasible area  
3 formed by constraints, all the tassel weights are higher than this 10 g. One reason is  
4 that so far we do not know the relationship between cob and tassel quantitatively.  
5 Hence, it is difficult to set the threshold value. Another reason is that tassel sink  
6 strength variation is fixed and it does not change according to the cob sink strength  
7 variation, in this work.

8 From the optimal results, the ideotype of maize can be deduced. From a  
9 physiological point of view, the cob begins to absorb biomass from about the 20<sup>th</sup>  
10 growth cycle when the leaf area saturates, independently of the cob position. And then,  
11 it absorbs biomass smoothly or significantly, depending on the breeding objectives.  
12 Especially, if the objective is to have a maximal cob weight, the maize should have a  
13 bigger reproductive capacity, and the cob should grow with post-expansion and fast  
14 growth rate. From an architectural point of view, for the maize giving the maximal  
15 cob weight, the leaf size is reduced during the last vegetative and reproductive stages  
16 of growth. The harvest index is above 50%. It is coincident with the ideotype of maize  
17 proposed by Mock and Pearce (1975) by analysing research results of other people  
18 with experimental based approach. The *Pareto front* of the multi-objective  
19 optimization problem presents all the different optimal strategies, and the  
20 decision-maker could choose his optimal strategy according to market prices or the  
21 application purposes for example. The optimal results provide a reference to improve  
22 breeding strategies and to design a new ideotype of maize.

1 Even though GreenLab model can simulate plant growth in response to  
2 environmental conditions (light, temperature, water, competition), some  
3 complementary work is needed to describe simultaneously carbon balance and water  
4 balance that determine the distinction between fresh and dry biomass. In addition, the  
5 parameters that we optimized are oriented to those related to the cob sink variation  
6 function, whereas the others are fixed to be the estimated values. However, there  
7 might be some correlation between parameters. Due to the limited observation data  
8 (samples), we have not been able to assess the correlation between parameters so far.  
9 If these drawbacks are corrected correspondingly, the parameter estimation accuracy  
10 should be increased and the frame work for optimization shall be improved. If the  
11 estimated parameter values are changed, the optimal solutions may be different, as the  
12 optimization is based on the model with estimated parameters. However, the  
13 methodology that we proposed to maximize both cob weight and the vegetative  
14 compartment weight, is still valid. Furthermore, it is interesting to note that the  
15 relationship between sources and sinks as illustrated in Figure 3(b) and Figure 7 does  
16 not depend on parameter values. The qualitative results are not changed.

17 Actually, in cobs, only kernels give the food for human beings or for livestock.  
18 The number of kernels is a critical factor that affects the final kernel weight (Borrás  
19 and Otegui, 2001). Therefore, optimizing the number of kernels per cob could be an  
20 interesting work in future. So far, we do not have the information about the proportion  
21 of the kernel weight to the cob weight, which raises the difficulty to estimate  
22 parameters of GreenLab model. However, the corresponding experimental work is in

1 process this year.

2

### 3 **Conclusion**

4 Two kinds of optimization problems of either only maximization of cob weight  
5 or maximization of cob weight and total weight of leaves and stem simultaneously  
6 were formulated. The non-convex, multimodal or non-unique solution problems were  
7 solved by a heuristic optimization algorithm, Particle Swarm Optimization.

8 The source-sink dynamics is investigated through optimization in this study. The  
9 optimization results provide a reference for decision-makers to improve the breeding  
10 strategies or to design ideotypes of plants, especially in the current context of biofuel  
11 development, increase in agricultural products price and necessity to consider  
12 co-products when designing cultivation practices.

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### 19 **References**

20 Allen, M., Prusinkiewicz, P., DeJong, T., 2005. Using L-systems for modeling  
21 source-sink interactions, architecture and physiology of growing trees: the  
22 L-PEACH model. *New Phytologist* 166, 869-880.

- 1 Baenziger, P.S., Russell, W.K., Graef, G.L., Campbell, B.T., 2006. Improving Lives:  
2  
3  
4 50 years of Crop Breeding, Genetics, and Cytology (C-1). *Crop Sci.* 46,  
5  
6 2230-2244.  
7  
8  
9 Borrás, L., Otegui, M.E., 2001. Maize Kernel Weight Response to Postflowering  
10  
11 Source–Sink Ratio. *Crop Sci.* 41, 1816–1822.  
12  
13  
14 Borrás, L., Cura, J.A., Otegui, M.E., 2002. Maize Kernel Composition and  
15  
16 Post-Flowering Source-Sink Ratio. *Crop Sci.* 42, 781–790.  
17  
18  
19 Borrás, L., Westgate, M.E., Otegui, M.E., 2003. Control of Kernel Weight and Kernel  
20  
21 Water Relations by Post-flowering Souce-sink Ratio in Maize. *Ann. Bot.* 91,  
22  
23 857-867.  
24  
25  
26  
27  
28 Carson, E., Feng, D.D., Pons, M.N., Soncini-Sessa, R., van Straten, G., 2006. Dealing  
29  
30 with bio- and ecological complexity: Challenges and opportunities. *Annual*  
31  
32 *Reviews in Control* 30, 91–101.  
33  
34  
35  
36 Cilas, C., Bar-Hen, A., Montagnon, C., Godin, C., 2006. Definition of Architectural  
37  
38 Ideotypes for Good Yield Capacity in *Coffea canephora*. *Ann. Bot.* 97, 405-411.  
39  
40  
41  
42 Cournède, P.H., Mathieu, A., Houllier, F., Barthélémy, D., de Reffye, P., 2008.  
43  
44 Computing Competition for Light in the GREENLAB Model of Plant Growth: A  
45  
46 Contribution to the Study of the Effects of Density on Resource Acquisition and  
47  
48 Architectural Development. *Ann. Bot.* 101, 1207-1219.  
49  
50  
51  
52  
53 Dencic, S., 1994. Designing a Wheat Ideotype with Increased Sink Capacity. *Plant*  
54  
55 *Breeding* 112, 311-317.  
56  
57  
58  
59 Dieleman, J.A., Marcelis, L.F.M., Elings, A., Dueck, T.A., Meinen, E., 2006. Energy  
60  
61  
62  
63  
64  
65

- 1 Saving in Greenhouse: Optimal Use of Climate Conditions and Crop  
2 Management. *Acta Hort. (ISHS)* 718, 203-210.
- 3 Donald, C.M., 1968. The breeding of crop ideotypes. *Euphytica* 17, 385-403.
- 4 Dong, Q., Louarn, G., Wang, Y., Barczi, J.F., de Reffye, P., 2008. Does the  
5 Structure–Function Model GREENLAB Deal with Crop Phenotypic Plasticity  
6 Induced by Plant Spacing? A Case Study on Tomato. *Ann. Bot.* 101, 1195 –  
7 1206.
- 8 van Evert, F.K., de Visser, P.H.B., Heinen, M., 2006. Operational Optimization of  
9 Organic Fertilizer Application in Greenhouse Crops. *Acta Hort. (ISHS)* 718,  
10 165-172.
- 11 Ferentinos, K.P., Arvanitis, K., Tantau, H., Sigrimis, N., 2006. Special Aspects of IT  
12 for Greenhouse Cultivation. In : *CIGR Handbook of Agricultural Engineering:*  
13 *Information Technology.* American Society of Agricultural and Biological  
14 Engineers, St. Joseph, Michigan, pp. 294-312.
- 15 Fieldsend, J.E., 2004. Multi-objective particle swarm optimization methods.  
16 [url=citeseer.ist.psu.edu/735591.html](http://citeseer.ist.psu.edu/735591.html).
- 17 Fink, M., 1993. Effects of Short-Term Temperature Fluctuation on Plant Growth and  
18 Conclusions for Short-Term Temperature Optimization in Greenhouse. *Acta Hort.*  
19 *(ISHS)* 328, 147-154.
- 20 Fourcaud, T., Zhang, X.P., Stokes, A., Lambers, H., Korner, C., 2008. Plant Growth  
21 Modelling and Applications: The Increasing Importance of Plant Architecture in  
22 Growth Models. *Ann. Bot.* 101, 1053-1063.

- 1 Guo, H., Letort, V., Hong, L., Fourcaud, T., Cournède, P.H., Lu, Y., de Reffye, P.,  
2  
3 2006. Adaptation of the GreenLab Model for Analyzing Sink-Source  
4  
5 Relationships in Chinese Pine Saplings. In: Fourcaud, T., Zhang, X.P. (Eds.),  
6  
7 Plant growth Modeling, and Applications, IEEE Computer Society (Los  
8  
9 Alamos, California), pp. 236-243.  
10  
11  
12 Guo, Y., Ma, Y.T., Zhan, Zh.G., Li, B.G., Dingkuhn, M., Luquet, D., de Reffye, P.,  
13  
14 2006. Parameter Optimization and Field Validation of the Functional-Structural  
15  
16 Model GREENLAB for Maize. *Ann. Bot.* 97, 217–230.  
17  
18  
19 Haverkort, A.J., Grashoff, C., 2004. IDEOTYPING-POTATO a modelling approach to  
20  
21 genotype performance. In: MacKerron, D.K.L., Haverkort, A.J. (Eds.), *Decision*  
22  
23 *Support Systems in Potato Production - Bringing Models to Practice*,  
24  
25 Wageningen Academic Publisher, pp. 199–211.  
26  
27  
28 He, S., Wu, Q.H., Wen, J.Y., Saunders, J.R., Paton, R.C., 2004. A particle swarm  
29  
30 optimizer with passive congregation. *BioSystems* 78, 135–147.  
31  
32  
33 van Henten, E.J., Buwalda, F., de Zwart, H.F., de Gelder, A., Hemming, J., Bontsema,  
34  
35 J., 2006. Toward an Optimal Control Strategy for Sweet Pepper Cultivation – 2.  
36  
37 Optimization of the Yield Pattern and Energy Efficiency. *Acta Hort. (ISHS)* 718,  
38  
39 391-398.  
40  
41  
42 Herndl, M., Shan, C., Wang, P., Graeff, S., Claupein, W., 2007. A Model Based  
43  
44 Ideotyping Approach for Wheat Under Different Environmental Conditions in  
45  
46 North China Plain. *Agricultural Sciences in China* 6, 1426-1436.  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1 architecture for water and phosphorus acquisition. *Journal of Theoretical Biology*  
2  
3 226, 331–340.  
4  
5  
6 3 Kang, M., Heuvelink, E., de Reffye, P., 2006. Building Virtual Chrysanthemum based  
7  
8 on Sink-source Relationships: Preliminary Results. *Acta Hort. (ISHS)* 718,  
9 4  
10 129-136.  
11 5  
12  
13 6 Kang, M., Evers, J.B., Vos, J., de Reffye, P., 2008. The Derivation of Sink Functions  
14  
15 of Wheat Organs using the GREENLAB Model. *Ann. Bot.* 101, 1099 – 1108.  
16 7  
17  
18 8 Kennedy, J., Eberhart, R.C., 1995. Particle swarm optimization. In: *Proc. IEEE Conf.*  
19  
20 on Neural Networks, IV, Piscataway, NJ, pp. 1942–1948.  
21 9  
22  
23 10 Kennedy, J., Eberhart, R.C., 2001. *Swarm Intelligence*. Morgan Kaufmann Publishers.  
24  
25  
26 11 King, R.E., Sigrimis, N., 2001. Computational intelligence in crop production.  
27  
28 Computers and Electronics in Agriculture 31, 1–3.  
29 12  
30  
31 13 Kurth, W., 2000. Towards universality of growth grammars: Models of Bell, Pagès,  
32  
33 and Takenaka revisited. *Ann. For. Sci.* 57, 543–554.  
34 14  
35  
36 15 Lauri, P., Costes, E., 2004. Progress in Whole-Tree Architecture Studies for Apple  
37  
38 Cultivar Characterization at INRA, France - Contribution to the Ideotype  
39 16  
40 Approach. *Acta Hort. (ISHS)* 663, 357-362.  
41 17  
42  
43 18 Letort, V., Cournède P.H., Lecoer, J., Hummel, I., de Reffye, P., Chiustophe, A., 2006.  
44  
45 Effect of topological and phenological changes on biomass partitioning in  
46 19  
47 Arabidopsis thaliana inflorescence: a preliminary model-based study. In:  
48 20  
49 Fourcaud, T., Zhang, X.P. (Eds.), *Plant growth Modeling, and Applications*, IEEE  
50 21  
51 Computer Society (Los Alamitos, California), pp. 65-69.  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1 Letort, V., Mahe, P., Cournède, P.H., de Reffye, P., Courtois, B., 2008a. Quantitative  
2 Genetics and Functional–Structural Plant Growth Models: Simulation of  
3 Quantitative Trait Loci Detection for Model Parameters and Application to  
4 Potential Yield Optimization. *Ann. Bot.* 101, 1243-1254.
- 5 Letort, V., Cournède, P.H., Mathieu, A., de Reffye, P., Constant, T., 2008b. Parametric  
6 Identification of a Functional-Structural Tree Growth Model and Application to  
7 Beech Trees (*Fagus sylvatica* ). *Functional Plant Biology* 35, in press.
- 8 Linker, R., Seginer, I., Gutman, P.O., 1998. Optimal CO<sub>2</sub> control in a greenhouse  
9 modeled with neural networks. *Computers and Electronics in Agriculture* 19,  
10 289–310
- 11 Luquet, D., Dingkuhn, M., Kim, H., Tambour, L., Clement-Vidal, A., 2006.  
12 EcoMeristem, a model of morphogenesis and competition among sinks in rice. 1.  
13 Concept, validation and sensitivity analysis. *Functional Plant Biology* 33,  
14 309-323.
- 15 Ma, Y.T., Li, B.G., Zhan, Zh.G., Guo, Y., Luquet, D., de Reffye, P., Dingkuhn, M.,  
16 2007. Parameter Stability of the Functional–Structural Plant Model GREENLAB  
17 as Affected by Variation within Populations, among Seasons and among Growth  
18 Stages. *Ann. Bot.* 99, 61-73.
- 19 Ma, Y.T., Wen, M.P., Guo, Y., Li, B.G., Cournède, P.H., de Reffye, P., 2008. Parameter  
20 Optimization and Field Validation of the Functional–Structural Model  
21 GREENLAB for Maize at Different Population Densities. *Ann. Bot.* 101,  
22 1185-1194.



- 1 Mathieu, A., Zhang, B.G., Heuvelink, E., Liu, S.J., Cournède, P.H., de Reffye, P., 2007.  
2  
3 Calibration of fruit cyclic patterns in cucumber plants as a function of  
4  
5 source-sink ratio with the GreenLab model. In: Proceedings of the 5th  
6  
7 International Workshop on Functional-Structural Plant Models, Napier, New  
8  
9 Zealand, pp. 5-1 - 5-4.  
10  
11  
12 Mathieu, A., Cournède, P.H., Barthélémy, D., de Reffye, P., 2008. Rhythms and  
13  
14 Alternating Patterns in Plants as Emergent Properties of a Model of Interaction  
15  
16 between Development and Functioning. *Ann. Bot.* 101, 1233-1242.  
17  
18  
19 Mock, J.J., Pearce, P.B., 1975. An Ideotype of Maize. *Euphytica* 24, 613-623.  
20  
21  
22  
23 Morimoto, T., Takeuchi, T., Hashimoto, Y., 1993. Growth optimization of plant by  
24  
25 means of the hybrid system of genetic algorithm and neural network. In: *Neural*  
26  
27 *Networks, IJCNN '93-Nagoya Proceedings of 1993 International Joint*  
28  
29 *Conference on*, 3, pp. 2979 – 2982.  
30  
31  
32  
33  
34  
35  
36 Morimoto, T., Torii, T., Hashimoto, Y., 1995. Optimal control of physiological  
37  
38 processes of plants in a green plant factory. *Practice* 3, 505-511.  
39  
40  
41  
42 Morimoto, T., De Baerdemaeker, J., Hashimoto, Y., 1997. An intelligent approach for  
43  
44 optimal control of fruit-storage process using neural networks and genetic  
45  
46 algorithms. *Computers and Electronics in Agriculture* 18, 205-224.  
47  
48  
49  
50  
51  
52  
53 Morimoto, T., Tu, K., Hatou, K., Hashimoto, Y., 2003. Dynamic optimization using  
54  
55 neural networks and genetic algorithms for tomato cool storage to minimize  
56  
57 water loss. *Trans. ASAE.* 46, 1151-1159.  
58  
59  
60  
61  
62  
63  
64  
65  
66  
67  
68  
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- 1 Multi-objective Particle Swarm Optimization (MOPSO). In: IEEE Swarm  
2 Intelligence Symposium, pp. 26-33.
- 3 Mustafa, G., 1989. Stochastic dynamic optimization approach for revegetation of  
4 reclaimed mine soils under uncertain weather regime. Thesis (Ph.D.), Blacksburg,  
5 VA (US), Virginia Polytechnic Institute and State Univ.
- 6 Peng, S., Khush, G.S., Virk, P., Tang, Q., Zou, Y., 2008. Progress in ideotype breeding  
7 to increase rice yield potential. *Field Crops Research* 108, 32-38.
- 8 Perttunen, J., Sievänen, R., Nikinmaa, E., 1998. LIGNUM: a model combining the  
9 structure and the functioning of trees. *Ecological Modelling* 108, 189-198.
- 10 Prasanna Kumar, G.V., Srivastava, B., Nagesh, D.S., 2008. Modeling and optimization  
11 of parameters of flow rate of paddy rice grains through the horizontal rotating  
12 cylindrical drum of drum seeder. *Computers and Electronics in Agriculture*, In  
13 Press.
- 14 Pratt, R.C., 2001. Specialty Corns. *Crop Sci.* 41, 1990.
- 15 Rasmusson, D.C., 1987. An Evaluation of Ideotype Breeding. *Crop Sci.* 27,  
16 1140-1146.
- 17 de Reffye, P., Hu, B.G., 2003. Relevant qualitative and quantitative choices for  
18 building an efficient dynamic plant growth model: GreenLab Case. In: Hu, B.G.,  
19 Jaeger, M., (Eds.), *Plant Growth Modeling and Applications. Proceedings -*  
20 *PMA03*, Tsinghua University Press and Springer, Beijing, China, pp. 87-107.
- 21 Sievänen, R., Nikinmaa, E., Nygren, P., Ozier-Lafontaine, H., Perttunen, J., Hakula,  
22 H., 2000. Components of functional-structural tree models. *Ann. For. Sci.* 57,

- 1 399–412.
- 2
- 3 2 van Straten, G., Challa, H., Buwalda, F., 2000. Towards user accepted optimal control
- 4
- 5
- 6 3 of greenhouse climate. *Computers and Electronics in Agriculture* 26, 221–238.
- 7
- 8
- 9 4 Tardieu, F., 2003. Virtual plants: modelling as a tool for the genomics of tolerance to
- 10
- 11
- 12 5 water deficit. *Trends in Plant Science* 8, 9–14.
- 13
- 14 6 Tripathi, P.K., Bandyopadhyay, S., Pal, S.K., 2007. Multi-Objective Particle Swarm
- 15
- 16
- 17 7 Optimization with time variant inertia and acceleration coefficients. *Information*
- 18
- 19
- 20 8 *Sciences* 177, 5033-5049.
- 21
- 22
- 23 9 Uribelarrea, M., Carcova, J., Otegui, M.E., Westgate, M.E., 2002. Pollen Production,
- 24
- 25 10 Pollination Dynamics, and Kernel Set in Maize. *Crop Sci.* 42, 1910–1918.
- 26
- 27
- 28 11 Vega, C.R.C., Sadras, V.O., Andrade, F.H., Uhart, S.A., 2000. Reproductive
- 29
- 30
- 31 12 Allometry in Soybean, Maize and Sunflower. *Annals of Botany* 85, 461-468.
- 32
- 33
- 34 13 Weiner, J., 1988. The influence of competition on plant reproduction. In: Lovett
- 35
- 36 14 Doust J., Lovett Doust L. (Eds.), *Plant reproductive ecology: patterns and*
- 37
- 38
- 39 15 *strategies*, Oxford University Press, New York, pp. 228-245.
- 40
- 41
- 42 16 Westgate, M.E., Lizaso, J., Batchelor, W., 2003. Quantitative Relationships between
- 43
- 44
- 45 17 Pollen Shed Density and Grain Yield in Maize. *Crop Sci.* 43, 934-942.
- 46
- 47
- 48 18 Wu, L., de Reffye, P., Hu, B.G., Le Dimet, F.X., Cournède, P.H., 2005. A Water
- 49
- 50
- 51 19 Supply Optimization Problem for Plant Growth Based on GreenLab Model.
- 52
- 53 20 ARIMA, 194-207.
- 54
- 55
- 56 21 Yan, H.P., Kang, M., de Reffye, P., Dingkuhn, M., 2004. A Dynamic, Architectural
- 57
- 58
- 59 22 Plant Model Simulating Resource-dependent Growth. *Ann. Bot.* 93, 591-602.
- 60
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61  
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64  
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1 Yin, X., Stam, P., Kropff, M.J., Schapendonk, A.H.C.M., 2003. Crop Modeling, QTL  
2 Mapping, and Their Complementary Role in Plant Breeding. *Agron. J.* 95, 90-98.  
3  
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1 Table 1. Estimated parameter values of GreenLab

Parameters	Values
$P_a$ (Sink strength of blade)	1 (fixed)
$a_a / b_a$ (Coefficients of beta function for blade)	3.59 / 5.38
$P_s$ (Sink strength of sheath)	0.6
$a_s / b_s$ (Coefficients of beta function for sheath)	3.05 / 3.69
$P_e$ (Sink strength of internode)	1.4
$a_e / b_e$ (Coefficients of beta function for internode)	3.34 / 1.65
$P_f$ (Sink strength of cob)	806.47
$a_f / b_f$ (Coefficients of beta function for cob)	8.34/ 2.60
$P_m$ (Sink strength of tassel)	4.23
$a_m / b_m$ (Coefficients of beta function for tassel)	1 / 1
$K_e$ (Coefficient of sink strength for short internode)	0.21
$\beta$ (Energetic efficiency)	12.36
$\gamma$ (Light interception coefficient)	1.90E-4

2

3

1 **Figure captions**

2 Figure 1. Example of sink variation function (Beta law), with sink strength  $P_o=10$ .

3 Figure 2. Simulation of biomass partition to (a) blade (b) sheath (c) internode (d) cob  
4 (e) tassel, with estimated parameter values by generalized non-linear least square  
5 method. “•” represents measured data at the 8<sup>th</sup> growth cycle corresponding to  
6 vegetative stage; “◦” measured data at the 18<sup>th</sup> growth cycle corresponding to  
7 flowering stage; “▼” measured data at the 33<sup>rd</sup> growth cycle corresponding to  
8 physiological maturity; “—” simulation result at the 8<sup>th</sup> growth cycle; “...” simulation  
9 result at the 18<sup>th</sup> growth cycle; “---” simulation result at the 33<sup>rd</sup> growth cycle.

10 Figure 3. (a) Maximal cob weight associated with cob position (b) Cob sink variations:  
11 the curve marked only with symbol represents the corresponding optimal cob sink  
12 variation; the curve marked by “—●—” represents the estimated cob sink variation.

13 Figure 4. Simulation result of leaf area index for maize with estimated parameter  
14 values marked by “—●—” and with the optimal one marked by “—○—” where the cob is  
15 born by the 1<sup>st</sup> phytomer counted from the bottom.

16 Figure 5. Comparison the ratio of cob weight to vegetative compartment weight  
17 during the plant growth. “—●—” represents the result with estimated parameter values  
18 and “--○--” represents the result with the optimal parameter values.

19 Figure 6. *Pareto front* of the multi-objective optimization problem with respect to cob  
20 position on the stem.

21 Figure 7. Area covered by all the optimal cob sink variations associated with the  
22 *Pareto front*. Two examples of the optimal cob sink variations are given. “—▲—”

1 represents the optimal cob sink variation for maize with cob born by the 12th phytomer, where the cob weight is 792 g and the vegetative compartment is 1695 g; “—□—” the optimal cob sink variation for maize with cob born by the 15th phytomer, where the cob weight is 503 g and the vegetative compartment is 2050 g.

Figure 8. Tassel weight with respect to cob weight, associated with the *Pareto front*.

6

1	1	Appendix
2		
3	2	Symbol list
4		
5		
6	3	$Q$ biomass production of an individual plant
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8		
9	4	$Q_{seed}$ seed biomass
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11	5	$D$ total demand of plant
12		
13		
14	6	$E$ environmental function
15		
16		
17	7	$S$ total green leaf surface area
18		
19		
20	8	$\beta$ energetic efficiency
21		
22		
23	9	$\gamma$ light inception factor
24		
25	10	$N_n^o$ number of organ $o$ born at growth cycle $n$
26		
27		
28	11	$t_{x_o}$ expansion duration of organ $o$
29		
30		
31	12	$ta$ blade functioning duration
32		
33		
34	13	$p_o(j)$ sink value of organ $o$ with age $j$
35		
36	14	$P_o$ sink amplitude (or sink strength) of organ $o$
37		
38		
39	15	$f$ sink variation function
40		
41		
42	16	$be$ beta law function
43		
44		
45	17	$M$ normalization factor
46		
47		
48	18	$a_o$ coefficient of beta law function for organ $o$
49		
50		
51	19	$b_o$ coefficient of beta law function for organ $o$
52		
53	20	$\Delta q_o(n,j)$ biomass increment of organ $o$ with age $j$ , when plant age is $n$
54		
55		
56	21	$q_o(n,j)$ accumulated biomass of organ $o$ with age $j$ , when plant age is $n$
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59	22	$slw$ specific leaf weight
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- 1  $n$  plant age
  - 2  $j$  organ age
  - 3  $J$  objective function
  - 4  $g$  inequality constraint function
  - 5  $h$  equality constraint function
  - 6  $x$  variable of optimization problem
  - 7  $v$  velocity
  - 8  $w$  inertia weight
  - 9  $c$  acceleration coefficient
  - 10  $r$  uniformly distributed random value between 0 and 1
  - 11  $B$  particle best position
  - 12  $Bl$  particle local best position

Figure 1

Example of sink variation function (Beta law)

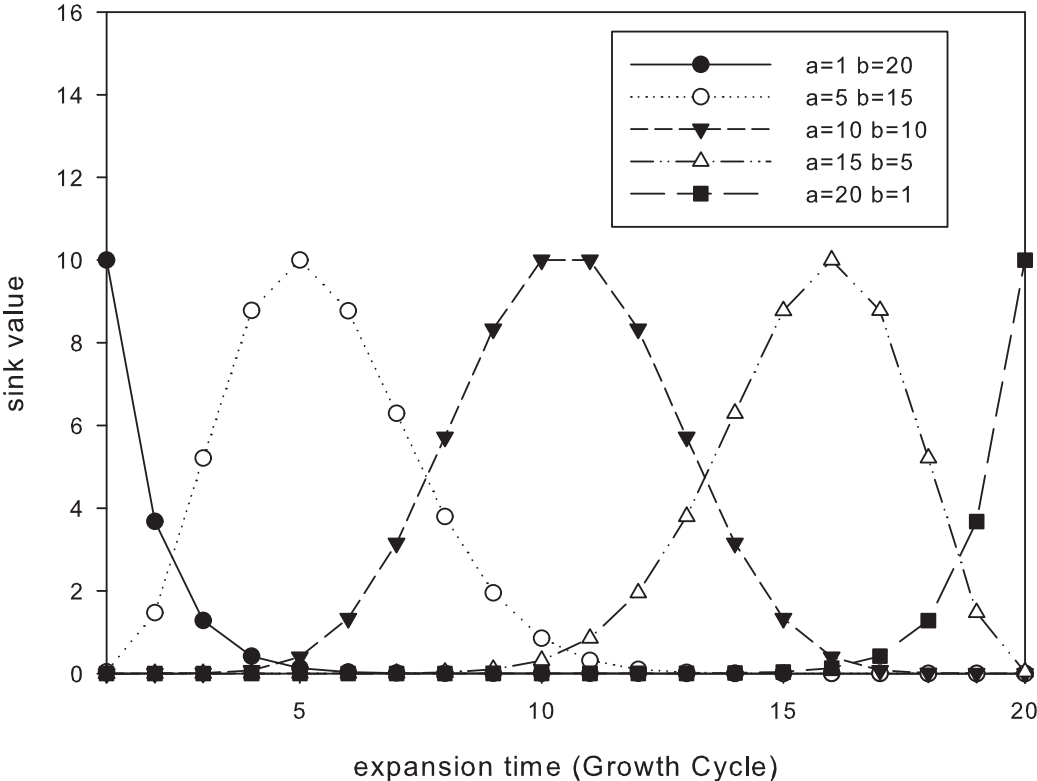


Figure 2(a)

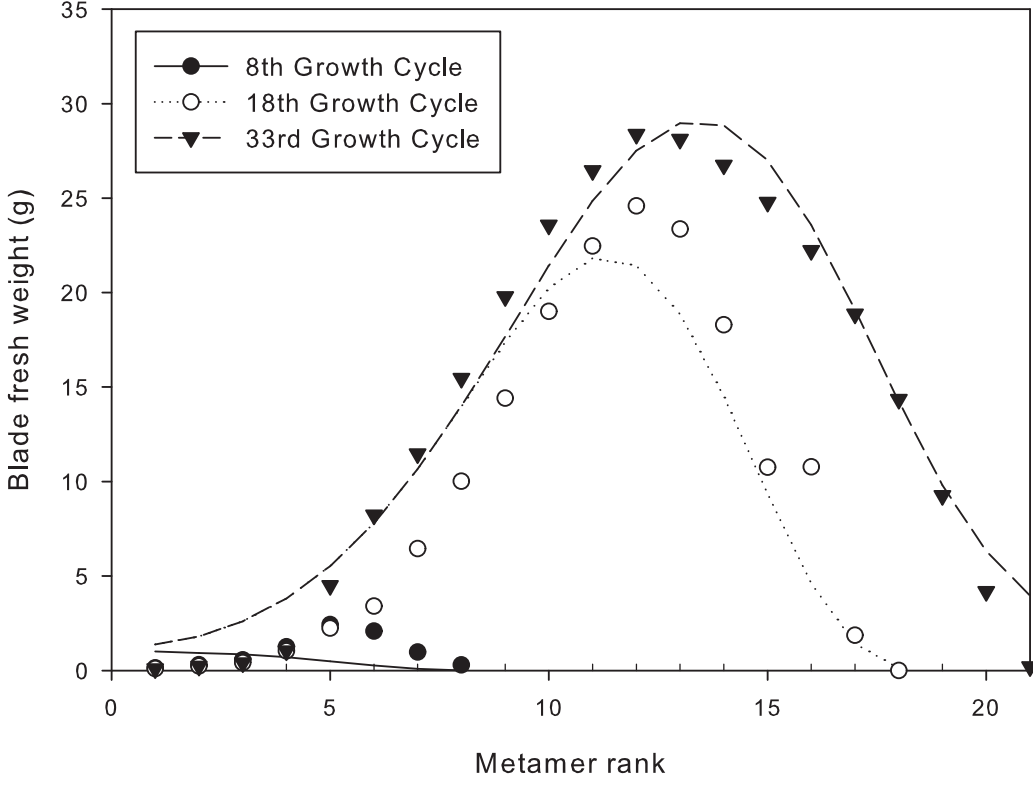


Figure 2(b)

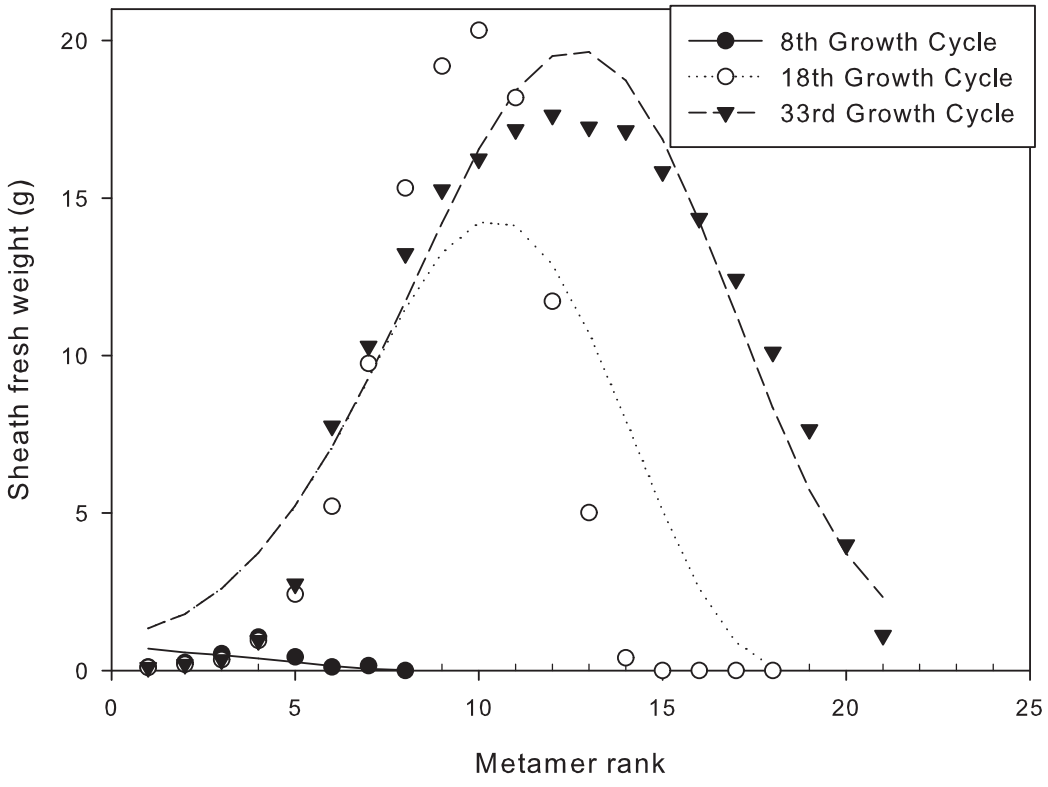


Figure 2(c)

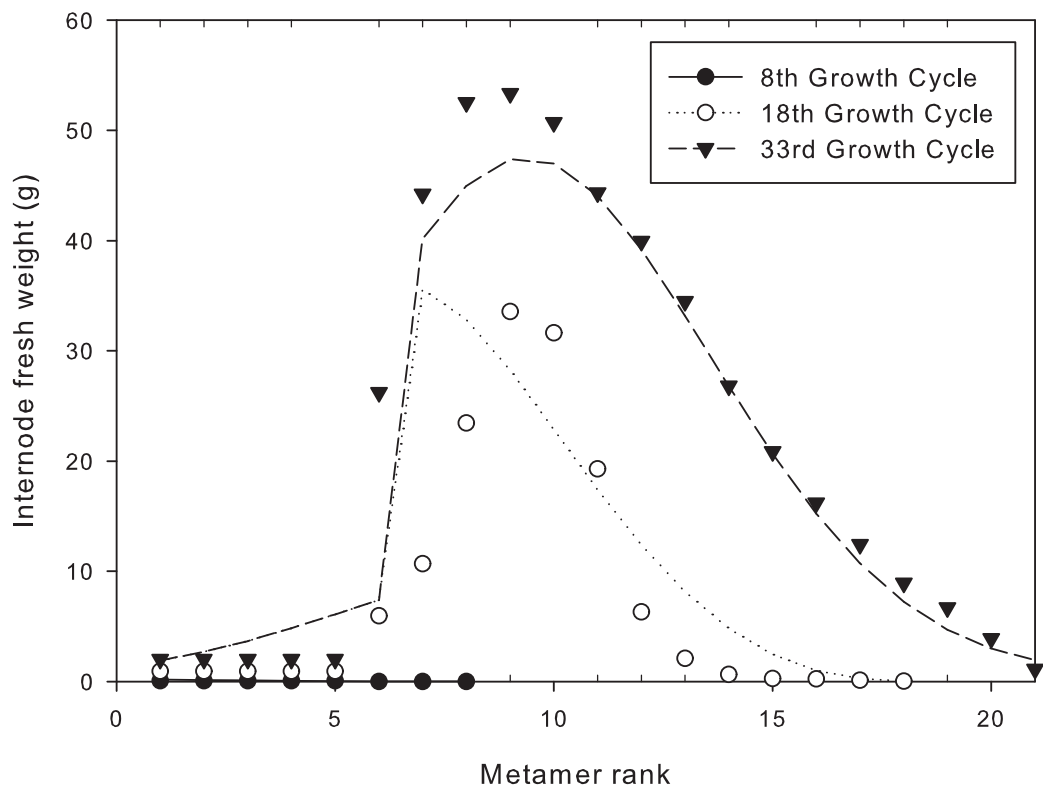


Figure 2(d)

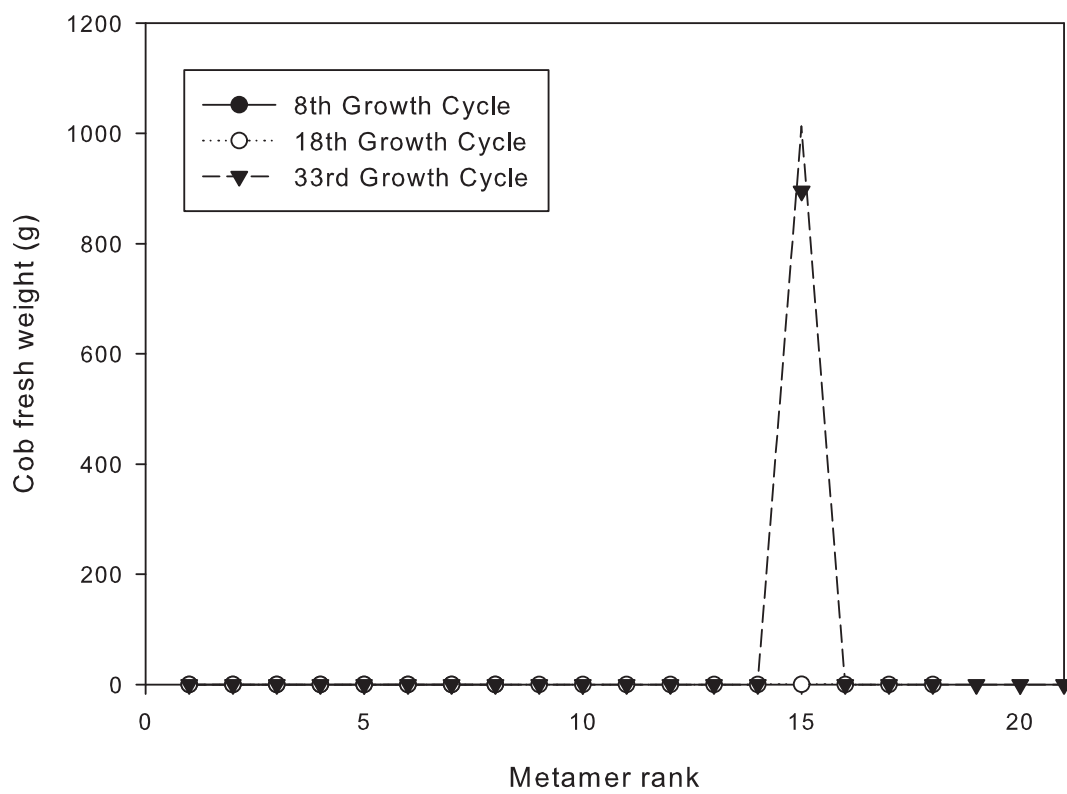


Figure 2(e)

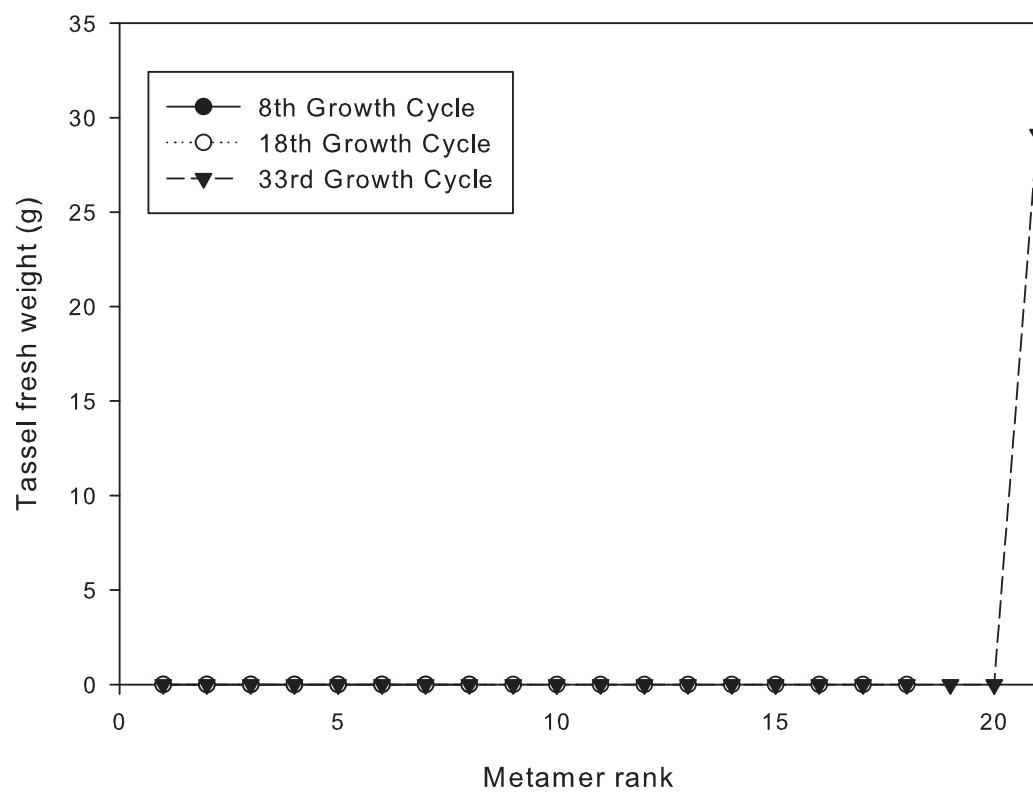


Figure 3(a)

Optimal cob weight associated with cob position

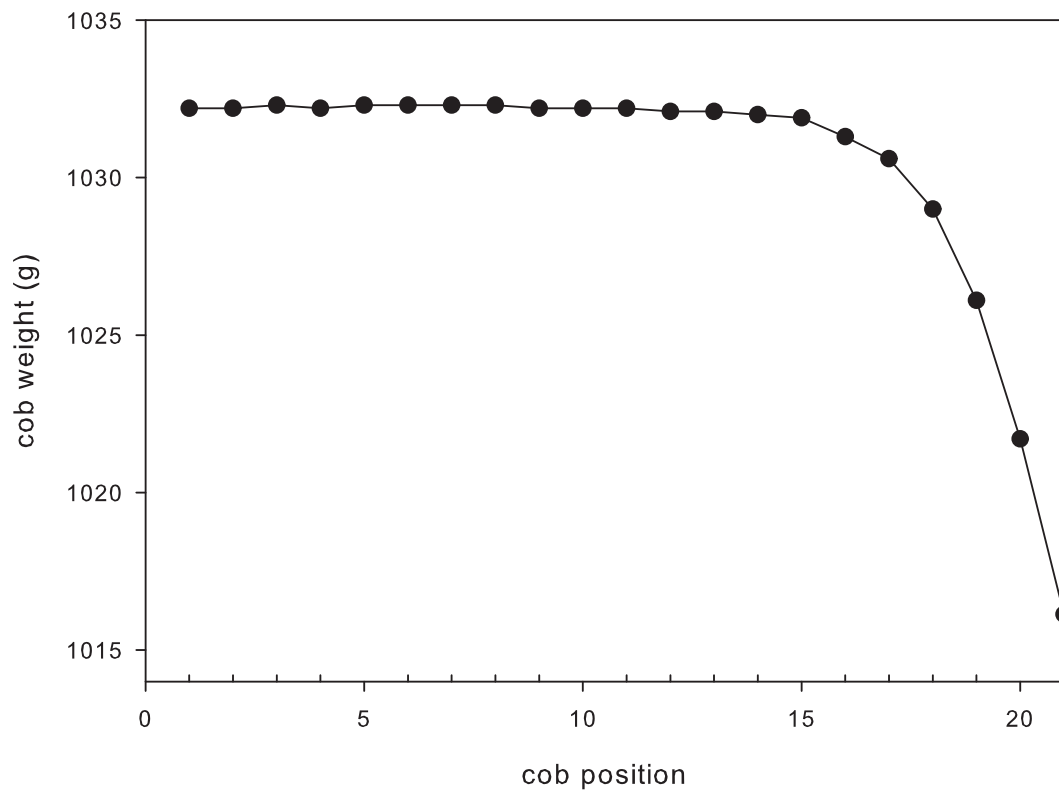




Figure 3(b)

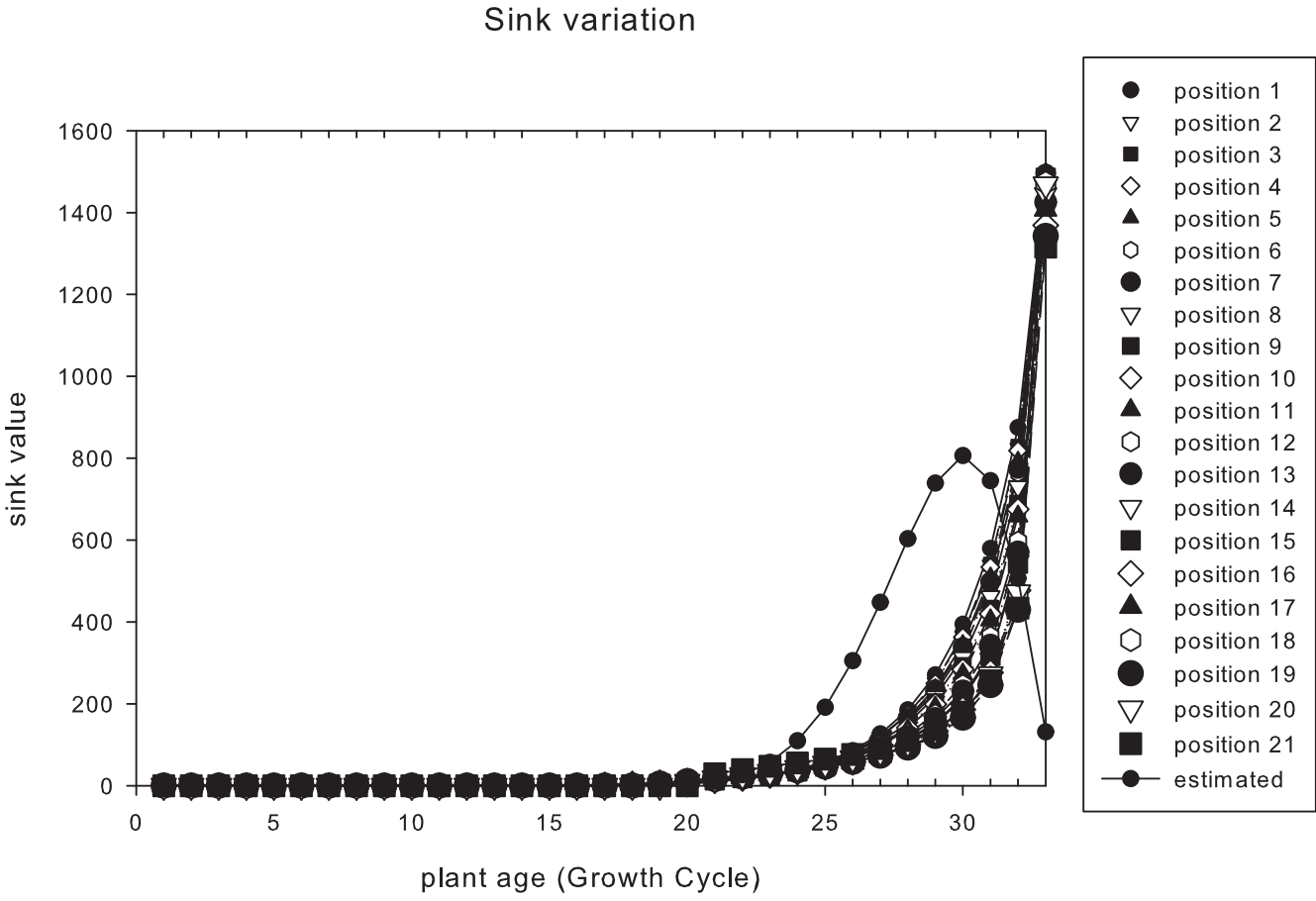


Figure 4

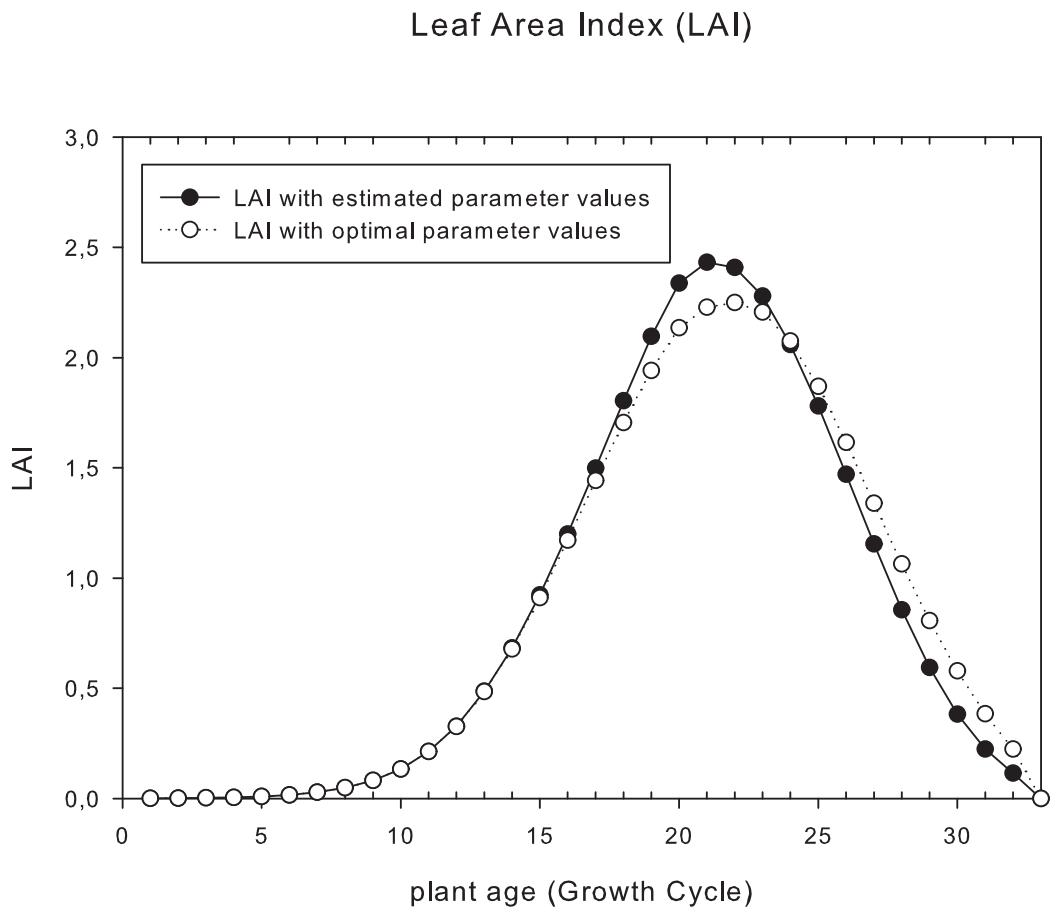


Figure 5

Ratio of cob weight to vegetative compartment weight

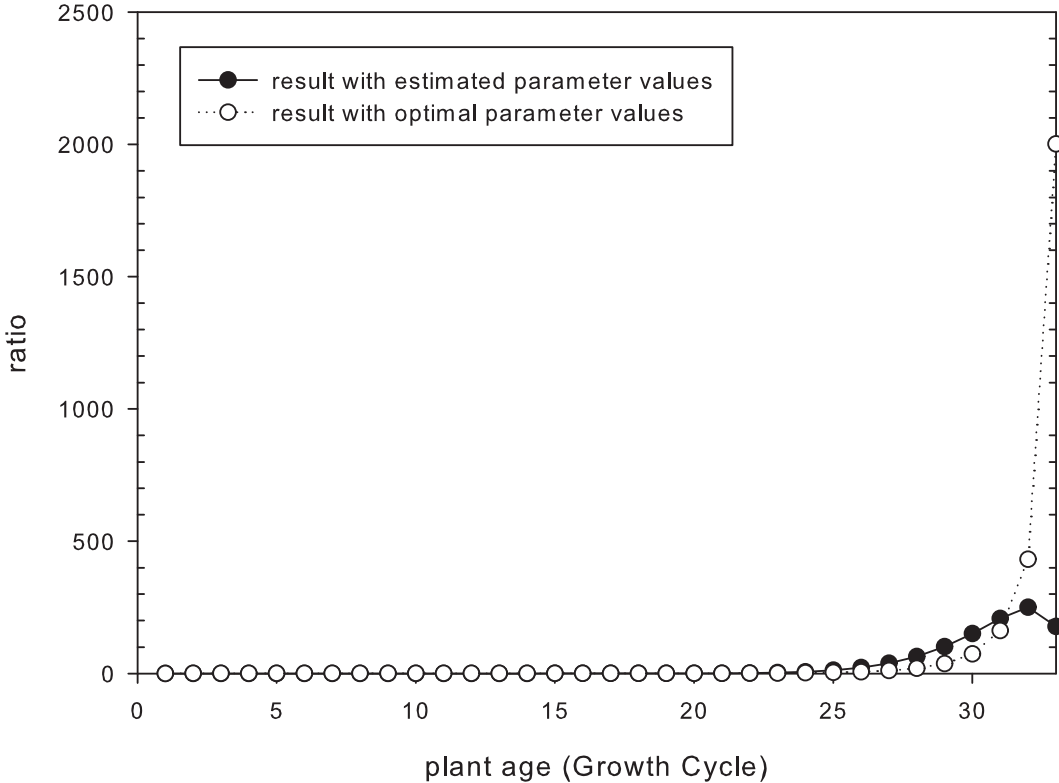


Figure 6

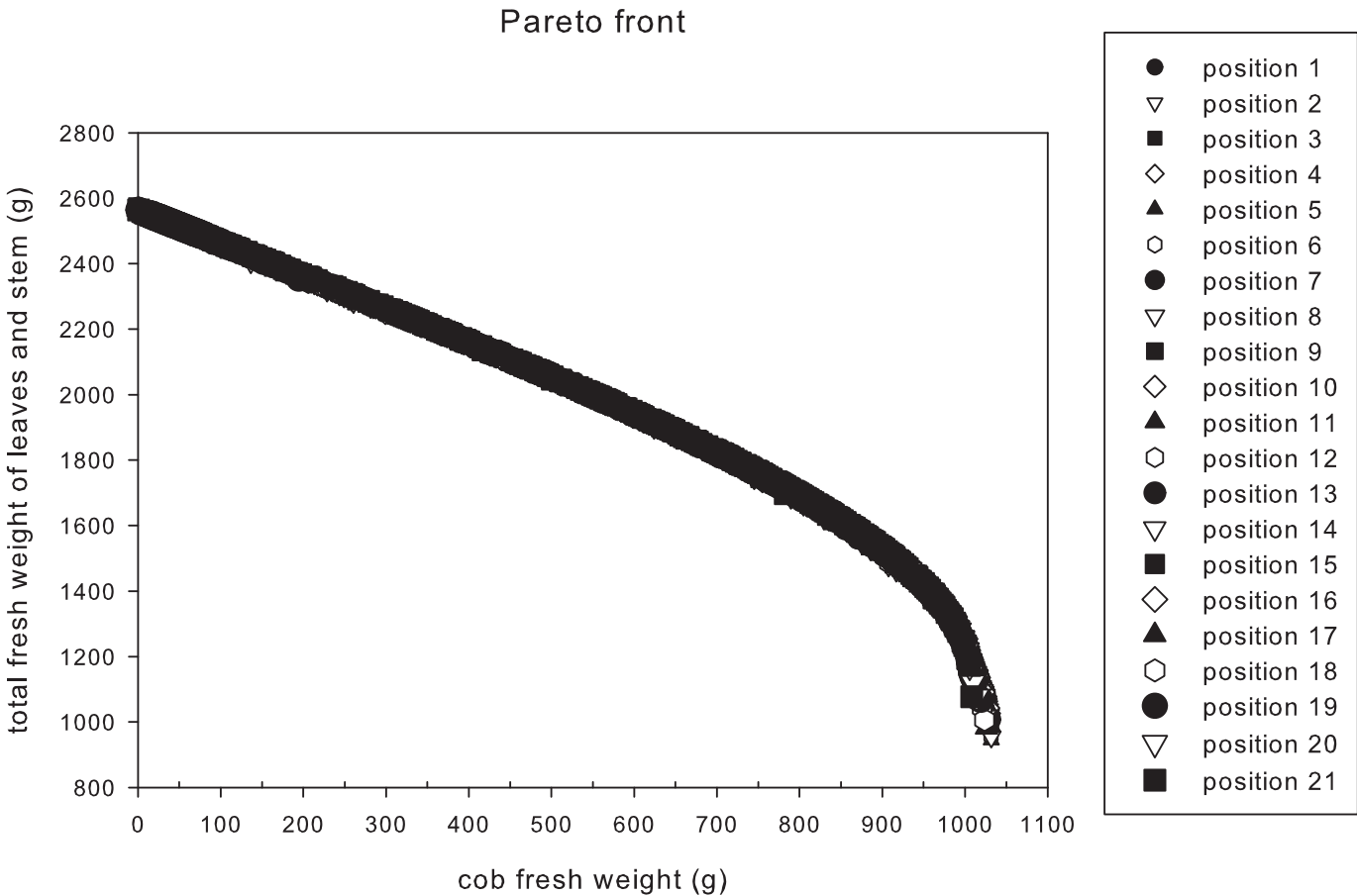


Figure 7

Area covered by all the optimal cob sink variations

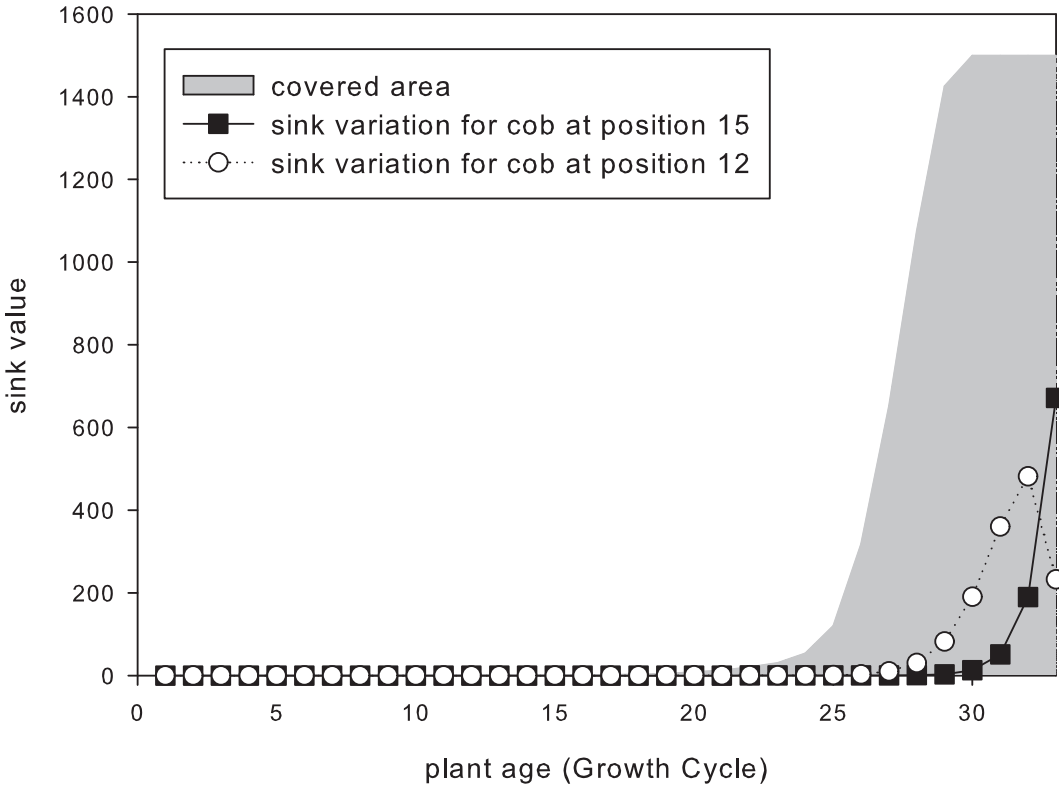


Figure 8

