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1 Optimization of source-sink dynamics in plant growth for ideotype breeding: a case
2 study on maize

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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 21st growth cycle,

1 but the plant is still alive until the 33rd 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 15th 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 β (linked to energetic
 12 efficiency) and γ (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⁻¹) 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 (8th GC corresponding to vegetative stage,
6 18th GC approximately corresponding to flowering stage and 33rd 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. Uribe Larrea *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:

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

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
4
5
6 will be missed. To avoid these two drawbacks, in this subsection, we suppose that cob
7
8
9 expansion duration depends on its position on the stem, to ensure that the cob has
10
11
12 possibility to obtain biomass until the end of the plant growth. For example, if the cob
13
14 appears at the 19th growth cycle, its expansion duration is 15 growth cycles with plant
15
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
21
22
23 strength variations are similar as shown in Figure 3(b) marked only with symbols, and
24
25 the estimated one is represented by the curve in “-.-”. Wherever the cob is and
26
27
28 whatever its expansion duration is, we found that the optimal cob development
29
30
31 strategies are similar. The optimal cob sink is almost zero at the beginning of cob
32
33
34 development, in order to reduce the competition for biomass with source organs and
35
36 to let leaf surface area increase, and then the sink increases monotonously till the end
37
38
39 of plant growth.

40 Comparing the estimated and optimal cob sink variations with cob particularly
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42 born by the 1st phytomer counted from the bottom shown in Figure 3(b), we can
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45 separate the cob development process into 4 stages. During the first stage from the 1st
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48 growth cycle to 15th 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 1st phytomer to by the 15th phytomer;
3 meanwhile, it leads to a slight difference among the optimal cob weights when the cob
4 position is higher than the 15th phytomer, as shown in Figure 3(a). The second stage is
5 from the 16th growth cycle to the 23rd 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 23rd growth cycle to the 31st 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 12th 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 15th
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 21st 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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3
4 optimal source-sink dynamics. In order to obtain the maximal yield of cob, the cob
5
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
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16 phenomenon can be derived from the monotonously increasing cob sink variation as
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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)
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24 and Vega *et al.* (2000): there is a threshold size for plants to produce flowers and fruits,
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26 the plant will grow as much as it can until its biomass reaches a threshold, and then
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28 the biomass may be distributed to fruits and flowers.

29 The interaction between cob and tassel is also deduced from the single and
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31 multi-objective optimization problems. The optimal solutions of cob sink variation
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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 20th growth cycle, while
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37 the tassel appears and absorbs biomass at the 21st growth cycle, and stops growing one
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39 growth cycle later, i.e. at the 22nd growth cycle. Considering this strong interaction
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41 between cob and tassel (Borrás *et al.*, 2002; Uribelarrea *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 20th
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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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
β (Energetic efficiency)	12.36
γ (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 8th growth cycle corresponding to
6 vegetative stage; “◦” measured data at the 18th growth cycle corresponding to
7 flowering stage; “▼” measured data at the 33rd growth cycle corresponding to
8 physiological maturity; “—” simulation result at the 8th growth cycle; “...” simulation
9 result at the 18th growth cycle; “---” simulation result at the 33rd 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 1st 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*.

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
10		
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	β energetic efficiency
21		
22		
23	9	γ 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		
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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)

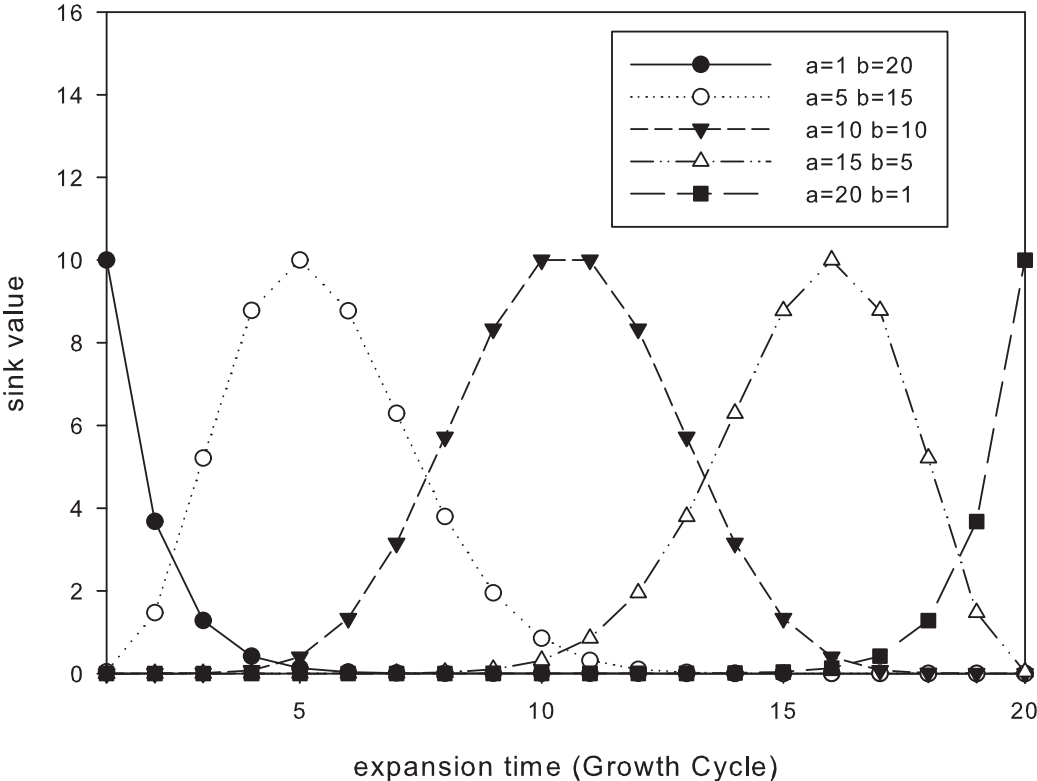


Figure 2(a)

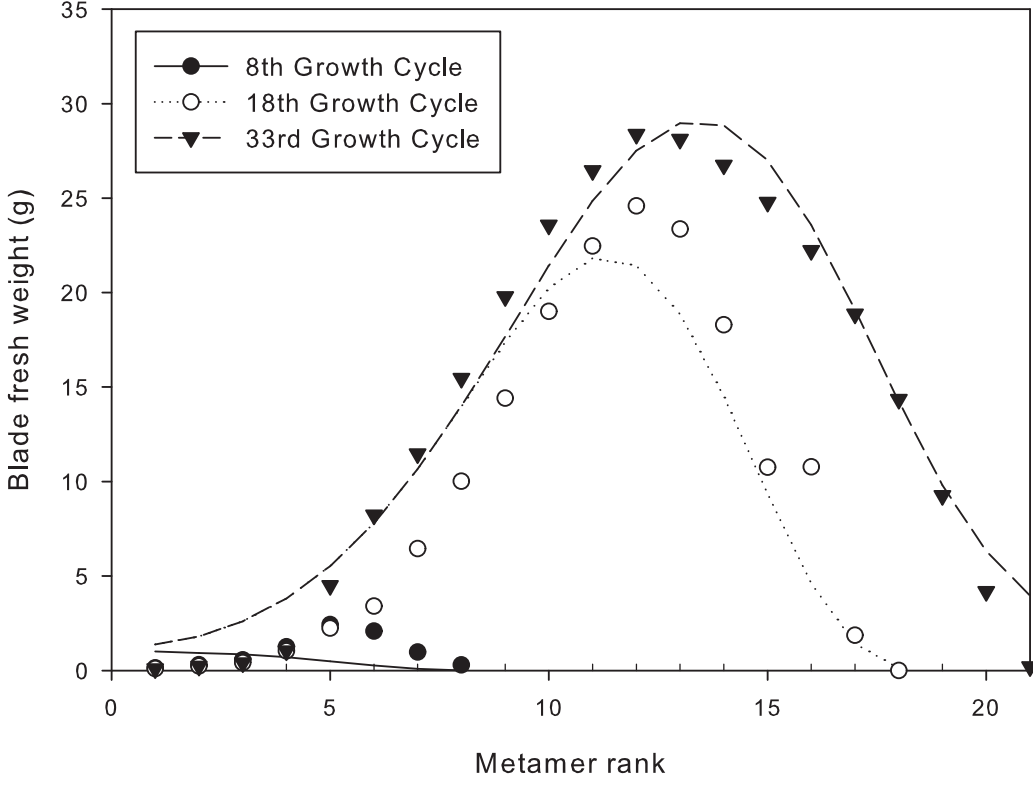


Figure 2(b)

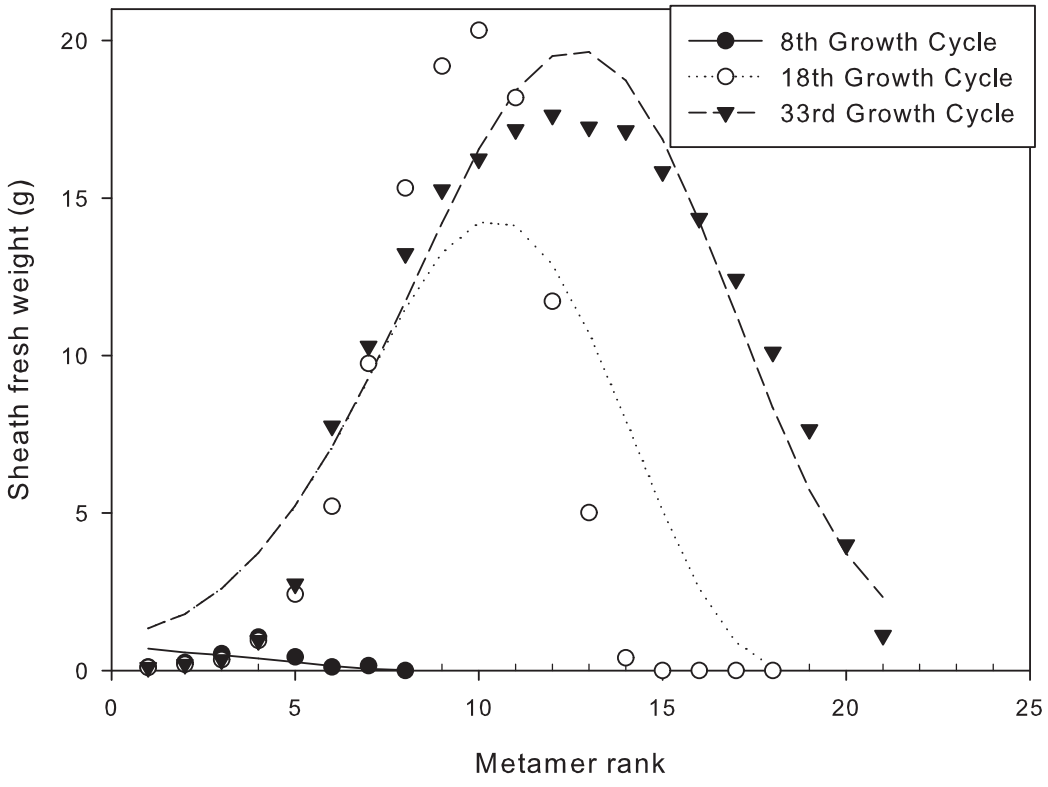


Figure 2(c)

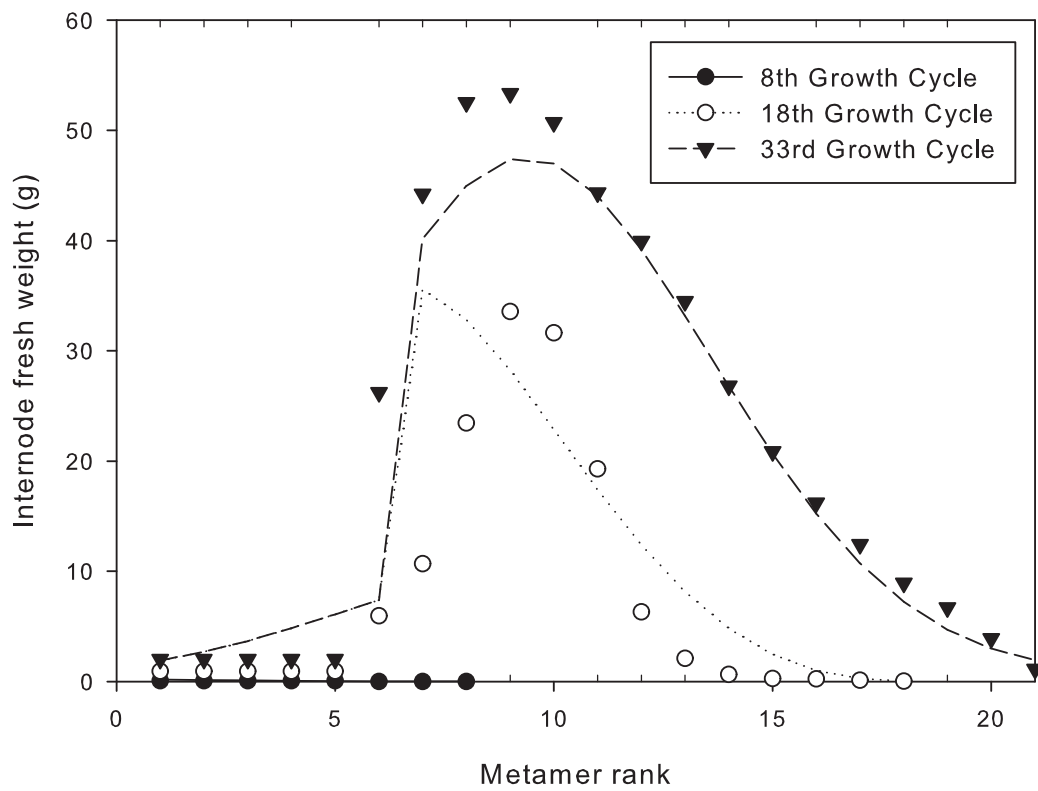


Figure 2(d)

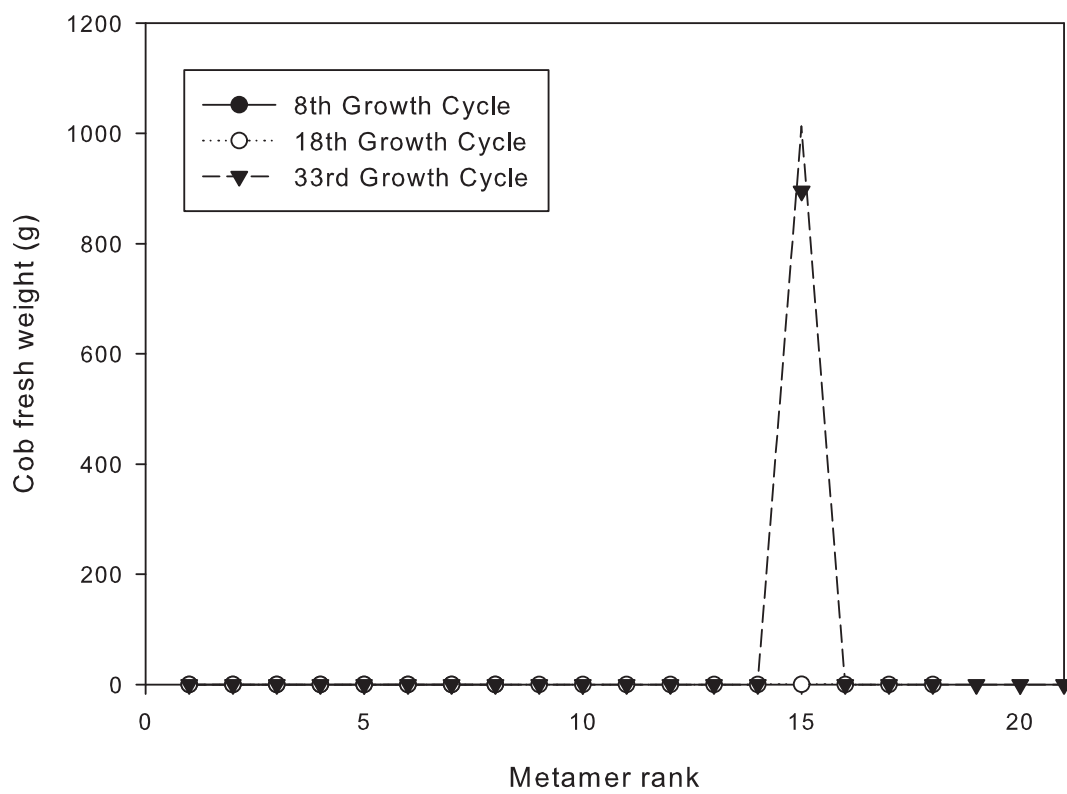


Figure 2(e)

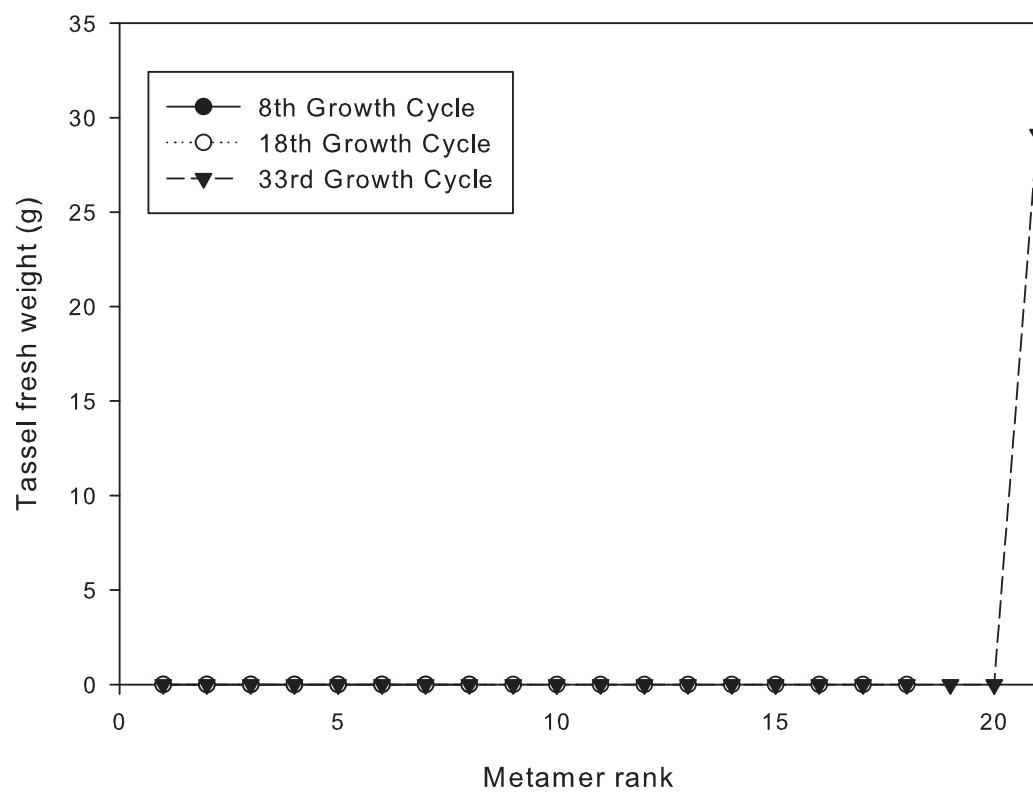


Figure 3(a)

Optimal cob weight associated with cob position

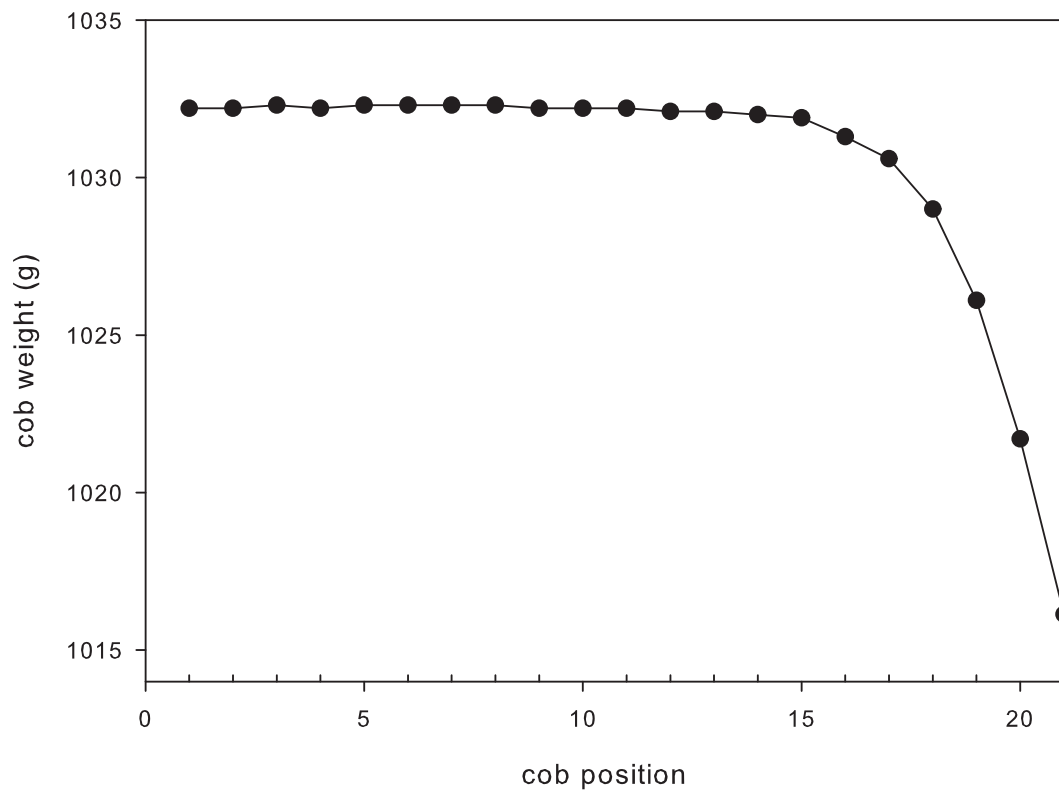


Figure 4

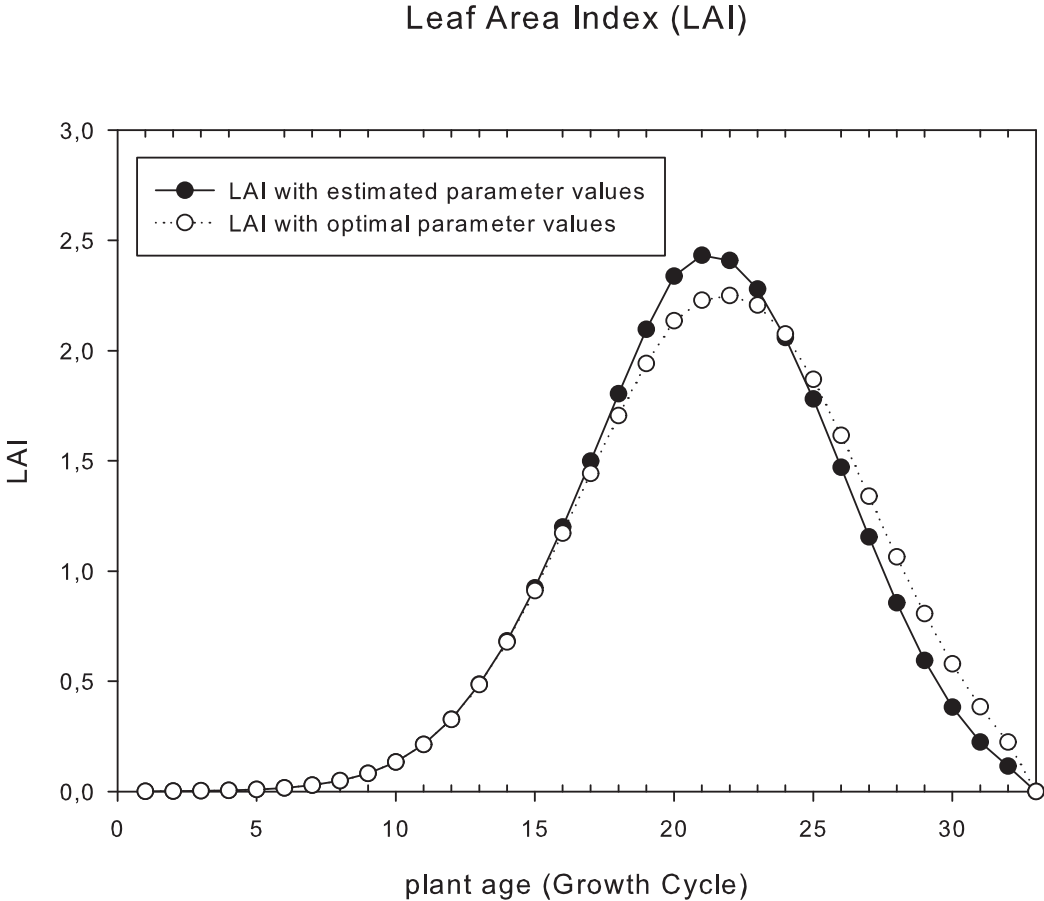


Figure 5

Ratio of cob weight to vegetative compartment weight

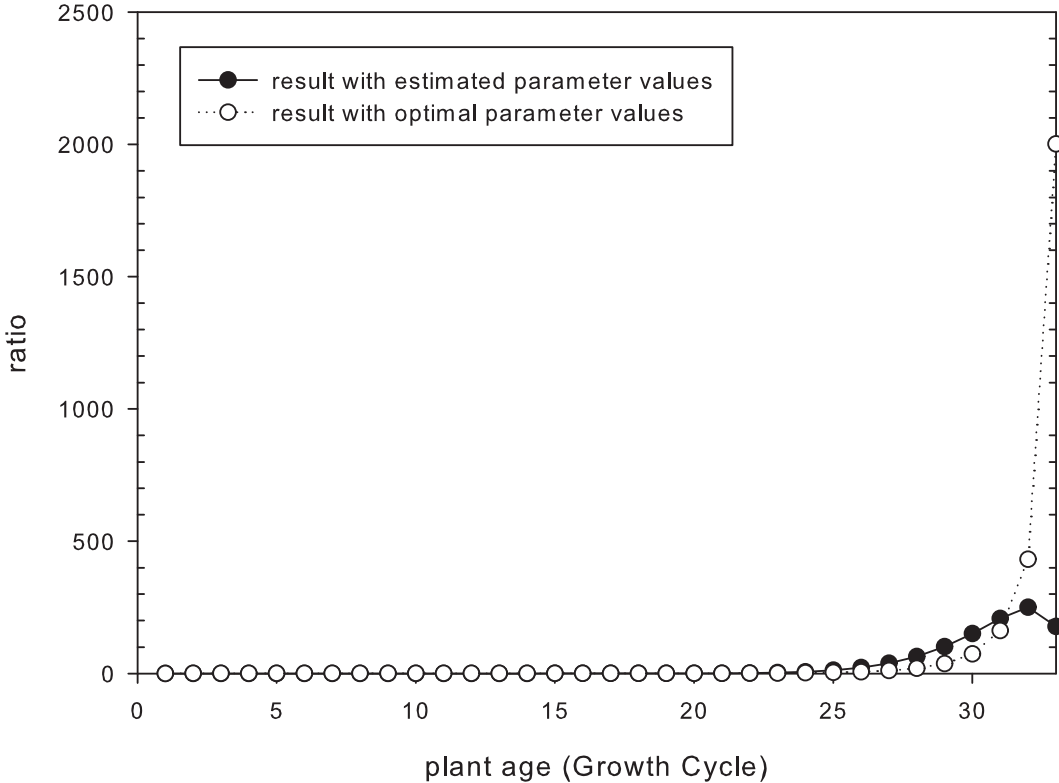


Figure 6

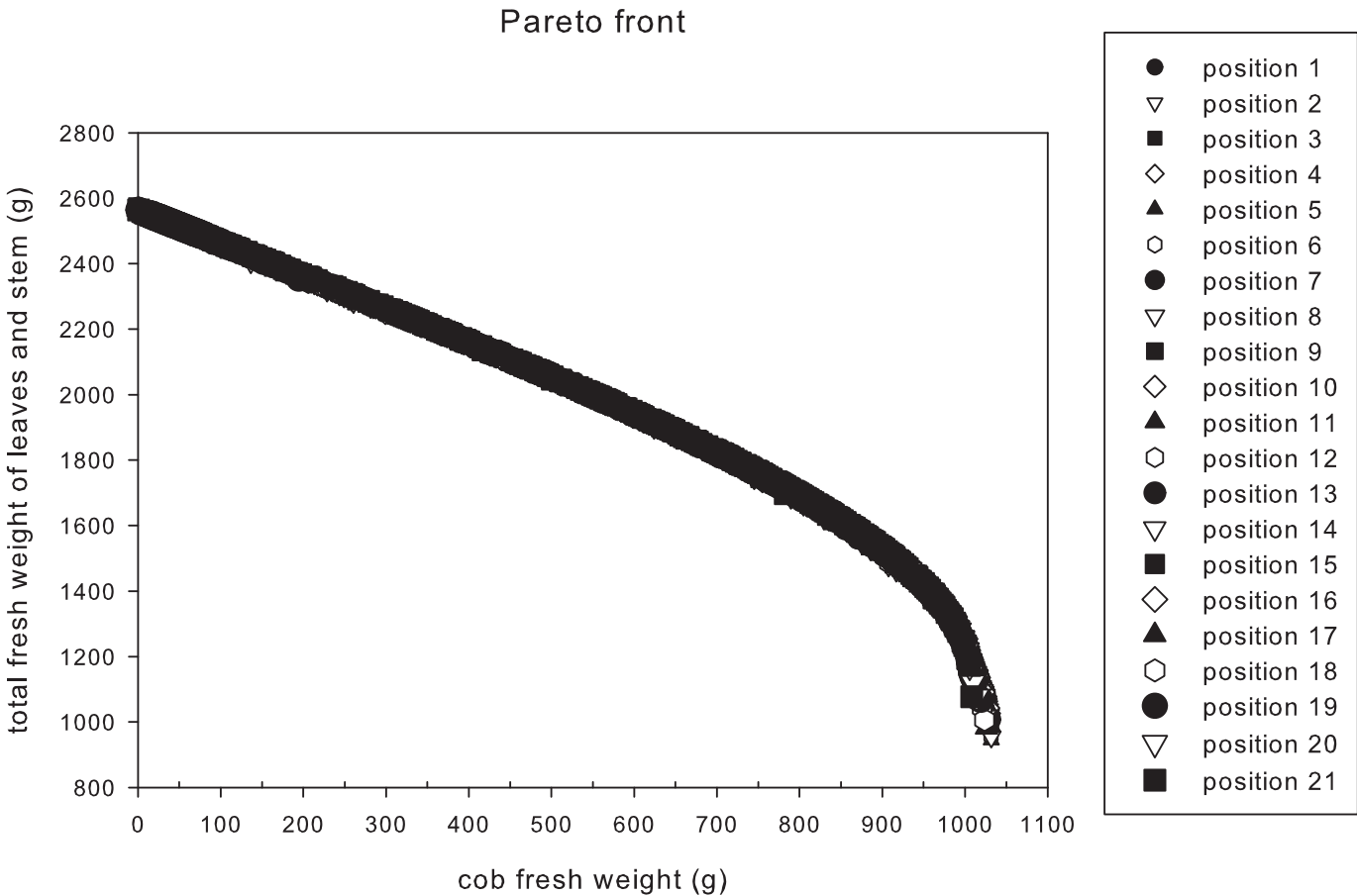


Figure 7

Area covered by all the optimal cob sink variations

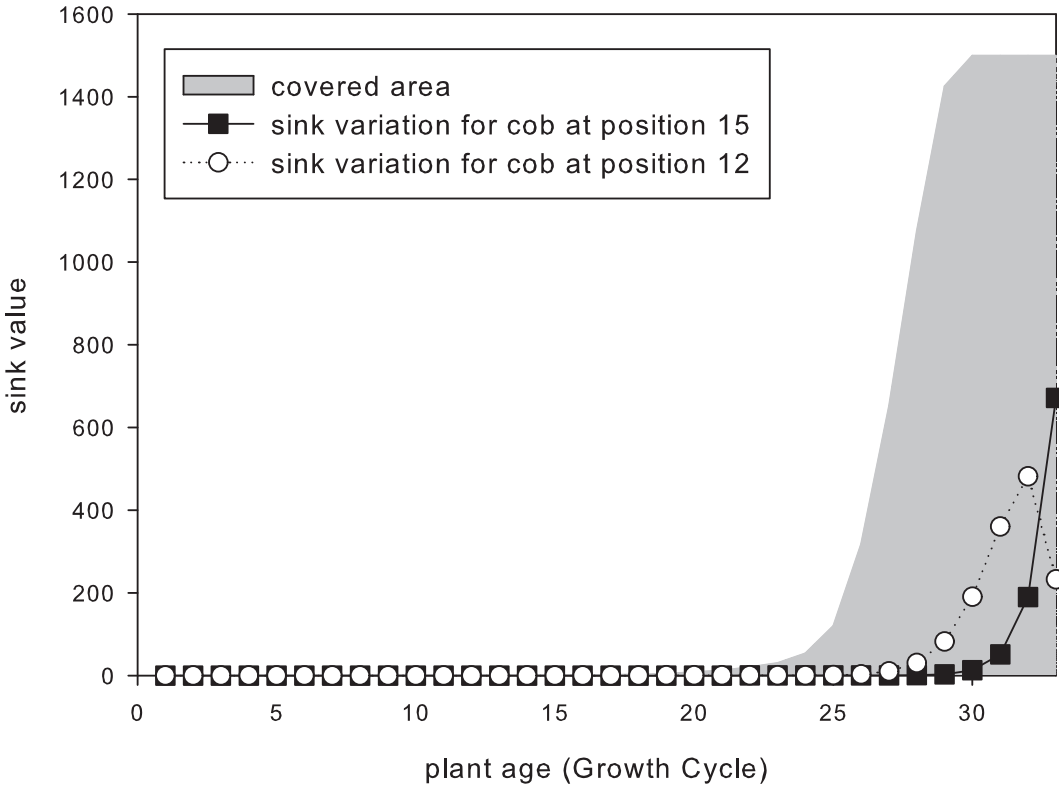


Figure 8

