



Optimization of source–sink dynamics in plant growth for ideotype breeding: A case study on maize

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ABSTRACT

The objective of this work is to illustrate how a mathematical model of plant growth could be possibly used to design ideotypes and thus leads to new breeding strategies based on the guidance from optimization techniques. As a test case, maize (*Zea mays* L., cv. DEA), which is one of the most widely cultivated cereals all over the world, is selected for this study. The experimental data reported in a previous study are used to estimate parameters of a functional–structural plant growth model, namely, “GreenLab”. As the corn cob and its leaves and stem can be benefited from economically, a single objective optimization problem (maximization of cob weight) and a multi-objective optimization problem (maximization of cob weight, maximization of leaf and stem weight) are formulated, respectively. The Particle Swarm Optimization approach is applied to solve these two kinds of optimization problems based on the GreenLab model. The optimized variables are specific parameters of the GreenLab model, which are the cob sink strength and the coefficients of the cob sink variation function. The optimization results revealed that to achieve breeding objectives, the optimal trade-offs of source–sink dynamics should be considered. Moreover, the optimization results of the multi-objective optimization problem revealed that the harvest index may not be the evaluation factor for yield improvement. The work described in this paper showed that such optimization approaches relying on plant growth models may help improve breeding strategies and design ideotypes of high-yield maize, especially in the current agricultural context with the increasing importance of co-products when designing cultivation practices.

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1. Introduction

In plant breeding, the concept of ideotype is first defined in Donald (1968): “a plant model which is expected to yield a greater quantity or quality of useful product when developed as a cultivar”, “plants with model characteristics known to influence photosynthesis, growth, and (in cereals) grain yield”. Since then, the design of ideotype has been a major issue in genetic improvement in order to optimize crop yield. There are two main strategies to investigate ideotype breeding: experimental based and plant model based approaches. The critical drawback of experimental based approach is that the time consumed for experiments is long (10 years needed by Dencic, 1994 and by Lauri and Costes, 2004, and 20 years by Peng et al., 2008) and it consumes resources that are limited (field,

water, labor) due to the cultivation of thousands of plants (Dencic, 1994). Moreover, the performance of the improved plant might prove disappointing in terms of grain yield compared with the original variety when the environmental conditions vary (Peng et al., 2008). Nowadays, it becomes widely accepted that plant growth models may provide efficient tools to study plant growth behavior (Tardieu, 2003; Herndl et al., 2007; Letort et al., 2008a), since they can not only complement field experiments, but also save time and resources. Therefore, researchers dedicated themselves to study ideotype breeding based on plant models (Yin et al., 2003; Cilas et al., 2006). Even though Cilas et al. (2006) investigated ideotype breeding from the architectural point of view, and Yin et al. (2003) from the physiological point of view using a process-based plant growth model, they all agree that there exist critical relationships between plant architectures and physiological processes during plant growth, with other researchers like Rasmusson (1987), Kaitaniemi et al. (2000), Sievänen et al. (2000), Luquet et al. (2006), and Fourcaud et al. (2008). The design of ideotypes should thus take into account both architectural and physiological aspects. In parallel, functional–structural plant growth models were developed (see

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Sievänen et al., 2000 or de Reffye et al., 2008 for reviews), combining the description of organogenesis (plant development), photosynthesis and biomass partitioning. They offer interesting perspectives to improve plant breeding.

For this study, the GreenLab plant growth model (Cournède et al., 2008) is chosen. It can be considered as a process-based model taking into account the dynamics of organogenesis. Its mathematical formalism as a dynamic system has allowed the estimation of model parameters from experimental data for a wide range of species and environmental conditions. The relative stability of parameters among seasons and treatments (Ma et al., 2007, 2008) leads us to consider a possible link of model parameters to the genotype of the species (Letort et al., 2008b), even though assessing such links would claim a considerable amount of work. Moreover, GreenLab's mathematical formulation makes it suitable for solving optimization problems arising in breeding.

Maize (*Zea mays* L., cv. DEA) is chosen for ideotype breeding in the present work, as it is one of the most widely cultivated cereals all over the world. Moreover, it has been studied in depth with the GreenLab model in different environmental conditions (Guo et al., 2006; Ma et al., 2007, 2008) and the model was shown to well describe the source–sink dynamics of maize growth.

Commonly, maize is used in the human diet in both fresh and processed forms; the grain and vegetative parts of maize are fed to livestock, and the components of the grain (e.g. starch) may be refined for direct consumption (Pratt, 2001). Moreover, the fact that the cob, and leaves and stem can be used as biofuel becomes of important economical interest (Baenziger et al., 2006). Therefore, the objective of this work is to optimize maize first with the potential best cob yield, and second with high yields of both cob and the vegetative part consisting of leaves and stem.

Haverkort and Grashoff (2004) and Herndl et al. (2007) have already used plant models to find ideotypes of plants with the optimum product with respect to physiological parameters. The results they found were through trial and error method based on simulations, as well as Habekotté (1997) through a sensitivity analysis approach. In the domain of agriculture, several works studied multi-objective optimization problems (Raju and Kumar, 1999; Angelis and Stamatellos, 2004; Francisco and Ali, 2006; Buddadee et al., 2008). However, these works mainly focused on agricultural systems and logistics. The objectives are land utilization, labor employment, crop production, water management, measurement techniques, for various crops (e.g. maize, wheat, tomato). The factors they considered are all related to cultivation modes (e.g. irrigation planning, water planning). None of them did optimization on the parameters that describe the inner physiological processes of plant growth, the factors related to genetic parameters or new genotype investigations for a specific species. In this study, we take advantage of the GreenLab dynamic system of plant growth to formulate proper optimization problems with respect to plant physiological processes in order to exhibit ideotypes of maize that satisfies the requirement of high-yield capacity in a given environment. Numerical methods are used to solve these optimization problems.

In the first section of this article, we recall the principles of the GreenLab model of maize growth and introduce the DEA cultivar on which our study is based. An experimental data set is used to estimate the model parameters which will serve as the reference when designing the ideotype. As mentioned above, from an economical point of view, there are potential benefits from both cob weight and the total weight of leaves and stem (to feed animals as forage, or to be used as biofuel). Firstly, an optimization problem with single objective maximization of cob weight is formulated and investigated, and then, a multi-objective optimization problem with two conflict objectives: maximization of cob weight and of the total weight of leaves and stem at the same time, is formulated with

a constraint. The constraint is that the tassel weight should be bigger than a threshold. A heuristic optimization algorithm, Particle Swarm Optimization (PSO) (He et al., 2004), is then used to solve both problems. Finally, the optimization results and their potential use as guidance for breeding are discussed.

2. Materials and methods

2.1. Description of the GreenLab model

GreenLab is a functional–structural plant growth model combining the descriptions of plant architecture and physiological processes of plant growth at organ level, in interaction with the environment (light, water, temperature and density). The dynamic mechanisms to generate plant architecture (organogenesis) and to calculate plant biomass production and partitioning to organs are introduced in detail in de Reffye et al. (2008). Here, only the necessary points to understand our approach are recalled.

In the usual cultivation conditions, maize is a single stem crop. The phytomer appearance is controlled by thermal time in the GreenLab model for maize. The model time step, also called growth cycle (GC), is thus equivalent to thermal time requirement for each phytomer appearance. The topology of maize cultivar ND108 as observed in the field is as follows: first six phytomers with short internodes appear; they are followed by 15 phytomers with longer internodes; the last one bears the male flower (tassel). Therefore, the organogenesis terminates at the end of the 21st growth cycle, but the plant is still alive until the 33rd growth cycle. Even though several phytomers may bear female flowers (cobs), Guo et al. (2006) chose to gather all the potential cob weights on the 15th phytomer. This simplification was proved very effective for plant modelling and model calibration (Guo et al., 2006).

The functional processes of plant growth are described by a source–sink model in GreenLab, with a common pool of biomass. GreenLab simulates plant growth from the seed stage, hence the initial plant biomass is from seed and the initial organs are driven by seed. And then, at the following growth cycle n , biomass production Q_n (g) of an individual plant is calculated by Beer–Lambert's law (McMurtrie, 1985) as expressed by Eq. (1). It depends on the total green leaf surface area at the end of the previous growth cycle $n-1$ (S_{n-1} (cm²)), on environmental factors gathered in the function E_n (g/cm²) and on light use efficiency μ (unitless) and light interception coefficient k (unitless):

$$Q_n = E_n \mu S_p \left(1 - \exp \left(-\frac{k}{S_p} S_{n-1} \right) \right), n \geq 1 \quad (1)$$

$$Q_0 = Q_{\text{seed}}$$

where Q_{seed} (g) is seed biomass; S_p (cm²) is the total ground projection area available of the leaf surface for plant modulated by the effects of self-shading and neighbour competition that is related to planting density; hence, S_{n-1}/S_p is leaf area index (LAI) adapted to individual plant.

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

$$D_n = \sum_{o=0}^{\min(n, t_{x,o})} \sum_{j=1} N_{n-j+1}^o p_o(j) \quad (2)$$

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

The biomass increment of an organ o of age j at growth cycle n , denoted by $\Delta q_o(n,j)$ (g), is proportional to its sink value $p_o(j)$ and

the ratio of biomass production to the total demand of plant, as detailed in Eq. (3):

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

The accumulated biomass, denoted by $q_o(n, j)$ (g), for an organ o of age j at growth cycle n is given by

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

As a consequence, the total green leaf surface area at growth cycle n , denoted by S_n (cm²), is

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

where t_a (growth cycle) is the blade functioning duration, and slw (g/cm²) is the specific leaf weight.

The family of Beta functions was chosen to describe the sink variation during the expansion, as expressed by Eq. (6):

$$f_o(j) = \begin{cases} be_o(j)/M_o & (1 \leq j \leq t_{x,o}) \\ 0 & (j > t_{x,o}) \end{cases} \quad (6)$$

with $be_o(j) = (j - 0.5)^{a_o-1} \cdot (t_{x,o} - j + 0.5)^{b_o-1}$
and $M_o = \max(be_o(j), 1 \leq j \leq t_{x,o})$

where a_o (unitless) and b_o (unitless) are the coefficients of the sink variation function be_o ; M_o (unitless) is normalization factor. Diverse sink variations can be obtained by adjusting values of the coefficients: a_o and b_o .

The sink value of an organ of age j , denoted by $p_o(j)$, is $f_o(j)$ multiplied by the sink amplitude (also called sink strength) P_o (unitless) as expressed by Eq. (7):

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

2.2. Field experiment and field measurements on maize

Maize cultivar ND108 (*Z. mays* L., cv. DEA) 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. The experiments had four replications. Samples were taken destructively on 12 dates. One plant was collected per replication and sampling date. Only above-ground organs are considered like in Guo et al. (2006). Fresh weights of blades, sheaths, internodes, cob and tassel; lengths and widths of sheaths; lengths, widths and areas of blades; and lengths and diameters of internodes, were measured and recorded individually at each sampling date. The specific leaf weight is 0.025 g/cm², for all leaves. The detailed information about the environmental conditions, sampling strategy, measured data and expansion duration and longevity of organs is given by Guo et al. (2006).

2.3. Parameter estimation of GreenLab

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

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

The same set of parameters is estimated simultaneously by fitting with several plants of a species at different development stages, which is called multi-fitting. In this paper, the data of fresh weight of all organs measured at three stages (8th growth cycle corresponding to vegetative stage, 18th growth cycle approximately corresponding to flowering stage and 33rd growth cycle corresponding to physiological maturity) are used as target data. A generalized non-linear least-square method adapted from Levenberg–Marquardt algorithm is used to estimate parameters of GreenLab (Zhan et al., 2003).

2.4. Multi-objective optimization

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

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

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

For multi-objective optimization problems, generally, objectives are in conflict with each other. In comparison with single objective optimization problems for which we may have results on the existence and uniqueness of the solution, the situation of multi-objective problems is more complex, since there is no canonical relationship in the solution space. Thus, the optimal solutions for multi-objective optimization problems are defined such that for these solutions, performance on one objective cannot be improved without sacrificing performance on at least another. The solutions satisfying this property form the Pareto front (Mostaghim and Teich, 2003).

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

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

It is also of economical interest to maximize the total weight of leaves and stem, which is the second objective of the multi-objective optimization problem. The equation for calculating the total weight of leaves and stem when plant age is n is given by

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

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

Cob weight and tassel weight are interrelated. Cob weight is controlled by pollen production, while pollen production depends on tassel size of maize. Moreover, Uribealrea et al. (2002) showed that if the tassel size is reduced, the cob size will be limited. Therefore, a constraint on tassel weight that should be beyond a threshold is imposed to the multi-objective optimization problem. The formula

for calculating the tassel weight when plant age is n is as follows:

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

Finally, the formula of the multi-objective optimization for maize is given by

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

where the threshold value is referred to experimental data.

It is acknowledged that cob weight is highly dependent on growth conditions during the early stages of grain filling and the final cob weight reflects the source–sink ratio of the entire grain filling period (Borrás et al., 2002); final cob weight of maize depends on the relationship between cob sink and availability of assimilates resulting from the biomass production of plant to fill this sink (Borrás et al., 2003). In addition, for potential applications in breeding, the parameters we optimize should be linked to plant genetics and therefore should be representative of some physiological processes. Therefore, for this preliminary study, we concentrate on the dynamics of biomass allocation to the cob, and the optimized variables of the problem are cob sink strength P_f and the coefficients of its sink variation function: a_f and b_f .

2.5. Particle Swarm Optimization (PSO)

The optimization problems that we study revealed non-convexity and multimodality as shown in Fig. 1, particularly there is no unique solution for multi-objective problems. Therefore, the iterative, population-based heuristic optimization algorithm PSO was used in our study.

PSO is first proposed by Kennedy and Eberhart (1995), which originally simulates the behavior of bird flocking. 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 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). 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 ; ω^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 specific algorithm that we used for the multi-objective optimization problem 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 problems and to find the Pareto front, the equations for changing the velocity and position of each particle are improved slightly, as given by Eq. (14):

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

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. 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 iteration, the algorithm is changed by replacing the unique global best position with a local guide best position for each particle, denoted by B_{lij} for the j th coordinate of particle i in Eq. (14). 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} .

All the optimal solutions are recorded in an archive with limited size. The Sigma method (Mostaghim and Teich, 2003) is used to determine the local guide best position of each particle. The solution in the archive which has the nearest distance from a given particle is decided to its local guide best position. For more details, we refer to Mostaghim and Teich (2003). The optimization program is developed in C++ by the authors and is run on Windows XP platform.

3. Results

3.1. Multi-fitting results

The estimated values of the hidden parameters of GreenLab by a generalized non-linear least-square method adapted from Levenberg–Marquardt method, which are listed in Table 1, are different from the ones in Guo et al. (2006) and Ma et al. (2007), as the sink variation function (Beta function) in this work is slightly improved as shown in Eq. (6): the sink strength is defined as the maximum sink value (sink amplitude) in this work, while it is defined as the total sink capacity in the previous studies. The

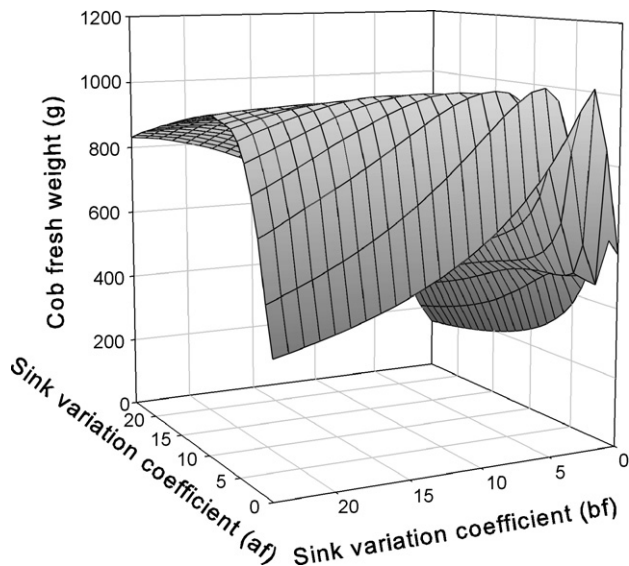


Fig. 1. Simulation results of the cob fresh weight (g) of maize ND108 with respect to the coefficients (a_f , b_f (unitless)) of the cob sink variation function, the other parameter values of GreenLab being the estimated ones as listed in Table 1.

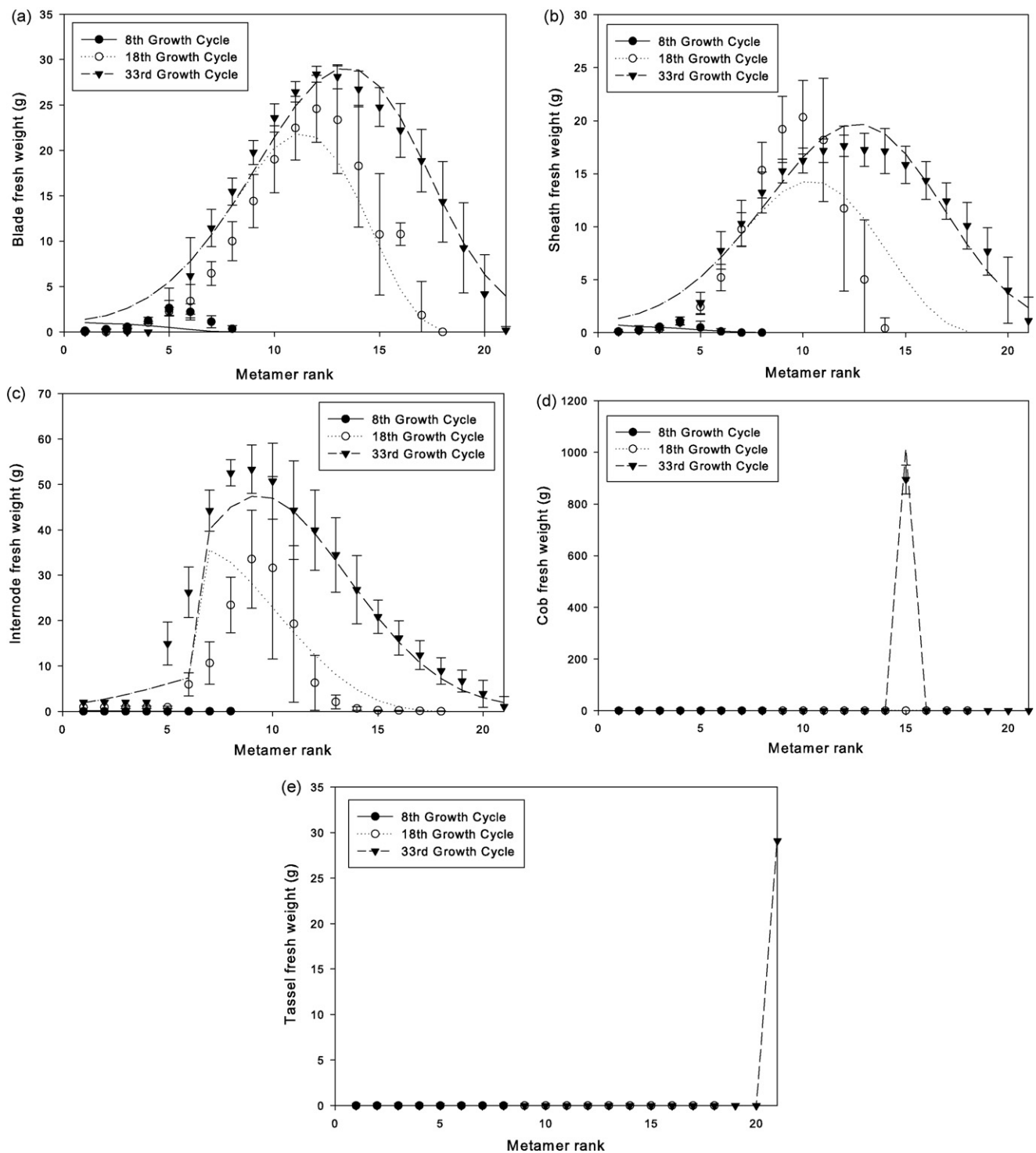


Fig. 2. Simulation of biomass partition to (a) blade, (b) sheath, (c) internode, (d) cob, (e) tassel, with estimated parameter values by generalized non-linear least-square method. “●” represents measured data at the 8th growth cycle corresponding to vegetative stage; “○” measured data at the 18th growth cycle corresponding to flowering stage; “▼” measured data at the 33rd growth cycle corresponding to physiological maturity; “—” simulation result at the 8th growth cycle; “...” simulation result at the 18th growth cycle; “- - -” simulation result at the 33rd growth cycle.

simulation results of organ fresh weight by GreenLab with the estimated parameters are given in Fig. 2, compared with the measured data. The root mean squared error (RMSE) is 10.50 for all data of three stages and the coefficients of determination (R^2) for blade, petiole, internode, cob and tassel at the maturity (33rd growth cycle) are 0.98, 0.95, 0.94, 1 and 1, respectively. The optimization results in the following sections are based on the maize modelled by GreenLab with the estimated parameter values listed in Table 1.

3.2. Single optimization problem of maximization of cob weight

The variation of the parameters on which we optimize is limited to a reasonable range referred to Ma et al. (2007, 2008), as listed in Table 2. The optimal cob sink as shown in Fig. 3 is almost zero at the beginning of cob development, in order to reduce the competition for biomass with source organs and to let leaf surface area increase. And then the sink increases monotonously till the end of

Table 1

Estimated parameter values of GreenLab by multi-fitting of maize ND108 measured at three different development stages simultaneously, using a generalized non-linear least-square method.

Parameters (definition)	Values	Unit
P_a (sink strength of blade)	1.00 (fixed)	–
a_a/b_a (coefficients of beta function for blade)	3.59/5.38	–
P_s (sink strength of sheath)	0.60	–
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 both long and short 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)	1.00/1.00	–
K_e (proportional coefficient of sink strength for short internode)	0.21	–
μ (light use efficiency)	3.43E–3	–
S_p (plant projection area on the ground)	3600	cm ²
k (light interception coefficient)	0.68	–

“–” represents that the parameter is unitless.

Table 2

Definitions and variation ranges of the GreenLab parameters that are optimized in the optimization problems.

Parameter*	Definition	Range
P_f	Sink strength of cob	[0,1500]
a_f	Coefficient of beta function for cob	[0,25]
b_f	Coefficient of beta function for cob	[0,25]

“*” represents that the parameters are unitless.

plant growth. The cob weight with the optimal cob sink variation is 1032 g.

Comparing the estimated and optimal cob sink variations as shown in Fig. 3, we can separate the cob development process into three stages. The first stage is from the 15th growth cycle to the 21st growth cycle. Even though the optimal cob sink is a little larger than the estimated one, it does affect the source organ (leaves) development. The cob competes for biomass with the source organs and the other organs. This competition leads to the decrease of the leaf surface area as shown in Fig. 4. During the second stage from the 22nd

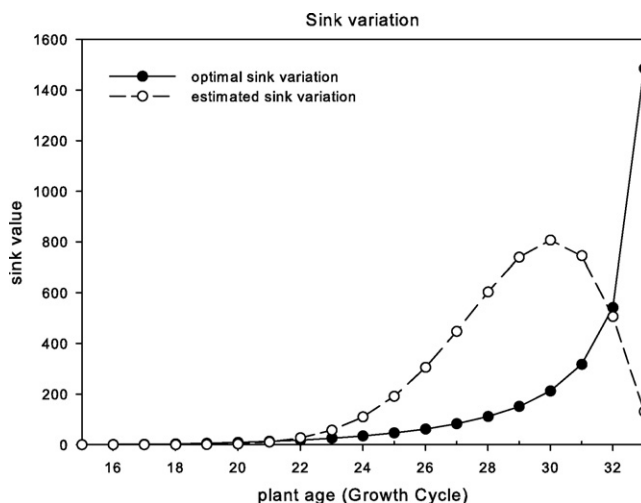


Fig. 3. Comparison of optimal and estimated cob sink variations. The curve marked by “—●—” represents the corresponding optimal cob sink variation; the curve marked by “—○—” represents the estimated cob sink variation.

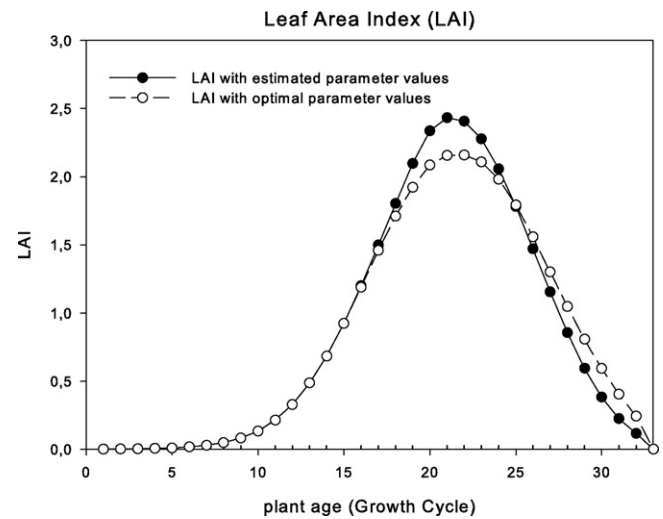


Fig. 4. Simulation result of leaf area index for maize with estimated parameter values marked by “—●—” and with the optimal one marked by “—○—”.

growth cycle to the 31st growth cycle, the optimal cob sink value keeps increasing, but smoothly. On the contrary, for the observed plant, the cob sink increases significantly, biomass allocation to the cob is done to the detriment of leaves (i.e. less biomass is allocated to leaves). Hence, the leaf surface area begins to decrease. During the last stage of plant growth within two growth cycles, the optimal cob sink begins to increase significantly and quickly. Since the other organ sinks are negligible, all the biomass is allocated to the cob as shown in Fig. 5: the ratio of cob weight to total weight of leaves and stem in this period tends to infinity.

The comparison results of the cob sink variation reveal the source–sink dynamics. The increment of the cob weight is the product of the cob sink value and the ratio of the plant biomass production, which depends on the leaf surface area, to the plant demand that is the sum of all the organ sinks, as described in Eq. (3). Even though the cob sink value is smaller than the estimated one, the leaf surface area is higher and the biomass production may thus be bigger. On the contrary, even though bigger cob sink value results in more biomass allocated to the cob instantaneously, it leads to less biomass allocated to other organs, especially leaves and less biomass production at the following cycles. Hence, to

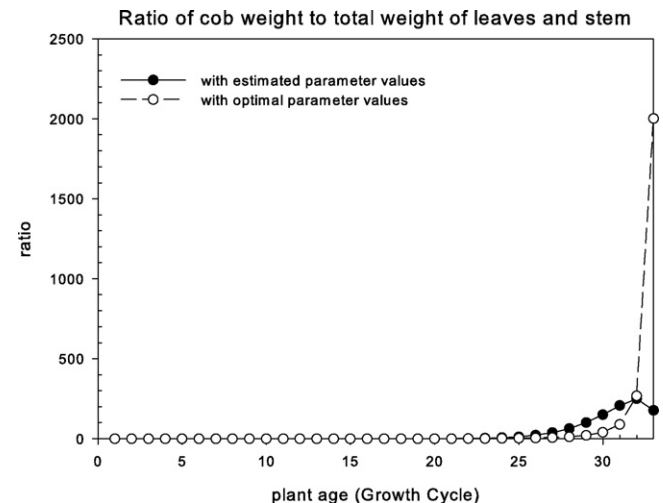


Fig. 5. Comparison of the ratio of cob weight to total weight of leaves and stem during the plant growth. “—●—” represents the result with estimated parameter values and “—○—” represents the result with the optimal parameter values.

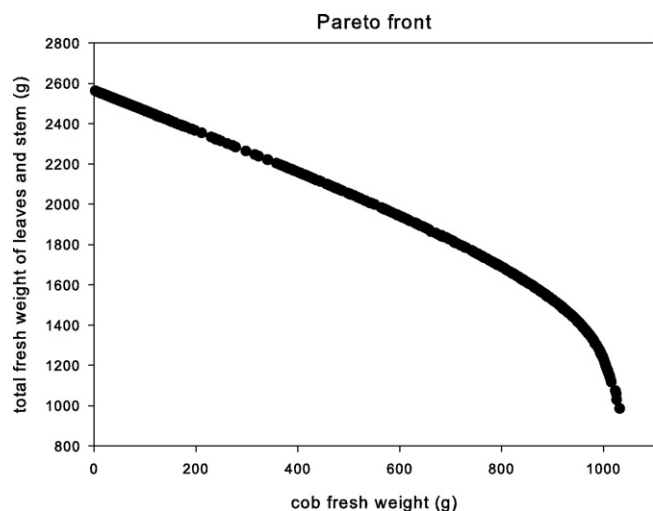


Fig. 6. Pareto front of the multi-objective optimization problem.

obtain maximal cob weight, the optimal trade-offs between sources and sinks should be considered. Compared with the estimated cob weight (1013 g), the optimal cob weight (1032 g) is 2% greater. The maize cultivar ND108 that we study, which results from long-term breeding programs, may already be close to optimum regarding cob yield. Hence, multi-objective optimization considering co-products is more interesting than the single objective optimization of maximization of cob weight for maize cultivar ND108, since it may provide new information.

3.3. Multi-objective optimization problem

The optimal result of the multi-objective optimization problem as described by Eqs. (9)–(12), known as Pareto front, is shown in Fig. 6. Pareto front is given by about 500 optimal solutions of cob sink variation. Hence in Fig. 7, we outlined the area covered by all the optimal solutions of cob sink variation. Particularly, one example of the optimal cob sink variation is given, the corresponding cob weight being 503 g and total weight of leaves and stem being 2050 g.

The Pareto front of our multi-objective optimization problem is characteristic of source–sink dynamics and reveals the necessary

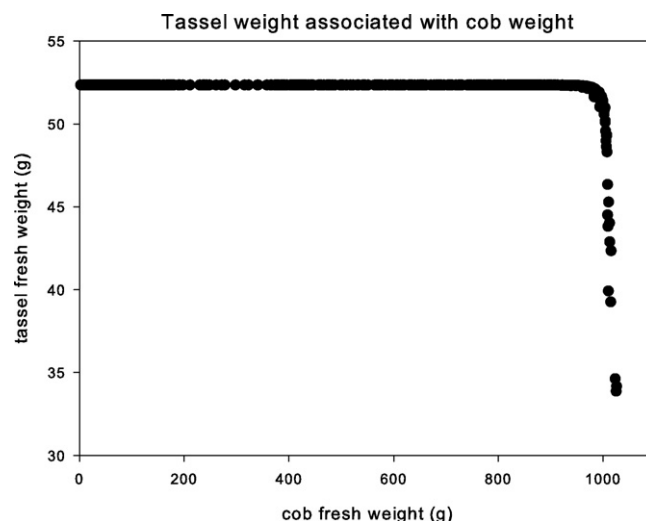


Fig. 8. Tassel weight with respect to cob weight, associated with the Pareto front.

balance between both objectives. Maximization of the total weight of leaves and stem leads to a zero cob sink strength. On the other hand, to maximize the cob weight, the cob sink value cannot be maximal all the way, otherwise there would not be enough leaf surface area, and the reduced biomass production would decrease the final cob weight. For this reason, the left extremity of the Pareto front corresponds to a zero cob weight whereas the right extremity corresponds to a strictly positive weight of stem and leaves. For maize cultivar ND108 (*Z. mays* L., cv. DEA), the tassel appears and begins to develop at the 21st growth cycle, with a very quick expansion (2 growth cycles). From the optimal results shown in Fig. 7, we found that the tassel expansion corresponds to the early stages when the cob sink begins to increase.

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

The cob weight simulated by GreenLab with the estimated parameter values is 1013 g, the corresponding total weight of leaves and stem is 927 g and the tassel weight is 29 g. With the optimal parameter values, the maximal cob weight among the Pareto front in Fig. 6 is 1032 g, the corresponding total weight of leaves and stem is 959 g and the tassel weight is 29 g. Comparing the Harvest Index (HI), which is defined by the ratio of the cob weight to the weight of plant, of the estimated and the optimal plants, HI of the optimal one is surprisingly a little smaller than the estimated one, even though both the cob weight and the total weight of leaves and stem are higher than the estimated one. It revealed the trade-offs between sources and sinks. Post-expansion and fast growing rate as shown in Figs. 3 and 7 will enhance not only the cob weight but also the weight of leaves and stem. This optimal cob development strategy is in agreement with Weiner (1988) and Vega et al. (2000): there is a threshold size for plants to produce flowers and fruits, the plant will grow as much as it can until its biomass reaches a threshold, and then the biomass may be distributed to fruits and flowers.

4. Discussion

In this paper, we have illustrated how the optimization of the parameters of plant growth models could be used as the first step

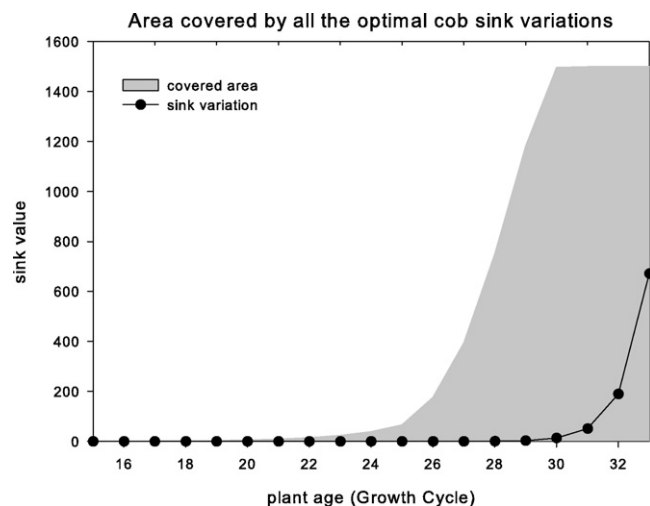


Fig. 7. Area covered by all the optimal cob sink variations associated with the Pareto front. One example of the optimal cob sink variations is given. “—●—” represents the optimal cob sink variation for maize where the cob weight is 503 g and the total weight of leaves and stem is 2050 g.

to design ideotypes for genetic selection. The GreenLab model was chosen for the simplicity of its parameterization. Moreover, it describes plant growth, both from ecophysiological and architectural points of view, at the individual organ scale. Breeders can get information about physiological characteristics in determining yield.

In plant breeding, the criteria for segregating or introducing accessions are mostly based on intuition or convention, but also increasingly on mechanistic knowledge of how traits contribute to the performance of interest. There is a recent agreement among plant breeders and physiologists that plant growth models based on ecophysiological knowledge can be applied to improve ideotype breeding efficiency (Yin et al., 2003; Hammer et al., 2006). They can help to provide quantitative answers to “what if . . .” questions for alternative plant types (Dingkuhn et al., 1993). Dingkuhn et al. (1993) and Yin et al. (2003) also pointed out that the model properties required for ideotype design are (1) to quantify feedback between physiological processes and environmental variables and (2) to have the ability of yield prediction without restricting to the environment in which the model parameters are derived. Ma et al. (2007, 2008) studied the stability of GreenLab parameters to different environmental conditions, e.g. seasonal variation and planting density. Most parameters revealed stable. Dong et al. (2008) also studied the stability of GreenLab parameters for tomato in different planting densities. The parameters characterising organ sink strengths and governing light interception were shown to be environment-dependant. These two studies lead us to consider a possible genotypic determination of GreenLab parameters and yet enhance the necessity to build up more sophisticated model versions, in order to fully unravel the genetic and environmental effects. It implies a better modelling of the effects of the environmental stresses. Preliminary results were introduced in Wu et al. (2005) and Le Chevalier et al. (2007) regarding water. Taking into account the current time step in GreenLab, which is equal to 2 or 3 days corresponding to thermal time interval for successive phytomer appearance for maize cultivar ND108 in this study, it may be long for the simulation of environmental stresses. However, the time step in GreenLab can be changed to calendar time, e.g. 1 day or 1 h (Li et al., to appear). In this way, the environmental stresses can be well simulated.

In quantitative genetics, many methods have been developed to identify particular loci in plant chromosomes that contribute to phenotypic traits (de Vienne, 1998), by establishing statistical correlations between quantitative traits that can be measured on plant (e.g. plant height, yield) and the values of particular genes, known as quantitative trait loci (QTL) analysis. Many researchers have raised the potential benefits and possibilities of coupling these genetic models to plant models, for genetic improvement (Tardieu, 2003; Yin et al., 2004; Hammer et al., 2006). A simulation study of linking the GreenLab model to a genetic model is presented by Letort et al. (2008b). The theoretical study illustrated how QTL analysis should give better results when performed on model parameters than on phenotypic traits, the latter being the results of complex interacting phenomenon difficult to statically assess with QTL analysis.

The parameters that we optimized are oriented to those related to the cob sink variation function, whereas the others are fixed to be the estimated values. However, there might be some correlation between parameters that we were not able to estimate. Such correlations could only be assessed if the model parameters were available on a large number of genotypes. Therefore, in this context, even if the link of GreenLab model parameters to genetics has not been proved yet and the information of correlations between all the parameters are missing, at least optimal parameters should provide some useful information for ideotype design, by unravelling the source–sink complex interactions.

In our test case, the ideotype of maize can be deduced from the optimal results. It provides a reference to improve breeding strategies. From a physiological point of view, the cob begins to absorb biomass from about the 20th growth cycle when the leaf area saturates. And then, it should absorb biomass smoothly or significantly, depending on the breeding objective. If the objective is to have a maximal cob weight, the maize should have a bigger reproductive capacity, and the cob should grow with post-expansion (i.e. a long delay for expansion) and fast growth rate (i.e. expand within a short period). From an architectural point of view, the leaf size is reduced during the last vegetative and reproductive stages of growth. The harvest index is above 50%. It is coincident with the ideotype of maize proposed by Mock and Pearce (1975) by analysing the research results of other people with an experimental based approach. The Pareto front of the multi-objective optimization problem presents all the different optimal strategies, and the decision-maker could choose his optimal strategy according to market prices or the application purposes for example.

Particle Swarm Optimization (PSO), which is a population-based heuristic optimization algorithm, is used to solve the single and multi-objective optimization problems. As it does not require the differentiation of the objective functions, and it returns several solutions at the same time, we can benefit from it to solve non-convex, single objective or multi-objective optimization problems, with potentially non-unique solutions. Theoretically speaking, it obtains global optimal solutions of optimization problems. Compared to other population-based heuristic optimization algorithms, such as Genetic Algorithm, the PSO has a high convergence rate for some problems and a better accuracy (Kennedy and Eberhart, 2001). Moreover, it has few parameters to adjust and is easy to implement thanks to its simple single operator, contrary to Genetic Algorithm that has evolutionary operators such as crossover and mutation. It is computationally inexpensive in terms of both memory and speed. Even though the optimal solutions found by the PSO cannot be proved to be global, it is generally good enough to practically guide genetic selection.

The maize that we optimized is assumed to have only one cob like the experimental data used for parameter estimation. However, the methodology that we used in this work is not restricted by the number of cobs on the stem. For the objective of the optimization problem, which is the maximization of cob weight, the crucial factor is not the number of cobs, but the optimal trade-offs between sources and sinks. However, in order to have more realistic optimal values, more constraints should be concerned. Since the cob growth requires pollen from the tassel and since there exists a strong interaction between cob and tassel (Borrás et al., 2002; Uribealarea et al., 2002), we integrate the tassel weight into the multi-objective optimization problem as a constraint. A threshold is set for tassel weight (not less than 10 g referred from experimental data). However, for all optimal solutions this constraint is not active (tassel weights strictly above 10 g). One reason is that so far we do not know the relationship between cob and tassel quantitatively. Hence, it is difficult to set the threshold value. Another reason is that tassel sink variation is fixed and it does not change according to the cob sink variation, in this work. The understanding of the interaction between cob and tassel should be improved in our future works. Finally, in cobs, only kernels give the food for human beings or for livestock. The number of kernels is a critical factor that affects the final kernel weight (Borrás and Otegui, 2001). Therefore, taking into account the number of kernels per cob could be an interesting complement to this study. So far, we do not have the information about the proportion of the kernel weight to the cob weight, which raises the difficulty to estimate the corresponding model parameters. Experiments are conducted in 2009 for this purpose.

5. Conclusion

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

In this study, the optimization problems investigate the optimal source–sink dynamics and results provide a reference for decision-makers to improve the breeding strategies or to design ideotypes of plants, especially in the current context of biofuel development, increase in agricultural products' prices and necessity to consider co-products when designing cultivation practices. Finally, the crucial and difficult issue that remains to be solved for a more efficient use of this methodology is to establish quantitative relationships between genes and model parameters.

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Appendix A.

Symbol list

Plant variables (symbols in the parenthesis after the variable definition represent the variable units, while “–” represents that the variables are unitless.)

Q	biomass production of an individual plant (g)
Q_{seed}	seed biomass (g)
D	total demand of plant for biomass (–)
E	environmental function (g/m ²)
S	total green leaf surface area (cm ²)
μ	light use efficiency (–)
k	light interception factor (–)
Sp	plant projection area on the ground (cm ²)
N_n^o	number of organ o born at growth cycle n (–)
$t_{x,o}$	expansion duration of organ o (growth cycle)
t_a	blade functioning duration (growth cycle)
$p_o(j)$	sink value of organ o of age j (–)
P_o	sink amplitude (or sink strength) of organ o (–)
f	sink variation function (–)
b_e	beta function (–)
M	normalization factor (–)
a_o	coefficient of beta function for organ o (–)
b_o	coefficient of beta function for organ o (–)
$\Delta q_o(n,j)$	biomass increment of organ o of age j , when plant age is n (g)
$q_o(n,j)$	accumulated biomass of organ o of age j , when plant age is n (g)
slw	specific leaf weight (g/cm ²)
n	plant age (growth cycle)
j	organ age (growth cycle)

Optimization problem variables

J	objective function
g	inequality constraint function
h	equality constraint function
x	variable of optimization problem

Particle Swarm Optimization algorithm variables

v	velocity
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w	inertia weight
c	acceleration coefficient
r	uniformly distributed random value between 0 and 1
B	particle best position
Bl	particle local best position

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