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Simulation of environmental and genotypic variations of final leaf number and anthesis date for wheat

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ABSTRACT

The rate of organ emergence and the duration of developmental phases are key components of plant fitness to its environment. Here, we describe a hybrid genetic algorithm for the estimation of the parameters of complex non-linear simulation models that we used to estimate the varietal parameters of a well-evaluated ecophysiological model (Sirius) of wheat phenology. The aim of this study was to analyze the correlations between the varietal parameters of Sirius and to determine the minimum number of parameters that need to be estimated in order to accurately simulate the effect of the genotype and environment on wheat anthesis date. A panel of 16 bread wheat cultivars was grown under controlled conditions with different vernalization and daylength treatments and in a field nursery with different sowing dates in order to characterize their vernalization and photoperiodic requirements and earliness *per se*. These cultivars were also grown in the field in two consecutive growing seasons in France and in the UK along a 800 km latitude transect, where the dynamics of leaf appearance and anthesis date were determined. Variation in both final leaf number and anthesis date in response to the environment and the genotype was predicted with a mean error of 0.55 leaves and 3.94 d, respectively, after estimation of only three of the seven varietal parameters of Sirius: the phyllochron, the response of vernalization rate to temperature, and the daylength response of leaf production. Among them, the phyllochron was reasonably well estimated and showed a positive association with earliness *per se* (Spearman's coefficient of rank correlation = 0.59). This study showed that the number of varietal parameters in Sirius was overestimated and that considering only three varietal parameters reduced the correlations between the parameters and the root mean square error of prediction for final leaf number and anthesis date. We conclude that a phenomenogical model of wheat development can be used to estimate key phenological parameters that are difficult to determine in the field; offering the possibility to conduct large-scale quantitative genetic studies to understand better the genetic control of flowering time in cereals.

1. Introduction

Plant phenology, the timing and duration of organ formation, drives plant resource acquisition and is a key component of plant fitness. Numerous studies have shown that wheat (*Triticum aestivum* L.) phenology, in particular anthesis date, is the main determinant of genetic adaptation to the environment (e.g. Iwaki et al., 2001; Law and Worland, 1997; Goldringer et al., 2006) and many genetic studies have reported co-location between genomic regions determining grain yield and major flowering time loci (e.g. Crossa et al., 2007; Hanocq et al., 2007; Zhang et al., 2010). In temperate environments, the optimal flowering time for wheat is governed by the risk of late frost in the spring and by late water deficit and high temperature during the grain filling period. Flowering time is thus a major target of all wheat breeding programs (Snape et al., 2001). Accurate prediction of phenology

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Table 1
Name, symbol, definition, nominal, minimal, and maximal value and unit of the non-varietal and varietal parameters of Sirius phenology sub-model.

Name	Symbol	Definition	Value			Unit
			Nominal	Min	Max	
Non-varietal parameters						
maxDL	DL_{sat}	Saturating photoperiod above which final leaf number is not influenced by daylength	15	–	–	h
MaxLeafSoil	L_{max}^{soil}	Haun stage up to which thermal time is calculated based on soil temperature (0–2 cm deep)	4	–	–	Leaf
Ldecr	L_{decr}	Haun stage up to which Phyll is decreased by $Phyll_{decr}$	2	–	–	Leaf
Lincr	L_{incr}	Haun stage above which Phyll is increased by $Phyll_{incr}$	8	–	–	Leaf
Pdecr	$Phyll_{decr}$	Factor decreasing the phyllochron for leaf number less than L_{decr}	0.75	–	–	Dimensionless
Pincr	$Phyll_{incr}$	Factor increasing the phyllochron for leaf number higher than or equal to L_{incr}	1.25	–	–	Dimensionless
Rp	R_P	Rate of decrease of the P_{SD} for winter sowing	0.003	–	–	°C d d^{-1}
PFLLAnth	t_{flag}^{anth}	Phyllochronic duration of the period between flag leaf ligule appearance and anthesis	1.39	–	–	Phyllochron
SDWS	$SD_{W/S}$	Sowing date for which P_{SD} is minimum	90	-	-	Day of the year
SDSA	$SD_{S/A}$	Sowing date for which P_{SD} is maximum	200	-	-	Day of the year
IntTvern	T_{int}^{ver}	Intermediate temperature for vernalization to occur	8	–	–	°C
MaxTvern	T_{max}^{ver}	Maximum temperature for vernalization to occur	17	–	–	°C
MinTvern	T_{min}^{ver}	Minimum temperature for vernalization to occur	0	–	–	°C
Varietal parameters						
D_{se}	D_{se}	Thermal time from sowing to emergence	175	100	250	°C d
MaxL	L_{max}^{abs}	Absolute maximum leaf number	24	13	28	Leaf
MinL	L_{min}^{abs}	Absolute minimum possible leaf number	5.5	4	11	Leaf
Phyll	Phyll	Phyllochron	100	70	150	°C d
SLDL	SLDL	Daylength response of leaf production	0.15	0	3	Leaf h^{-1} (daylength)
VAI	VAI	Response of vernalization rate to temperature	0.001	0	0.01	d^{-1} °C^{-1}
VBEE	VBEE	Vernalization rate at temperature equal to T_{min}^{ver}	0.01	0	2	d^{-1}

is also essential when using a crop simulation model to assess the sustainability of crop production in different environments or the impacts of global climatic changes on wheat productivity and quality (Porter and Semenov, 2005).

Flowering time in wheat can be described as a function of (1) the number of leaves produced by the main-stem; (2) the rate of leaf appearance (i.e. the inverse of phyllochron); (3) the thermal time between flag leaf appearance and flowering; and is under the control of temperature and photoperiod (Hay and Kirby, 1991; McMaster, 2005). Most of the environmental and genetic variation in thermal time from seedling emergence to anthesis results from variation in the number of leaves produced by the main-stem, hence phyllochron, between emergence and flag leaf ligule appearance (Kirby et al., 1985a,b). In contrast with most wheat simulation models in which phenology is described by a series of major events on the shoot apex with fixed durations in thermal time (Weir et al., 1984; Ritchie, 1991), in the Sirius model the processes described above are modeled explicitly (Jamieson et al., 1998a,b). Although these two approaches differ substantially because the number of main-stem leaf at the terminal spikelet stage is strongly related to final leaf number they give similar results (Jamieson et al., 2007), but the approach used in Sirius differentiates the effects of temperature and photoperiod on main-stem development (i.e. the rate of organ appearance) and on the state of the shoot apex (Brooking et al., 1995; Brooking, 1996). A similar approach was recently used to simulate the effect of the environment and of major flowering genes in the model species *Arabidopsis thaliana* (Wilczek et al., 2009).

In Sirius seven varietal parameters need to be estimated for each genotype (Table 1). A procedure has been proposed to estimate some of these parameters for spring wheat cultivars using field observations (Jamieson and Munro, 1999, 2000), but it requires at least two field sowing date treatments, in each of which should be determined (1) the exact Haun stage (Haun, 1973) when 6–7 leaves have been produced; (2) the dates of emergence of the flag leaf ligule; and (3) the date of anthesis. Therefore, the estimation of varietal parameters for new cultivars is usually done ad hoc by fine-tuning these varietal parameters until simulated and observed anthesis date and final leaf number (when available) match. No systematic study has been undertaken to determine the correlation between these varietal parameters and if varietal differences in phenology could be predicted using a reduced number of parameters. This situation with regard to calibration of varietal phenological parameters significantly constrains the use of this model as a research tool and its present application to solve practical problems.

A common approach used for the calibration of model parameters is to define an ad hoc criterion of goodness-of-fit and then provide software to search for the parameter values that minimize the criterion (Mercau et al., 2007; Bhatia et al., 2008). There are several available computer algorithms for model parameter estimation, such as gradient-based methods of Levenberg–Marquardt (Dennis and Schnabel, 1983), down-hill simplex methods (Nelder and Mead, 1965), simulated annealing methods (Ingber, 1993), and genetic algorithms (Holland, 1992). Genetic algorithms have been developed and used to solve complex optimization problems (Park and Froment, 1998; Marseguerra et al., 2003; Katare et al., 2004; Fazal et al., 2005; Dai et al., 2009). They mimic the processes of natural evolution and selection (Ooka and Komamura, 2009). Compared with other optimization methods, genetic algorithms are more appropriate for models with high levels of complexity and discontinuity, because no gradient information is required and only evaluation of the objective function and the constraints are necessary to evaluate the fitness function (Barth, 1992). Moreover, they usually show very good robustness and global convergence properties (Barth, 1992; Hu et al., 2007). As a derivative-free technique genetic algorithms are versatile and can deal with problems with complex objective functions for which a derivative is difficult or impossible to obtain.

In this study, we developed a hybrid genetic algorithm that we implemented in the latest version of the Sirius wheat simulation model (*SiriusQuality*2; Martre et al., 2006, 2008). This algorithm was used to estimate the varietal phenological parameters of 16 modern wheat cultivars grown in eight site-years. The main objectives were (1) to quantify the correlation between these parameters; (2) to determine the minimum set of varietal parameters needed to predict genetic and environmental variations of anthesis date; and (3) to assess the associations between these estimated parameters, the main phenology components (photoperiod response, vernalization requirement, and earliness *per se*) and measured parameters.

2. Materials and methods

2.1. Phenology model

Responding to environmental factors the apical meristem of the wheat shoot switches from a vegetative phase where it produces leaf primordia to a reproductive phase where it produces floral primordia. The successive appearance of leaves on the main-stem and tillers is the expression of the vegetative development, while anthesis is a particular stage in the reproductive development of wheat plants. Vegetative and reproductive development is coordinated and overlap in time (Kirby, 1990; Hay and Kirby, 1991), so that much of the reproductive development occurs early in unison with vegetative development. This means that, as far as timing of events is concerned, vegetative and reproductive processes are not independent. Within this framework, in the phenology model proposed by Jamieson et al. (1998a), the variations associated with vernalization requirement and daylength sensitivity are described in terms of primordium initiation, leaf production, and final main-stem leaf number. The duration of three developmental phases are simulated. First, the pre-emergence phase (sowing to emergence) is simulated as a fixed duration in thermal time which may differ between cultivars (D_{se}; parameter definitions and values are given in Table 1; Weir et al., 1984). Second, the leaf production phase from crop emergence to flag leaf appearance integrates the effects of vernalization and photoperiod. Third, the duration of the flag leaf ligule appearance-anthesis phase is proportional to the phyllochron ($t_{\mathrm{flag}}^{\mathrm{anth}}$; Brooking et al., 1995). The equations describing the leaf production phase implemented in *Siriusquality*2 (Martre et al., 2006, 2008) are described below.

The leaf production phase is modeled based on two independently controlled processes, leaf initiation (primordia formation) and emergence (leaf tip appearance) rates and organ identity defining the fate of the apex primordia whether vegetative or floral. The interaction between these processes leads to the determination of the final number of leaves ($\mathrm{LN_f}$) that will be produced on the main-stem. Thermal time since emergence (T_t) is calculated with a base temperature of 0 °C. Initially the controlling temperature (apex temperature) is assumed to be that of the near soil surface (0–2 cm), and then that of the canopy after Haun stage 4 ($L_{\max}^{\mathrm{soil}}$). Sirius calculates near soil surface temperature and canopy temperature based on the surface energy balance as described by Jamieson et al. (1995).

Leaf production follows a segmented linear model in thermal time (Boone et al., 1990; Jamieson et al., 1995; Slafer and Rawson, 1997; González et al., 2002). The first two leaves appear more rapidly than the next six, and then leaf appearance slows again for the subsequent leaves independently of the total number of leaves produced:

$$\mathrm{LN} = \begin{cases} \mathrm{Phyll_{decr}} \times \mathrm{Phyll_{SD}} \times T_t, & \mathrm{LN} < \mathrm{L_{decr}} \\ \mathrm{Phyll_{SD}} \times T_t, & L_{\mathrm{decr}} \leq \mathrm{LN} < L_{\mathrm{incr}} \\ \mathrm{Phyll_{incr}} \times \mathrm{Phyll_{SD}} \times T_t, & \mathrm{LN} \geq L_{\mathrm{incr}} \end{cases} \tag{1}$$

where LN is the actual number of visible leaves on the main-stem (equivalent to the Haun stage); T_t is the thermal time accumulated by the apex since emergence; $\mathrm{Phyll_{SD}}$ is the phyllochron from Haun stages 2 to 8 modified for the sowing date; $\mathrm{Phyll_{decr}}$ is a factor decreasing the phyllochron for leaf number less than L_{decr}; $\mathrm{Phyll_{decr}}$ is a factor increasing the phyllochron for leaf number higher than or equal to L_{incr}; L_{decr} is the Haun stage up to which Phyll is decreased by $\mathrm{Phyll_{decr}}$; and L_{incr} is the Haun stage above which Phyll is increased by $\mathrm{Phyll_{incr}}$. Many studies have shown that phyllochron depends on the sowing date, several authors have discussed putative physiological causes of theses variations (Slafer and Rawson, 1997; McMaster et al., 2003); while others have shown that most of the observed variations in phyllochron are due to apex-air temperature differences (Vinocur and Ritchie, 2001; Jamieson et al., 2008). In Sirius, as a surrogate for the apex-air temperature correction, for a winter sowing (day of the year 1 to 90 for the Northern hemisphere), the phyllochron decreases linearly with the sowing date and is minimum until mid July for the Northern hemisphere (day of the year 200):

$$\mathrm{Phyll_{SD}} = \begin{cases} \mathrm{Phyll} \times (1 - R_{\mathrm{P}} \times \min(\mathrm{SD}, \mathrm{SD_{W/S}})), & 1 \leq \mathrm{SD} < \mathrm{SD_{S/A}} \\ \mathrm{Phyll}, & \mathrm{SD} \geq \mathrm{SD_{S/A}} \end{cases} \tag{2}$$

where SD is the sowing date in day of the year; Phyll is a varietal parameter defining the phyllochron for autumn sowing; R_{P} is the rate of decrease of $\mathrm{Phyll_{SD}}$ for winter sowing; $\mathrm{SD_{W/S}}$ and $\mathrm{SD_{S/A}}$ are the sowing dates for which P_{SD} is minimum and maximum, respectively.

At any time during vegetative development apex primordia number (PN) is calculated through a simple metric relationship with leaf number (Kirby, 1990) under the assumption that the apex contains four primordia at emergence and that they accumulate at twice the rate of leaf emergence (Brooking et al., 1995; Jamieson et al., 1998a):

$$\mathrm{PN} = 2 \times \mathrm{LN} + 4 \tag{3}$$

Concomitant processes governing apical progress toward a reproductive state and defining $\mathrm{LN_f}$ (i.e. vernalization requirements and photoperiodic responses) are modeled sequentially. Vernalization commences once the seed has imbibed water. The daily vernalization rate (V_{rate}) increases at a constant rate (VAI) with daily mean soil or canopy temperature from its value (VBEE) at the minimum vernalizing temperature ($T_{\min}^{\mathrm{ver}}$) to a maximum for an intermediate temperature ($T_{\mathrm{int}}^{\mathrm{ver}}$). Above this temperature V_{rate} reduces to zero at the maximum vernalizing temperature ($T_{\max}^{\mathrm{ver}}$):

$$V_{\mathrm{rate}} = \times \begin{cases} \mathrm{VAI} \times T_t + \mathrm{VBEE}, & T_{\min}^{\mathrm{ver}} \leq T_t \leq T_{\mathrm{int}}^{\mathrm{ver}} \\ (\mathrm{VAI} \times T_{\mathrm{int}}^{\mathrm{ver}} + \mathrm{VBEE}) \times \dfrac{(T_{\max}^{\mathrm{ver}} - T_t)}{(T_{\max}^{\mathrm{ver}} - T_{\mathrm{int}}^{\mathrm{ver}})}, & T_{\mathrm{int}}^{\mathrm{ver}} < T_t \leq T_{\max}^{\mathrm{ver}} \\ 0, & T_{\min}^{\mathrm{ver}} > T_t \;\; \text{or} \;\; T_t > T_{\max}^{\mathrm{ver}} \end{cases} \tag{4}$$

where VAI and VBEE are two varietal parameters (Table 1). The progress toward full vernalization (V_{prog}) is simulated as a time integral:

$$V_{\mathrm{prog}} = \sum_{\mathrm{day}=1}^{n} V_{\mathrm{rate}}, \quad \text{with} \quad V_{\mathrm{prog}} \in [0, 1] \tag{5}$$

Two varietal parameters define the minimum ($L_{\min}^{\mathrm{abs}}$) and maximum ($L_{\max}^{\mathrm{abs}}$) number of leaves that can emerge on the main-stem. The model assumes that plants start their lives with a high potential leaf number ($\mathrm{LN_{pot}}$ set to an initial value of $L_{\max}^{\mathrm{abs}}$) which decreases with vernalization progress:

$$\mathrm{LN_{pot}} = L_{\max}^{\mathrm{abs}} - (L_{\max}^{\mathrm{abs}} - L_{\min}^{\mathrm{abs}}) \times V_{\mathrm{prog}} \tag{6}$$

Vernalization is complete when one of three conditions is met. Either V_{prog} has reached a value of 1, $\mathrm{LN_{pot}}$ has reached a value that equals $L_{\min}^{\mathrm{abs}}$, or $\mathrm{LN_{pot}}$ has reduced to PN. These primordia are all assumed to produce leaves.

The crop responds to daylength (DL) only once vernalization is complete (or at emergence for a spring cultivar for which the vernalization routine is skipped). It is assumed that DL sensitivity leads to an increase in the number of leaf primordia resulting from the vernalization routine. DL is calculated following the treatment of Sellers (1965) with a correction for atmospheric refraction equivalent to 50′. If DL of the day when vernalization is completed exceeds a given value (DL_{sat}), then LN_f is set to the value calculated at the end of the vernalization routine (Brooking et al., 1995). For DL shorter than DL_{sat}, Brooking et al. (1995) have shown that LN_f is determined by DL at the stage of two leaves after the flag leaf primordium has formed. This creates the need for an iterative calculation of an approximate final leaf number (LN_{app}) that stops when the required leaf stage is reached:

$$LN_{app} = \min(LN_{pot}, LN_{pot} + SLDL \times (DL_{sat} - DL)) \tag{7}$$

where SLDL is a varietal parameter defining the daylength response as a linear function of DL. The attainment of the stage "two leaves after flag leaf primordium" is reached when half of leaves have emerged (Brooking et al., 1995):

$$\text{if}\quad 0.5 \times LN_{app} \le LN, \quad \text{then}\quad LN_f = LN_{app} \tag{8}$$

2.2. *Hybrid genetic algorithm for parameter calibration*

The hybrid genetic algorithm developed in this study comprises global and local search behaviors. Crossover, mutation, and selection operators perform a global search in the entire parameter space, while a local hill climbing operator explores the vicinity of convergence generated by the iterations of the genetic algorithm. The algorithm has been designed and parameterized to balance these two search behaviors (Fig. 1).

The algorithm starts with an initial population of N_I vectors generated by Monte-Carlo uniform random sampling of each input parameter within its predefined initial range (Table 1). The model is then run using the N_I vectors and their fitness value is calculated. The N_S fittest vectors (see below) are then selected and randomly divided into $N_S/2$ pairs of vectors (parents). Randomly chosen pairs are then split at a random point and their end parts are swapped (one-cut-point crossover). The two fittest vectors from each pair of vectors and their two offsprings are then selected. The parameters of N_M randomly sampled vectors are mutated. For each sampled vector the number of parameters and which parameters to mutate are also randomly determined. The value of each selected parameter is replaced with a random value generated assuming a uniform distribution. In order to narrow the search space and increase the rate of convergence of the algorithm, the range of the parameter values is reduced by 1% of its initial length at each generation (self-adaptive strategy). The absolute range of each parameter is then calculated so that the centre of the new range equals the current parameter value. The main operator of space exploration has the ability to escape from local optimum. If after 10 generations the maximum fitness value does not increase, then the searching space is expanded by 2 times G_S. Then an extra round of crossover is also done after resampling $N_S/2$ new pairs of vectors.

If the fitness value of the fittest vector is greater than a fixed threshold value (T_{FV}), then a local optimal solution is sought before injecting it into the next generation (Fig. 1; Gen and Cheng, 2000). N_L new vectors are randomly generated in the vicinity of the fittest one. Then the fitness value of the N_L new vectors is calculated and only the fittest vector is added to the next generation. After the global and local search, the fitness of the newly generated vectors might all be deteriorated compared with those of the previous generation. Thus the N_{S2} fittest vectors are also added to the next generation, which guarantee that the fitness value of the fittest vector does not decrease with the generations. The sequence of successive population generation is stopped when a pre-assigned number of generations is reached.

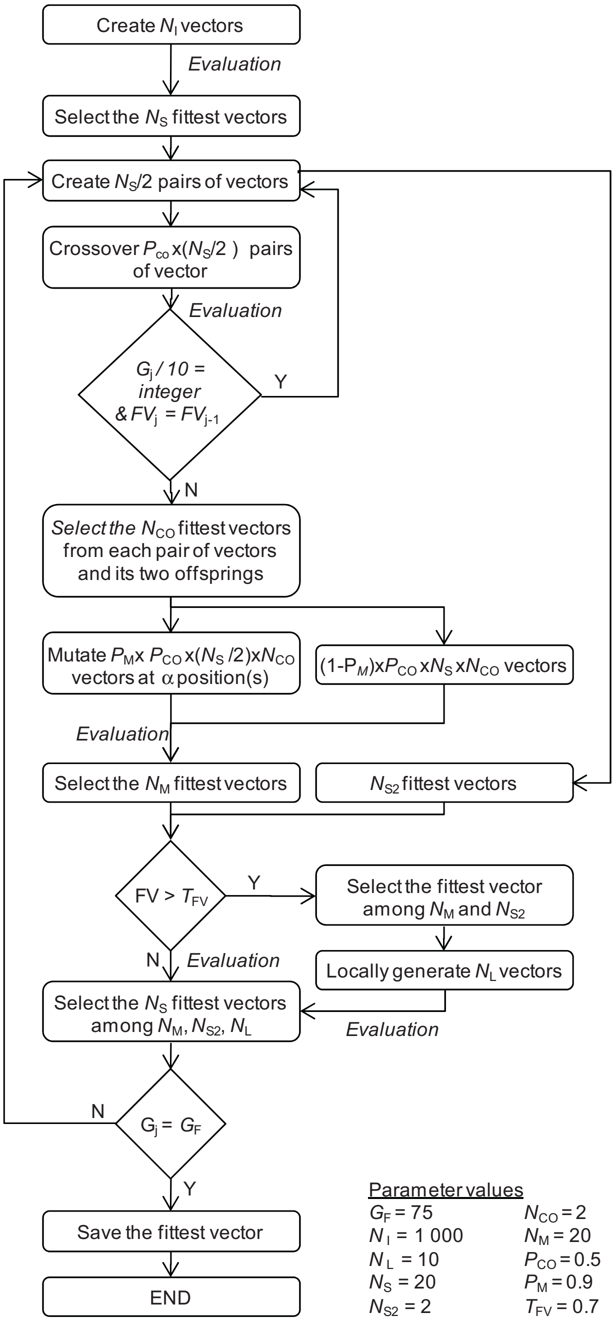

Fig. 1. Simplified flow chart of the genetic algorithm implemented in *SiriusQuality*2. FV_j, highest fitness value at the *j*th generation; *G*, current generation; G_F, final number of generation; N_I, number of vectors of the initial population; N_L, number of vectors generated by the local hill climbing operator; N_M, number of vectors selected after the mutation operator; N_S, number of vectors selected from one generation to the next one; N_{S2}, number of vectors from the previous population kept after the mutation operator; N_{CO}, number of vector selected after cross-over of each pairs of vectors; N_M, number of vectors selected after mutation; P_{CO}, cross-over probability; P_M, mutation probability; T_{FV}, fitness value threshold to go through the local-hill climbing operator; α, random number of mutated position(s) in each mutated vector.

The fitness function was defined as:

$$\text{Fitness}\left[\theta_i\right] = \prod_{k=1}^{V}\prod_{j=1}^{N}\exp\left(-\frac{(O_{jk} - P_{jk}(\theta_{ik}))^2}{2 \times (CV_k \times O_{jk})^2}\right) \tag{9}$$

where θ_i is the *i*th parameter vector, O_{jk} is the *j*th observation for the *k*th variable, $P_{jk}(\theta_{ik})$ is the *j*th prediction of the *k*th variable with

Table 2
Summary of the experiments used in this study.

Environment abbreviation	Site name	Coordinates	Plot size (m^2)	Sowing density (seed m^{-2})	Sowing date	Average emergence date[a]	Average anthesis date	N application[b] (kg N ha^{-1})
CF07	Clermont-Ferrand	45°46′N, 03°09′E	7.5	250	10 Nov. 2006	27 Nov. 2006	15 May 2007	240
CF08				250	06 Nov. 2007	06 Dec. 2007	26 May 2007	240
EM07	Estrées-Mons	49°08′N, 03°00′E	6.5	250	17 Oct. 2006	24 Oct. 2006	20 May 2007	250
EM08				250	22 Oct. 2007	ND	31 May 2007	210
NO07	Norwich	52°38′N, 1°18′E	7.2	400	18 Oct. 2006	ND	28 May 2007	180
NO08				400	19 Oct. 2007	05 Nov. 2007	8 Jun. 2007	200
SB07	Sutton Bonington	52°50′N, 1°14′W	39.6	300	04 Oct. 2006	13 Oct. 2006	31 May 2007	210
SB08				250	10 Oct. 2007	19 Oct. 2007	07 Jun. 2007	210

[a] ND, not determined.

[b] N was applied using either three (at SB and NO) or four (at EM and CF) split applications. All N fertilizer was applied as granules of ammonium nitrate (34.5%N) except for the first three applications in EM that were applied as a liquid solution (15% ureic acid, 7.5% ammonium, 7.5% nitrate). Each split was applied on the same calendar date for all the cultivars.

the *i*th vector, CV is the average coefficient of variation of the k_{th} variable, *N* is the total number of observations, and *V* is the total number of variables. This function gives a value between 0 and 1 to reflect the goodness of fit between model predictions and relevant observation variables.

2.3. Experiments

For this study 16 genotypes were selected as UK and French-bred cultivars/advanced breeding lines to represent feed wheat (Alchemy, Arche, Beaver, Consort, Rialto, Robigus and Savannah) and bread-making wheat (CF9107, CF99102, Paragon, Perfector, Quebon, Recital, Renan, Soissons and Toisondor) types. CF9107 and CF99102 are advanced INRA breeding lines that, for simplicity, are referred to hereafter as cultivars.

Field experiments were carried out at two sites in the UK (University of Nottingham, Sutton Bonington and John Innes Centre, Norwich) and in France (INRA Clermont-Ferrand and INRA Estrées-Mons) in 2006–2007 (07) and 2007–2008 (08). The experiments sites represent a 800 km latitudinal transect and are representative of the climate of main wheat growing regions in Europe. The 16 cultivars were tested in these eight site-season combinations (hereafter referred as environments) in fully replicated trials with three replicated plots. Details of the experiments could be found in Gaju et al. (2011). All experiments were sown at the recommended date and seed density (Table 2). All crop inputs including pest, weed and disease control, and nitrogen, potassium, phosphate and sulfur fertilizers, were applied at levels to prevent nutrients or pests, diseases and weeds from limiting yield. Plant growth regulator was applied as chlormequat at onset of stem extension in the experiments at Estrées-Mons (EM), Norwich (NO) and Sutton Bonington (SB). All the crops were rain fed.

LN was determined in 2007 and 2008 at Clermont-Ferrand (CF) and SB on 10 randomly chosen main-stems per plot every 20–100 °C d from Haun stage 1.5 (at CF) or 8.5 (at SB) to flag leaf ligule emergence. In 2008 at SB, LN was determined only for six cultivars. LN was not determined in the other experiments because it is very resource and time consuming. Leaves were tagged every 3–4 leaves in order to keep track of the total leaf number. Non-integer LN$_f$ values reflect the fact that in most cases there were a few main-stems with either one more or one less leaf. The phyllochron of each cultivar was calculated as the inverse of the slope of the linear regression of LN against T_t for leaves 3–8. Phyllochron was thus calculated only at CF. Main-stem were observed daily for anthesis. Anthesis date was recorded in each experiment when 50% of the main-stem ears carried visible stamens in all plots.

The photoperiod response, earliness *per se*, and vernalization requirement of all the cultivars were determined as previously described (Hanocq et al., 2004; Goldringer et al., 2006). In brief, eight seeds per cultivar were sown in a *Sphagnum* peat moss mix on 13 October 2006 and were maintained for 5 d after emergence in a greenhouse where the temperature was controlled at 18/14 °C (day/night) with a 10 h photoperiod. The plants were watered as needed to maintain the peat moss wet. Plants were then vernalized for 8 wks in a growth chamber with a 8-h photoperiod and a day/night temperature regulated at 6/4 °C. After vernalization the plants were transferred to a controlled photoperiod greenhouse where half of the plants received 10 h photoperiod and the rest 20 h. The photoperiod response was calculated as the difference in thermal time between the end of vernalization and heading for plants grown with 10 and 20 h photoperiod. Plants that did not head in short days were assigned the degree–day value at the end of the experiment (2683 °C d). The earliness *per se* was calculated as the thermal time between the end of vernalization and heading for plants transferred under long days. In order to estimate the vernalization requirement seeds of each cultivar were sown in a commercial mix and vernalized as described above. Plantlets vernalized for 0, 4, and 8 wks were transplanted on 18 April 2007 (i.e. under long days) in single-rows (30 seeds) in a replicated nursery at INRA Le Moulon (48°42′N, 02°08′E). Heading date (Zadok's stage 55) was scored on five plants per row and vernalization requirement was calculated as the difference in thermal time between transplantation and heading for fully and unvernalized or partially vernalized plants. In addition, all the cultivars were typed using perfect markers of the *Ppd-B1* (D. Laurie, personal communication) and *Ppd-D1* (Beales et al., 2007) loci responsible for photoperiod sensitivity and of the *Vrn-A1*, *Vrn-B1*, and *Vrn-D1* loci responsible for vernalization requirement (Yan et al., 2004; Fu et al., 2005).

2.4. Implementation of the genetic algorithm and statistical analysis

Observed anthesis date for the 16 cultivars in the eight environments was used to estimate the varietal parameters of the phenology model implemented in *SiriusQuality*2. The initial range of the parameters (Table 1) was significantly larger than that reported in the literature (Brooking, 1996; Robertson et al., 1996; Brooking and Jamieson, 2002; Martre et al., 2007). First, all the seven varietal parameters were estimated simultaneously. In order to assess the correlation between these parameters, their attainability, and the mean square error between observed and simulated anthesis date, several independent rounds of calibration were carried out. Based on these results (see Section 3), several varietal parameters were fixed at their nominal values to identify the minimum number of varietal parameters to predict anthesis date and LN$_f$ without significant increase in the model error.

All the statistical analyses were done in R-2.9.2 for windows (R Development Core Team, 2007). Simulated and observed duration

Table 3
Genotype at the PPD-B1, PPD-D1 and VRN-1 loci and photoperiod response, vernalization requirement, and earliness *per se* for the 16 wheat cultivars used in this study.

Cultivar	Photoperiod response			Vernalization requirement					Earliness *per se*
	Ppd-B1[a]	*Ppd-D1*[b]	Degree–days difference in heading dates between LD and SD[c]	*Vrn-A1*[d]	*Vrn-B1*[e]	*Vrn-D1*[e]	Degree–days difference in heading dates between non/partially and fully vernalized plants[f]		Thermal time between transplanting and heading[g] (°C d)
							0–8 wks	4–8 wks	
Alchemy	w	b	>1524	c	nd	nd	–	278	1159
Beaver	w	b	>1476	c	nd	nd	–	–	1207
Consort	w	b	>1508	c	nd	nd	–	–	1175
Paragon	w	b	>1669	a	nd	nd	290	120	1014
Rialto	w	b	882	c	nd	nd	–	236	1159
Robigus	w	b	>1588	c	nd	nd	–	173	1095
Savannah	w	b	>1540	c	nd	nd	–	322	1143
Soissons	w	a	411	c	nd	nd	–	376	982
Arche	w	b	>1572	b	nd	nd	557	156	1111
CF9107	w	b	940	c	d	nd	–	0	1030
CF99102	w	b	1116	c	nd	nd	–	124	998
Perfector	w	b	>1556	c	nd	nd	–	–	1127
Québon	w	b	>1604	c	nd	nd	–	694	1079
Récital	m	a	312	c	nd	nd	–	253	1014
Renan	w	b	1134	c	nd	nd	–	545	998
Toisondor	w	a	627	c	nd	nd	–	202	1191

[a] The allele m (mutant) confers insensitivity to photoperiod, while the allele w (wild-type) confers sensitivity (Beales et al., 2007; D.A. Laurie, personal communication).
[b] The allele a confers insensitivity to photoperiod, while the allele b confers sensitivity (Beales et al., 2007).
[c] Determined on fully vernalized plants transferred in a greenhouse under either short (SD, 10 h photoperiod) or long (LD, 20 h photoperiod) days, plants that did not head in SD were assigned the degree–day value at the end of the experiment (2683 °C d).
[d] The alleles a and b confer a spring growth habit, while the allele c confers a winter growth habit (Yan et al., 2004)
[e] The allele d (deleted) confers a spring growth habit, while the allele nd (non deleted) confers a winter growth habit (Fu et al., 2005).
[f] Determined on plants transplanted in the field under long days after either 0, 4, or 8 wks of vernalization under controlled conditions. Hyphens indicate that the plants did not head.
[g] Determined on fully vernalized plants grown under long days (20 h photoperiod).

of the sowing to anthesis period, the anthesis date, and LN_f were compared using mean square error (MSE) and its square root (RMSE), and by the ordinary least square regression. Statistical analysis of the regression lines was done with the Smart library for R using standardized major axis regression (Falster et al., 2006). Correlations between parameters were estimated using Pearson's product moment correlation coefficient for paired samples. Associations between estimated parameter values and daylength response, vernalization requirement or earliness *per se* were analyzed using Spearman's coefficient of rank correlation (ρ). The choice of the best set of varietal parameters was validated using the leave-one-out cross-validation approach which provided an unbiased estimation of the root mean square error of prediction ($\widehat{\text{RMSEP}}_{\text{CV}}$) (Jones and Carberry, 1994; Wallach, 2006).

3. Results and discussion

3.1. Photoperiod response, vernalization requirement and earliness per se

The panel of cultivars used in this study showed a broad range of photoperiod response, vernalization requirement, and earliness *per se* (Table 3). Two cultivars had a low sensitivity to daylength (Soissons and Récital), while six (Rialto, CF9107, CF99102, Renan, and Toisondor) showed an intermediate response. The other cultivars did not head under short days and are therefore photoperiod sensitive. The analysis of nucleotide polymorphism in the *Ppd-B1* and *Ppd-D1* genes, responsible for the daylength sensitivity, confirmed these results, since Soissons, Récital, and Toisondor were found to carry a photoperiod insensitive allele at the *Ppd-D1* locus (*Ppd-D1a*), while the other cultivars carry photoperiod sensitive alleles. Récital also carries a photoperiod insensitive allele at the *Ppd-B1* locus (Beales et al., 2007).

When transplanted in the field under long days without vernalization treatment only Paragon and Arche headed (Table 3). For the 4 wks of vernalization treatment Beaver, Consort, and Perfector did not head when transplanted in the field under long days and have therefore a winter type growth habit. The other cultivars have intermediate vernalization requirements; ranging from CF9107 which headed on the same day for the 4 and 8 wks vernalization treatments, to Renan and Québon which had a difference in heading date of more than 545 °C d (i.e. ca 32 d) between the 4 and 8 wks vernalization treatments. In good agreement with these phenotypic results Paragon and Arche carry a spring type allele at the *Vrn-A1* locus, while CF9107 carries a spring type allele at the *Vrn-B1* locus, which has weaker effects than *Vrn-1A* (Zhang et al., 2008).

The range of earliness *per se*—i.e. the minimum thermal time between sowing and maturity independently from vernalization requirement and photoperiod sensitivity (Slafer and Rawson, 1995a)—among the 16 cultivars was 225 °C d (i.e. ca. 12 d). A cluster analysis suggested two major groups of earliness *per se* (data not shown). In the experimental network, averaged across the eight site-year combinations anthesis date ranged from 17 May for Récital to 4 June for Beaver (data not shown). Beaver had also the highest earliness *per se* value, while Récital had the 12th lowest earliness *per se* (Table 3). Within the individual trials the range of anthesis date was the highest in EM07 and NO07 (20 d) and the smallest in NO08 and SB08 (12 d; data not shown). Therefore, the genetic variability for anthesis in the studied panel is comparable to that observed in most wheat breeding programs (e.g. White et al., 2008).

3.2. Correlations between estimated parameters

After the first generation of the genetic algorithm, the fitness value varied significantly for 20 independent rounds of estimation (median range of 0.185). After 75 generations in 90% of the cases the range of fitness values narrowed down to less than 0.026 and the fitness value was higher than 0.99 for 14 of the cultivars. The fitness value did not increase significantly after 75 generations (Supporting Information Fig. S1). Therefore, in this study the maximum number of generations was set at 75. To overcome the drawback of genetic algorithms, due to their random nature, it is necessary to perform several independent rounds of estimation and to select the best solution among the different rounds (Gen and Cheng, 2000). Preliminarily analyses showed that 10 independent rounds of estimation were sufficient to find an accurate estimate of the fitness value (data not shown).

When the seven varietal parameters (Table 1) were optimized simultaneously, the daylength response (SLDL) was significantly correlated with the phyllochron (Phyll) and with the absolute minimum leaf number ($L^{\text{abs}}_{\text{min}}$; Table 4(A)). The estimated thermal time between sowing and emergence (D_{se}) was also significantly correlated with Phyll. Across 10 independent rounds of estimation the estimated value of the maximum absolute leaf number ($L^{\text{abs}}_{\text{min}}$) varied from 8.1 (Soissons) to 14.2 (Alchemy) leaves. D_{se} was also very variable across the ten independent rounds of estimation; its coefficient of variation ranged from 9.2% (Paragon) to 30.5% (Rialto). The identifiability problem encountered with these two parameters was most likely due to their low total sensitivity index compared with the other six varietal parameters and their comparatively high level of interactions with other parameters (P. Martre, J. He, and P. Stratonovitch, unpublished data). The estimation of the varietal parameters was therefore carried out again with these two parameters fixed at their nominal values.

When $L^{\text{abs}}_{\text{max}}$ and D_{se} were fixed at their nominal values, the correlation between Phyll and $L^{\text{abs}}_{\text{min}}$ became significant (Table 4(B)). The estimated values of the vernalization rate at the minimal vernalizing temperature (VBEE) and of the response of the vernalization rate to temperature (VAI) were scattered throughout their initial ranges (data not shown). Published values of VBEE and VAI for winter wheat range from 7.5 to $20.3 \times 10^{-3}\ \text{d}^{-1}$ and 0.3 to $3.6 \times 10^{-3}\ \text{d}^{-1}\ {}^{\circ}\text{C}^{-1}$, respectively (Brooking, 1996; Robertson et al., 1996; Brooking and Jamieson, 2002), and are significantly correlated ($r = -0.79$; P-value = 0.011; $d.f. = 8$). The large range of the estimated values of these two parameters was most likely due to compensation phenomena. Therefore, they were fixed at their nominal values in turn.

When VBEE was fixed at its nominal value the correlation between Phyll and SLDL was not significant anymore (Table 4(C)), while VAI was then strongly correlated with SLDL and $L^{\text{abs}}_{\text{min}}$. The coefficient of variation of VAI was reduced by 45% (Beaver) to 96% (Rialto). The estimated values of $L^{\text{abs}}_{\text{min}}$ ranged among the 16 cultivars from 5.74 (Toisondor) to 8.61 (Beaver) leaves (median was 6.41 leaves). These values are in good agreement with previous work that showed that $L^{\text{abs}}_{\text{min}}$ for spring wheats, or vernalized winter wheats, grown in long days varies from 5 to 8 leaves (Levy and Peterson, 1972; Rahman, 1980; Slafer and Rawson, 1995b). Therefore, this parameter can mostly likely be fixed at its nominal value without significant loss in the quality of the prediction of LN_{f}.

Table 4

Correlation matrixes for the varietal parameters of the phenology model used in Sirius estimated for 16 wheat cultivars grown in eight environments. ***, **, *Indicate significant correlation with P-values lower than 0.001, 0.01, and 0.05, respectively ($d.f. = 14$).

(A) Seven parameters

	Phyll	SLDL	VAI	$L^{\text{abs}}_{\text{min}}$	VBEE	$L^{\text{abs}}_{\text{max}}$
SLDL	-0.51^{*}					
VAI	0.28	−0.20				
$L^{\text{abs}}_{\text{min}}$	0.28	-0.67^{**}	0.26			
VBEE	0.00	−0.03	0.16	−0.01		
$L^{\text{abs}}_{\text{max}}$	−0.23	0.02	0.08	0.12	−0.22	
D_{se}	-0.42^{*}	0.27	0.22	−0.07	0.13	0.26

(B) Five parameters

	Phyll	SLDL	VAI	$L^{\text{abs}}_{\text{min}}$
SLDL	-0.59^{*}			
VAI	0.02	0.18		
$L^{\text{abs}}_{\text{min}}$	0.47^{*}	-0.77^{***}	−0.15	
VBEE	−0.03	−0.06	−0.31	0.05

(C) Four parameters

	Phyll	SLDL	VAI
SLDL	−0.10		
VAI	0.21	0.71^{**}	
$L^{\text{abs}}_{\text{min}}$	0.09	-0.66^{**}	-0.69^{**}

(D) Three parameters

	Phyll	SLDL
SLDL	−0.13	
VAI	0.25	0.57^{*}

Finally, when only Phyll, SLDL, and VAI were estimated simultaneously, only SLDL and VAI were significantly correlated (Table 4(D)). The correlation between these two parameters was

Table 5

Root mean square error (RMSE), root mean square error of prediction ($\widehat{\text{RMSEP}}$), and cross-validation estimate of the root mean square error of prediction ($\widehat{\text{RMSEP}}_{\text{CV}}$) for anthesis date and final leaf number after calibration of 7 (D_{se}, $L^{\text{abs}}_{\text{max}}$, $L^{\text{abs}}_{\text{min}}$, Phyll, SLDL, VAI, and VBEE), 5 ($L^{\text{abs}}_{\text{min}}$, Phyll, SLDL, VAI, and VBEE), 4 ($L^{\text{abs}}_{\text{min}}$, Phyll, SLDL, and VAI), and 3 (Phyll, SLDL, and VAI) varietal parameters for 16 wheat cultivars.

Number of estimated parameters	RMSE[b]			$\widehat{\text{RMSEP}}$								$\widehat{\text{RMSEP}}_{\text{CV}}$[c]
	Min	Max	MF	Leave-out environment								
				CF07	CF08	EM07	EM08	NO07	NO08	SB07	SB08	
Anthesis date (day)												
7	1.65	1.84	1.65	3.31	2.59	3.09	7.64	3.35	6.33	6.84	3.37	4.94
5	1.77	2.07	1.62	3.23	3.06	3.52	6.67	3.59	5.19	7.97	3.47	4.90
4	1.63	1.92	1.63	3.74	4.33	4.54	7.27	2.99	5.11	4.71	3.50	4.69
3	1.72	1.90	1.55	1.73	2.99	3.11	6.44	2.83	3.78	5.58	2.80	3.94
LN_{final} (leaf)[a]												
7	0.33	0.43	0.36	0.44	0.40	–	–	–	–	0.61	0.57	0.51
5	0.32	0.40	0.37	0.46	0.40	–	–	–	–	0.34	0.59	0.46
4	0.35	0.48	0.32	0.52	0.55	–	–	–	–	0.57	0.49	0.53
3	0.33	0.42	0.39	0.50	0.36	–	–	–	–	0.80	0.41	0.55

[a] $\widehat{\text{RMSEP}}$ for LN_{final} was calculated only for the environments where it was measured for the 16 cultivars.

[b] Minimum (Min) and maximum (Max) RMSE from 10 independent rounds of parameter estimation are reported, as well as RMSE calculated using for each of the 16 cultivars the parameter values from the round of parameter estimation that gave the maximum fitness value (MF).

[c] $\widehat{\text{RMSEP}}_{\text{CV}}$ is the square root of the average $\widehat{\text{MSEP}}$ for the eight leave-out environment scenarios.

significant in all the combination of parameters tested. Compared with the initial situation where seven varietal parameters were estimated simultaneously the average coefficient of variation of Phyll, SLDL, and VAI was reduced by 42%, 88%, and 80%, respectively. When only two parameters were estimated the algorithm cannot converge to an acceptable fitness value (data not shown). This is in good agreement with many studies that showed that when fewer parameters are estimated, without a significant sacrifice in the quality of the model predictions, the uncertainty in the estimated values of the parameters is reduced (Makowski et al., 2006). The correlation between the varietal parameters strongly depended on the set of the parameters that was estimated. This can most simply be explained by the high level of interactions between these parameters. In good agreement with these results, White et al. (2008) showed that three cultivar-specific parameters corresponding to the vernalization requirement, the photoperiod response, and the phyllochron are required to simulate the anthesis date of a panel of wheat cultivars using the wheat simulation model CSM-Cropsim-CERES. These authors showed that the vernalization requirement and photoperiodic response parameters of CSM-Cropsim-CERES could be estimated with linear effects of *Vrn* (*Vrn-A1*, *Vrn-B1*, and *Vrn-D1*) and *Ppd* (*Ppd-D1*).

3.3. Prediction of anthesis date and final leaf number

Differences in anthesis date among the 16 cultivars ranged from 12 d (SB08 and NO08) to 21 (NO07) d. LN_f was determined for the 16 cultivars only for CF07, CF08, and SB08. Differences in LN_f among the 16 cultivars ranged from 1.6 leaves (CF07) to 2.5 (SB08) leaves. Anthesis date and LN_f were not significantly correlated at the three sites ($0.28 \le r \le 0.50$; $0.288 \ge P\text{-value} \ge 0.051$). There was significant ($P\text{-value} < 0.001$) cultivar by environment interaction for both anthesis date and LN_f.

The root mean square error (RMSE) for anthesis date was similar for the calibration strategies with seven to three varietal parameters, averaging 1.61 d (Table 5). However, the root mean square error of prediction ($\mathrm{R\hat{M}SEP}$) was lower for the strategy with three varietal parameters than with any of the other strategies tested in five out of eight environments. The cross-validation root mean square error of prediction ($\mathrm{R\hat{M}SEP_{CV}}$) was similar for the strategies with seven, five, and four varietal parameters (averaging 4.84 d), but it was reduced by 19% when only three parameters were estimated simultaneously. Simulated and observed duration from sowing to anthesis ($r = 1.0$) and anthesis date ($r = 0.98$) were closely correlated ($P\text{-value} < 0.001$; Fig. 2). These results clearly showed that the reduced uncertainty in parameter estimation when only three parameters were estimated was accompanied by a reduction in the uncertainty in the model prediction.

The RMSE and $\mathrm{R\hat{M}SEP_{CV}}$ for LN_f were similar for the different calibration strategies, averaging 0.36 and 0.51 leaves, respectively (Table 5). This suggests that the estimation of LN_f was not significantly biased. As illustrated in Fig. 3 for four cultivars, the rate of leaf emergence was reasonably well simulated when only three parameters were estimated. Simulated and observed LN_f for the 16 cultivars were well correlated ($r = 0.97$; $P\text{-value} < 0.001$), with a slope not significantly different from one ($P\text{-value} = 0.71$) and an intercept not significantly different from zero ($P\text{-values} = 0.59$; Fig. 4).

3.4. Association between estimated and observed parameters

The reported genetic range of variation of phyllochron for wheat is 75–120 °C d (Kirby et al., 1985a; Mossad et al., 1995; Slafer and Rawson, 1995c; Ishag et al., 1998). Similar ranges of variations (i.e. ±15–25% of the mean value) have been reported for rice (*Oryza sativa* L.; Miyamoto et al., 2004) and barley (*Hordeum vulgare* L.; Dofing, 1999). In these two species the broad-sense heritability of the phyllochron is 70–90% (Dofing, 1999; Morita et al., 2005), indicating a strong genetic control. The range of phyllochron variation for wheat might account, for LN_f of 10 leaves, for 25 d (ca. 460 °C d) difference in anthesis. According to this simple calculation phyllochron can account for a very significant part of the genetic variability of anthesis in modern wheat germplasm.

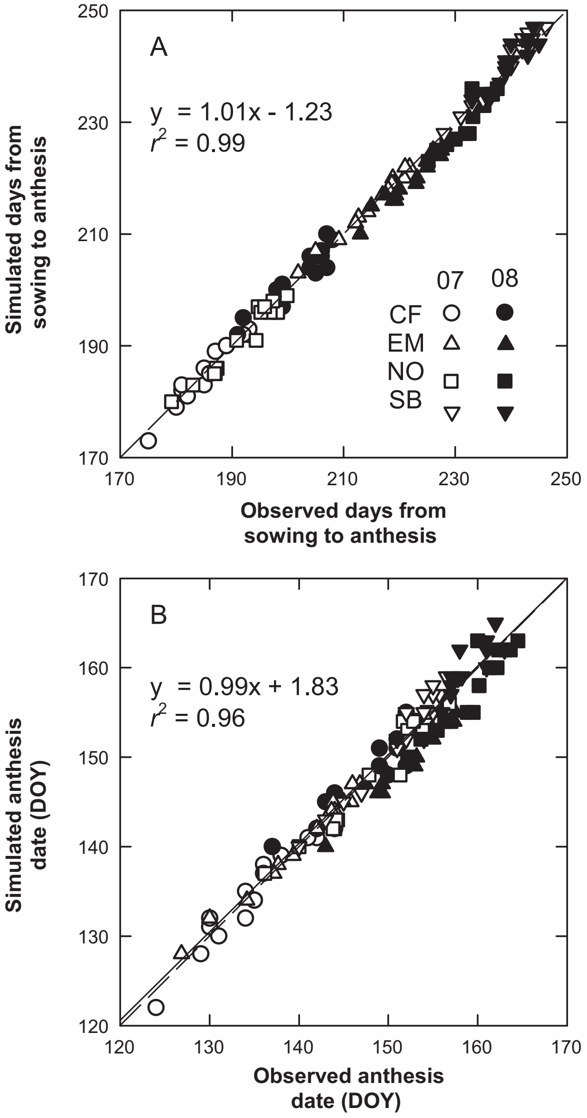

Fig. 2. Simulated versus observed duration from sowing to anthesis (A), and anthesis date (B) for 16 wheat cultivars grown at Clermont-Ferrand (CF, circles), Estrées-Mons (EM, triangle up), Norwich (NO, square), and Sutton Bonington (SB, triangle down) in 2006–2007 (07, open symbols) and 2007–2008 (08, closed symbols). The three varietal parameters Phyll, SLDL, and VAI were estimated simultaneously. The solid lines are linear regressions.

The estimated values of Phyll were within the reported range for 14 of the cultivars (Fig. 5A, see supplement A for tabular presentation of the estimated parameter values). Alchemy (124 °C d) and Consort (127 °C d) had slightly higher estimated Phyll values. Estimated and calculated values of Phyll were linearly correlated ($P\text{-value} < 0.001$), with a slope not significantly different from one ($P\text{-value} = 0.020$) and a Y-intercept not significantly different from zero ($P\text{-value} = 0.041$; Fig. 6). Deviations in slope and intercept were due to only few data points and if the regression was forced through the origin, the slope was close to unity (0.964 ± 0.07; $P\text{-value} < 0.001$). The correlation between observed and simulated

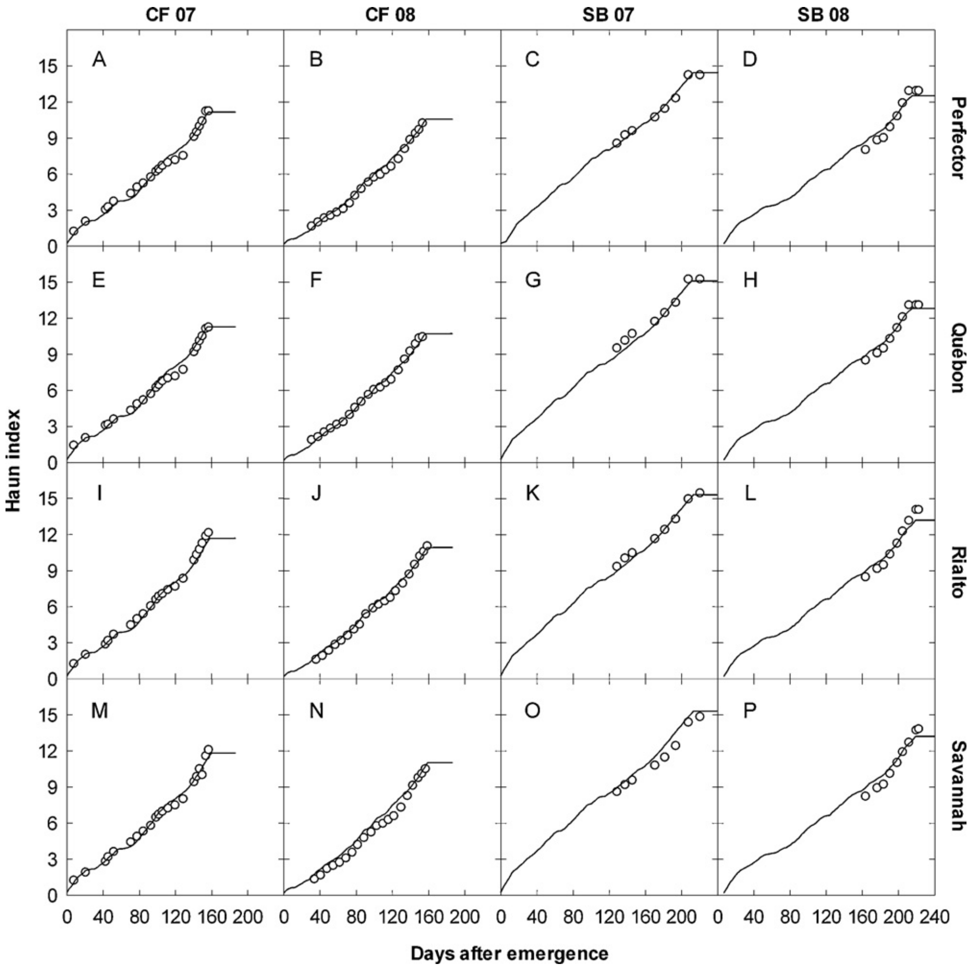

Fig. 3. Simulated (solid lines) and observed (open circles) Haun index versus days after emergence for the wheat cultivar Perfector (A–D), Québon (E–H), Rialto (I–L) and Savannah (M–P) grown in Clermont-Ferrand in 2006–2007 (CF07; A, E, I, and M) and 2007–2008 (CF08; B, F, J, and N) and in Sutton Bonington in 2006–2007 (SB07; C, G, K, and O) and 2007–2008 (SB08; D, H, L, P). The three varietal parameters *P*, SLDL, and VAI were estimated simultaneously.

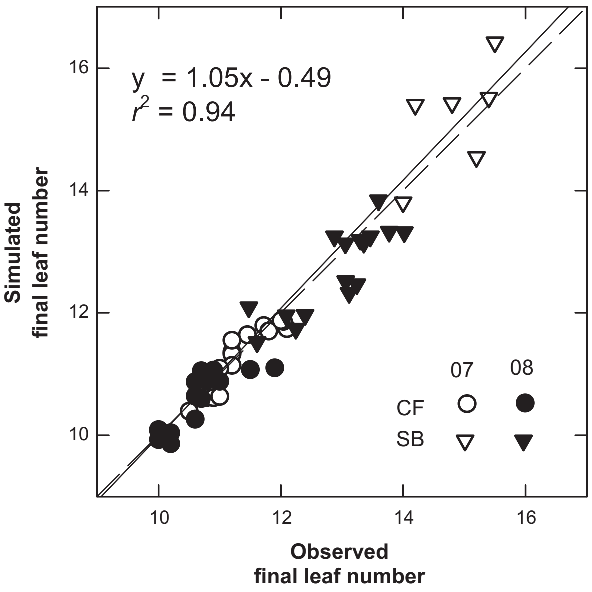

Fig. 4. Simulated versus observed final leaf number for 16 wheat cultivars grown at Clermont-Ferrand (CF, circles) and Sutton Bonington (SB, triangle down) in 2006–2007 (07, open symbols) and 2007–2008 (08, closed symbols). For SB07 the final leaf number was determined for only 6 cultivars. The three varietal parameters Phyll, SLDL, and VAI were estimated simultaneously. The solid line is the linear regression.

Phyll did not decline when the number of estimated parameters was reduced (0.86 when seven parameters were estimated versus 0.90 when only three parameters were estimated).

No correlation was found between LN_f (averaged across environments) and Phyll (*P*-value = 0.94). In good agreement with this result, in barley (*H. vulgare* L.) phyllochron and LN_f are controlled by different quantitative trait loci (QTL; Borràs-Gelonch et al., 2010). The estimated values of Phyll were significantly associated with the earliness *per se* of the cultivars estimated in the greenhouse (ρ = 0.59; *P*-value = 0.023). In good agreement, several rice (*PLASTOCHRON1*) and maize (*Zea mays* L.; *Teopod1-3*) mutations with extended duration of the juvenile phase have shorter phyllochron (Poethig, 1988; Ahn et al., 2002). However, our results contradict the statement of Hay and Ellis (1998) that "interpretation of the role of earliness *per se* genes in wheat and barley should concentrate upon their effect on collar initiation and mainstem leaf number [...], rather than on possible effects on phyllochron". Determination of the phyllochron in the field is very tedious and time consuming. The parameter estimation procedure described here could be used to estimate the phyllochron of large number of genotypes for genetic studies when only the sowing and anthesis dates (and weather data) are available. Knowledge of the genes controlling the phyllochron might allow breeders to fine-tune flowering time for regional variations in climate. It may also provide a better understanding of the genetic control of tillering. The coordination between leaf emergence rate and the pattern of tillering suggests that the phyllochron can substantially affect tillering rate and the

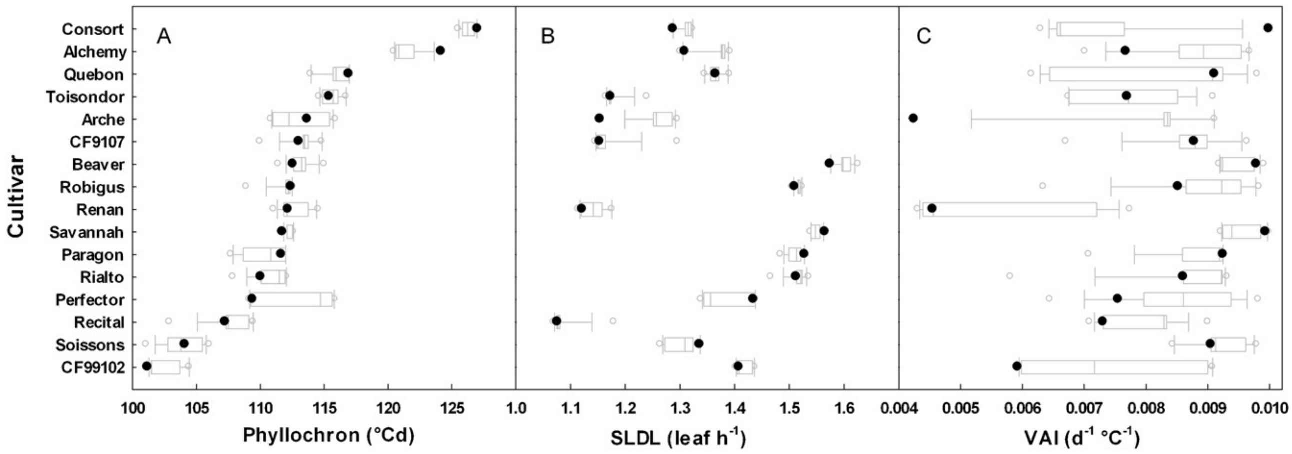

Fig. 5. Estimated values of the varietal parameters Phyll (A), SLDL (B), and VAI (C) for 16 wheat cultivars. The three parameters were estimated simultaneously. Closed circles are the fittest parameters sets for 10 independent rounds of estimation, the edges of the boxes represent the 25% and 75% percentiles, the solid horizontal bars the 10% and 90% percentiles, the open circles the outliers. Cultivars are ranked based on the fittest Phyll value.

potential number of tillers (Kirby et al., 1985b). This is supported by the common genetic basis of phyllochron and potential tiller number in rice (*O. sativa* L.; Dong et al., 2004; Miyamoto et al., 2004). This association could be due to the emergence of tillers earlier with low phyllochron values, although no correlation was found between these traits for barley (Borràs et al., 2009). But in barley phyllochron and potential tiller number are not systematically correlated (Borràs et al., 2009) and are controlled by different QTL (Borràs-Gelonch et al., 2010). Phyllochron is also an important trait for early vigor, a key adaptive trait for wheat, especially under Mediterranean conditions (Rebetzke and Richards, 1999). Phyllochron can affect early vigor, which can in turn affect tillering through the carbohydrate supply/demand balance (Bos and Neuteboom, 1998).

The estimated values of SLDL ranged from 1.08 leaf h^{-1} (Récital) to 1.57 leaf h^{-1} (Beaver) daylength (Fig. 5B). Values of SLDL calculated from published data are significantly lower, ranging from 0.33 to 1.28 leaf h^{-1} daylength (Levy and Peterson, 1972; Allison and Daynard, 1976; Rahman and Wilson, 1977; Brooking et al., 1995; Slafer and Rawson, 1995b). No significant association was found between the daylength response and the estimated SLDL values. The correlation between SLDL and VAI might have led to overestimation of both parameters (see below). SLDL was significantly associated with the average (across the eight environments) anthesis date ($\rho = 0.67$; *P*-value = 0.010) and LN$_f$ ($\rho = 0.875$; *P*-value < 0.001).

VAI was significantly correlated with the average (across the eight environments) anthesis date ($\rho = 0.52$; *P*-value = 0.0475), but not with the LN$_f$ (*P*-value = 0.22). As mentioned above, the estimated values of VAI (Fig. 5) were ca. twice as large as that reported in the literature from growth chamber experiments (Brooking, 1996; Robertson et al., 1996; Brooking and Jamieson, 2002). Estimated values of VAI for the ten independent rounds of estimation were much more variable than that of Phyll and SLDL (Fig. 5C). This suggests that different values of VAI resulted in the same or similar model outputs. This phenomenon was explained by Beven and Binley (1992) as “equifinality”, where a given end state can be reached by many potential means and none can be rejected if without further proofs. This can also be due to the fact that under our experimental conditions with an autumn sowing all the cultivars were fully vernalized before the daylength approached DL$_{sat}$, which was not the case in the growth chamber experiments where these parameters were estimated. Under such conditions the final leaf number and the anthesis date would be mainly determined by the photoperiod at the end of the vernalization, and therefore SLDL would be more influential than VAI. This conclusion is supported by the positive correlation ($\rho = 0.54$; *P*-value = 0.036) between the photoperiod response estimated in the greenhouse and anthesis date in the field (averaged across the eight environments), while no significant correlation (*P*-value = 0.43) was found between the vernalization requirement and the anthesis date. Analysis of experimental dataset with different sowing dates would probably allow a more accurate estimation of VAI (McMaster et al., 2008) and might allow these two parameters to be uncoupled.

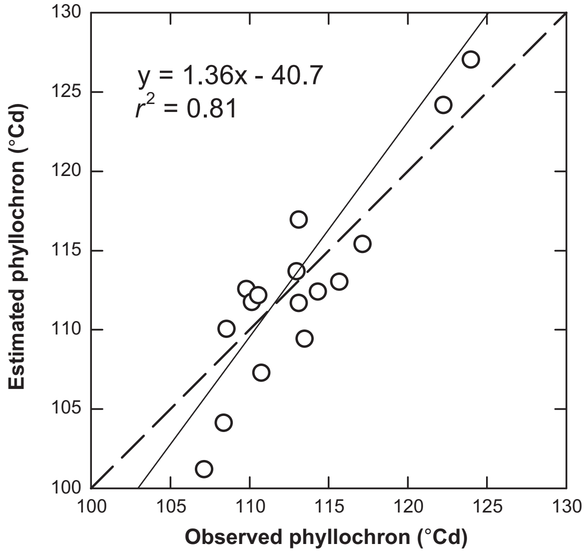

Fig. 6. Estimated versus measured phyllochron for 16 wheat cultivars. The estimated values are those who gave the maximum fitness values for each cultivar across 10 rounds of calibrations; the observed values are the average values of phyllochron calculated at Clermont-Ferrand, in 2007 and 2008. The dashed line is the 1:1 line, the solid line is the linear regression. The three varietal parameters Phyll, SLDL, and VAI were estimated simultaneously.

4. Conclusion

The estimation of parameters for complex non-linear models is still an open field, and there is no general consensus on the best approach (Makowski et al., 2006). Very few studies have rigorously analyzed the choice of varietal (genotypic) parameters and their associations with measured traits or parameters for complex process-based models. This study demonstrates that the previous version of *SiriusQuality* was over-parameterized for autumn sowing dates in northern Europe and modern cultivars and that several varietal parameters for phenology were significantly correlated. The results showed that only three varietal parameters need to be estimated: the phyllochron, the response of vernalization rate to temperature, and the daylength response of leaf production. The estimated and measured values of Phyll showed a strong linear correlation and Phyll was shown to be associated with earliness *per se*. Further studies are needed to analyze the correlation between SLDL and VAI using different sowing dates.

The varietal flowering time parameters have been experimentally determined for barley recombinant inbred lines by transferring the plant from long days to short days at regular intervals throughout development (Yin et al., 2005a,b). This approach is very time- and resource-consuming and, as noted by the authors, the estimation of parameters for vernalization requirement would require even more expensive temperature-controlled experimentations. The hybrid genetic algorithm developed here allows the estimation of these parameters solely from field observations of anthesis date in different environments. Since anthesis date is routinely recorded by geneticists, this approach could be applied for model calibration on large populations grown in multi-environment field networks without extra work. Estimated model parameters can then be used in classical QTL analysis to detect genetic loci which could then feed-back the model (Yin et al., 2005b; Letort et al., 2008). The analysis of the genetic basis of Phyll, SLDL and VAI would strengthen our understanding the genetic control of flowering time in wheat, the most important temperate cereal in the world.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.eja.2011.11.002.

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Table S1
Estimated values of the varietal parameters Phyll, SLDL, and VAI for 16 wheat cultivars. The three parameters were estimated simultaneously.

Cultivar	**Phyll (°C)**	**SLDL** leaf h^{-1} (daylength)	**VAI** d^{-1} $°C^{-1}$
Alchemy	124	1.31	0.00768
Beaver	113	1.57	0.00979
Consort	127	1.29	0.00999
Paragon	112	1.53	0.00925
Rialto	110	1.51	0.00861
Robigus	112	1.51	0.00853
Savannah	112	1.57	0.00994
Soissons	104	1.34	0.00906
Arche	114	1.15	0.00425
CF9107	113	1.15	0.00878
CF99102	101	1.41	0.00593
Perfector	109	1.43	0.00756
Québon	117	1.37	0.00911
Récital	107	1.08	0.00731
Renan	112	1.12	0.00456
Toisondor	115	1.17	0.00770