Process-based analysis of Thinopyrum intermedium phenological development highlights the importance of dual induction for reproductive growth and agronomic performance

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Process-based analysis of *Thinopyrum intermedium* phenological development highlights the importance of dual induction for reproductive growth and agronomic performance

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Keywords

Thinopyrum intermedium; perennial grains; flowering induction; photoperiod; modelling

Highlights

- IWG reproductive growth requires a vernalization treatment
- In spring, IWG reproductive growth is associated with GDD accumulation and photoperiodic response
- GDD-daylength coupled dynamics drive IWG sward functional changes during reproductive growth
- GDD-daylength coupled dynamics can inform and improve agronomic management.

Abstract

Intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey) is being developed for use as a new perennial grain crop through breeding and agronomic research. However, progress has been hampered by lack of understanding of environmental requirements for flowering and grain production. Therefore, we developed a phenology model for IWG adapted from the STICS soil-crop model. The model was compliant with experimental results (relative root mean square error = 0.03). The optimal vernalizing temperature was between 4 and 5°C, optimal daylength between 13 and 14h, while daylength below 11h slowed reproductive development. Vernalization requirement was found to be a constraining inductive process. Including a photoperiod limitation to the model with temperature improved its ability to predict induction at various latitudes. Therefore, timing and duration of vegetative vs. reproductive growth may differ between environments and change reproductive tiller elongation earliness, weed competitiveness, management timing, and stress conditions during phases critical to grain yield. Accurate phenology models will enable optimal field management and inform future breeding strategies. However, plasticity may lead to divergent ideotypes under various agroecosystems.

1. Introduction

The wheat-relative intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey) (IWG) is a winter-hardy cool-season perennial grass, which has recently undergone development as a perennial grain by several breeding programs (Bajgain et al., 2020). Improved IWG populations have been released by *The Land Institute* (Salina, Kansas, USA) under the trade name Kernza® (DeHaan et al., 2018). Intermediate wheatgrass can support the transition to agroecological systems because this perennial crop produces forage and grain for several years with minimal soil disturbance and associated environmental issues (Duchene et al., 2019; Ryan et al., 2018). Featuring large and deep roots, year-round soil cover, increased resource use efficiency and an extended growing season (Cattani and Asselin, 2018a; DeHaan, 2015; Glover et al., 2010; Sprunger et al., 2018),

50 the ‘perennialization’ of cropping systems would be one cornerstone of sustainable agriculture
51 (Crews, 2016).
52
53 Intermediate wheatgrass has relatively low grain yields compared with annual cereal grains (Jungers
54 et al., 2018, 2017; Tautges et al., 2018), which has limited the introduction and adoption of IWG into
55 grain systems and crop rotations. Seed production is the result of the interaction between genotype
56 and growth conditions. Breeding efforts have been mostly dedicated to improving shatter resistance
57 and free-threshing seeds, along with larger seed mass and seed number per head (DeHaan et al.,
58 2018). Little attention has been paid to IWG phenological milestones that determine its growth cycle
59 (inductive transition), from the initiation of inflorescence primordia to seed maturity. Current
60 worldwide endeavors and interest in IWG production is driving the need for deeper investigation of
61 the environmental requirements associated with IWG yield and yield components. Filling this
62 knowledge gap would provide direction in targeting specific breeding strategies, suitable growing
63 contexts, and best crop management practices to optimize IWG grain production.
64
65 Winter annual herbaceous grains, like winter wheat, and most perennial grasses have a dual
66 induction requirement for flowering (Cooper and Calder, 1964; Heide, 1994). The primary induction
67 includes exposure to winter conditions, including low temperatures (LT) and short daylength (SD),
68 which is followed by a secondary induction that includes a period of transition to longer days (LD)
69 and higher temperatures (HT; Heide, 1994). Primary induction is usually discussed as the
70 vernalization process, corresponding to a chilling treatment that induce reproductive primordia
71 (Seppänen et al., 2013). Cold resistance is gradually improved through low-temperature acclimation,
72 and then gradually lost with time, cooler temperatures and vernalization saturation (Fowler et al.,
73 1996; Limin and Fowler, 2006). The secondary induction follows as a critical accumulation of heat
74 units (growing degree-day) and increased daylengths that stimulate a crop’s phasic development,
75 tiller growth and flowering (Basu et al., 2012; Chouard, 1960; Trione and Metzger, 1970).

In winter grain crops and forage grasses, the achievement of primary induction (vernalization) needs either LT or SD, but sometimes requires both (e.g. *Bromus inermis*), or has a preferential temperature/photoperiod inductive pathway (e.g. *Phleum nodosum, Agrostis canina;* Cooper and Calder, 1964; Halevy, 1989). Temperature and photoperiod are interactive factors since a change in one parameter can modify inductive requirements of the other (Halevy, 1989; Heide, 1994; Limin and Fowler, 2006; Mahfoozi et al., 2000; Ritchie, 1991). However, warm-season perennial grasses (e.g. *Panicum virgatum, Andropogon gerardii*), and certain cool-season species (e.g. *Phleum pratense)* do not require vernalization to achieve flowering (Table S1). Moreover, population diversity, breeding, and plant life-history in fields leads to a certain variability or heterogeneity of inductive requirements among the same species, with the potential formation of cultivars or local ecotypes (Dubcovsky et al., 2006 Cooper and Calder, 1964; Jokela et al., 2015; Palit et al., 2014). Considering IWG, the need of primary induction (vernalization treatment) to ensure proper reproductive growth has been shown previously (Frischknecht, 1959) and has been recently confirmed by field observations and results from controlled experiments (Ivancic et al, *under review*).

The transition from winter dormancy to spring growth and flowering (secondary induction) vary greatly among perennial grasses in terms of timing and environmental requirements (Ansquer et al., 2009). Flowering earliness generally differentiates fast growing species with generally lower requirements. Conversely, late maturing species generally require greater heat unit accumulation, associated with higher phyllochrons, to achieve flowering (Duru et al., 1993, 2008b; Frank and Bauer, 1995). Photoperiod mediation of the growth period is observable in many species, with different degrees of importance, late flowering and single induction grasses would depend solely on photoperiod responsiveness (Castro et al., 2011; Esbroeck et al., 2003; Mitchell et al., 1997). Considering IWG, the role of photoperiod in reproductive growth has been suggested before and

would have been a driver of later tiller elongation as compared to other perennial grasses such as *Bromus inermis* (Mitchell et al., 1998).

Linking plant phenology to whole plant growth and resource use strategy, fast or slow growing patterns of forage grasses appears to be associated with several functional traits (e.g. organ turnover rate, specific leaf area, biomass density, leaf nitrogen concentration, net primary productivity; Cruz et al., 2010; Duru et al., 2008, 2009; Ryser and Lambers, 1995; Shipley, 2006) which, when combined, determine the resource-conservative or acquisitive growth strategies of these grass species in their native ecosystems.

This study used a large pool of phenological field observations from various regions and across different cropping seasons to evaluate IWG phasic development *in situ*. To complement other studies designed in controlled conditions (Ivancic et al., *under review*), this dataset offers an unprecedented opportunity to look at the influence of divergent temperature and daylength conditions on IWG growth. The use of integrative crop modelling concepts is then a powerful way to provide a more holistic understanding of the crop growth dynamic within a specific environment. Coupling field observations and modeling approaches notably enables the analysis of complex biotic and abiotic interactions through the integration of growth function and process-based data.

The objective was to accurately characterize the converging drivers of phenological development of IWG populations in diverse growth environments. In particular, three questions were addressed: i) How sensitive is IWG to vernalization and what are its vernalization requirements?; ii) How sensitive is IWG to photoperiod during secondary induction and what are the photoperiod thresholds of IWG?; and iii) How fast does IWG develop in various agronomic conditions? These questions were examined through field-based measurement analysis and crop model inversion of IWG phenological development. IWG phenology and environmental requirements are discussed and compared to the

existing literature on perennial grasses and annual winter grain crops, with the purpose to better place IWG growth among already characterized functional groups. Overall, this work aims to evaluate opportunities and challenges in terms of adequacy and integration of IWG as a perennial grain into farming systems.

2. Materials and methods

To characterize IWG phenological responses to contrasted growing environments, and compare its behavior to known perennial grasses or annual grain crops characterized in the literature (section 2.1), a database was constructed with experiments conducted across Western Europe and North America (section 2.2). In an attempt to better understand crop response to those conditions, field result analysis was coupled with crop modeling approaches. Classic field result analysis, consisting of comparing phenological stages and degree-day accumulation starting February 01 (shown to minimize GDD accumulation variability and corresponding to plant changes in assimilate allocation; Ansquer et al., 2009; Peacock, 1976), was first conducted (section 2.3). Crop modeling approaches were then deployed to further ascertain the impacts of vernalization and photoperiod on the phenological development (section 2.4).

2.1. Experimental sites and data collection

2.1.1. Site description and experimental conditions

From 2012 to 2019, IWG field experiments were conducted in four countries (USA, Canada, France and Belgium). Data were thus respectively collected under Köppen climate (Peel et al., 2007) type Dfb in Canada (humid continental climate conditions), type Dfa in the USA (hot summer continental climate conditions) and type Cfb in France and Belgium (temperate climatic conditions characterized by warm summers). These climatic contexts allowed evaluation of various temperature patterns and seasonal conditions to assess the accumulation of heat units and vernalization requirements.

Furthermore, latitudes of the different sites ranged between 38.77°N and 50.56°N (Table S2) inducing contrasted photoperiods.

2.1.2. Data collection

For each location, precipitation and average temperatures were measured daily. IWG growth stages were measured at the field level, representing the dominant growth stage of the stand, and were rated using the BBCH scale (Hess et al., 1997) and the timing of each observation was reported in DAE/DAH unit (day after emergence/ day after last harvest). In this paper the focus was put on four main phenological stages:

- stem elongation (BBCH 30), which characterize the end the juvenile phase and the beginning of shoot development;
- flag leaf (BBCH 39) accounts for the end of foliar development;
- flowering (anthesis) (BBCH 65) represents the end of shoot development and the beginning of grain filling;
- maturity (BBCH 89), which stands for the end of grain filling and the cessation of the reproductive cycle.

A total of 137 phenological observations were recorded on these main phenological stages.

2.2. Growing-degree-day calculation

Following the approach of Ansquer et al. (2009), growing-degree-day (GDD) in base 0 was computed as:

$$T_{mean}(i) = \frac{T_{max}(i) - T_{min}(i)}{2} \quad \textbf{Eq. 1}$$

$$GDD(i) = T_{mean}(i) - T_{base} \quad \textbf{Eq. 2}$$

In which *i* is a given day, T_{max},T_{min} *and* T_{mean} are respectively the maximal, minimal and mean air temperature recorded for day *i* and T_{base} is the base temperature (assumed to be 0 in this case).

As in Ansquer et al. (2009), and as usually done for perennial crops, the sum of GDD is usually computed starting Feb. 01 in France. In this paper, the sum of GDD was computed from February, 01 and accumulated up to flowering (BBCH 65). This approach has demonstrated its relevance to determine grass development milestones (Ansquer et al. 2009 ; Bartholomew and Williams, 2005 ; Brown et al., 1986 ; Chauvel et al., 2000 ; Frank and Hofmann, 1989 ; Mitchell et al., 1997). Using a constant base temperature over which any additional degree is accumulated as a temperature enabling developmental unit is largely used (e.g. Ansquer et al., 2004 ; Cruz et al., 2010 ; Duru et al., 2008c ; Luo et al. 2011 ; Parthasarathi et al., 2013). Such an approach has been integrated in most plant growth models (Wang et al., 2017).

2.3. Crop modelling

The crop model approach deployed in this paper adopts the formalisms used in the widely validated STICS soil-crop model (Brisson et al., 2009, 2002, 1998). We propose here a short description of the different formalisms. Further details are found in Brisson et al. (2009).

2.3.1. Phenological development

As for many crop models, the simulation of succession of different phenological stages is driven by the accumulation of "*development units*". To compute these, we kept from the STICS model the impacts of temperature, photoperiod and cold requirements, while we set aside the slowing impacts of water and nitrogen stress. The *development units* considered here are computed at the daily time step as follows:

$$UPVT(i) = GDD_t(i) \cdot SFP(i) \cdot SFV(i) \qquad \textbf{Eq. 3}$$

In which *i* is the considered day, *UPVT* are Photo-Vernalo-Thermic Units (UPVT in short), GDD_t are the growing degrees-days limited by thresholds, *SFP* is a Slowdown Factor accounting for Photoperiod, and *SFV* is a Slowdown Factor accounting for Vernalization.

Under this formalization, the accumulation of development units is firstly driven by the widely-accepted concept of growing degrees-days (Durand, 1967). Comparing to the simple Eq. 2, the concept of growing degree-day used here (GDD_t) is adapted to account for minimal, optimal and maximal temperature thresholds (Eq. 4). Photoperiod (Eq.5) and cold requirement (Eq.6) are used to slow down the accumulation of development units; as suggested by Brisson and Delecolle (1992), these effects are computed as a rate applied per unit of thermal time, implying the use of multiplicative terms in eq.3.

Finally, the last step of phenological development simulation was to sum UPVT over the cropping season. To do so, UPVT were summed starting from the day of emergence (establishment year) or the day following previous harvest (other years) up to the harvest of the considered crop season. Regarding the simulation of one particular stage (BBCH 30, 39, 65 or 89 – see section "Data collection"), the model calibration involved retrieving the sum of UPVT that was required to reach a specific stage while optimizing the model performances (see section "Assessment of model performance").

2.3.2. Effect of temperature

The impacts of temperature respond to a triangular function (Eq.4)

$$\begin{cases} GDD_t(i) = 0 & if \quad T_{mean}(i) \leq DT_{min} \; or \; T_{mean}(i) \geq DT_{max} \\ GDD_t(i) = T_{mean}(i) - DT_{min} & if \quad DT_{min} < T_{mean}(i) \leq DT_{opt} \\ GDD_t(i) = \dfrac{DT_{opt} - DT_{min}}{DT_{opt} - DT_{max}} . (T_{mean}(i) - DT_{max}) & if \quad DT_{opt} < T_{mean}(i) < DT_{max} \end{cases}$$

Eq. 4

In which DT_{min}, DT_{opt} and DT_{max} are the minimal, optimal and maximal temperature to allow for crop development. In particular, here, DT_{min} is the equivalent of T_{base} proposed at equation 2.

Under such conditions, the effects of temperature on crop development are linearly increasing between DT_{min} and DT_{opt} and are linearly decreasing between DT_{opt} and DT_{max}. DT_{opt} and DT_{max} have

been proposed in Brisson et al. (2008) to account for the slowdown in crop development that can be observed under hot conditions.

2.3.3. Photoperiod factor

Using classic astronomical functions, the photoperiod (PhotoP(i) in Eq.5) can be calculated on the basis of the calendar days and the latitude (Sellers, 1965). Based on the photoperiod, the slow-down photoperiodic effect SFP(i) can then be calculated using Eq. 5.

$$\begin{cases} SFP(i) = \frac{(PhotoP(i) - PhotoP_{sat})}{(PhotoP_{sat} - PhotoP_{base})} + 1 \\ SFP(i) = \max\left(\min(SFP(i), 1), 0\right) \end{cases} \quad \textbf{Eq. 5}$$

In which $PhotoP_{base}$ is the photoperiod below which there is no development and $PhotoP_{sat}$ is the saturation photoperiod, above which there is no limitation. The second term of Eq.5 ensures that SFP(i) is mathematically bounded between 0 and 1.

We assumed that IWG would be a long-day plant (Heide, 1994) similar to other grassland species and most annual grain crops such as wheat, barley and rye. This implies that $PhotoP_{base}$ would be lower than $PhotoP_{sat}$. As for the STICS model, photoperiod effect was inactivated after flowering stage and up to maturity.

2.3.4. Cold requirements

The cold requirement routine is a two-step procedure, in which the vernalizing value of a given day is firstly computed (VV(i) in Eq.6), and then the slow-down factor SFV(i) is calculated as the ratio of completion of the total vernalization requirements (Eq.7). We furthermore adapted the formalism proposed in STICS to introduce a sensitivity parameter to vernalization, as for Eq. 5, to determine what would be the degree of sensitivity of IWG to vernalization requirement.

$$VV(i) = max\left(1 - \left[\frac{T_{vern} - T_{mean}(i)}{Ampli_{vern}}\right]^2, 0\right) \quad \textbf{Eq. 6}$$

$$\begin{cases} SFV(i) = \frac{\left[\sum_{j=D_{emer}\ or\ D_{harv}}^{i} VV(j)\right] - VV_{min}}{VV_{req} - VV_{min}} \\ SFV(i) = \max\left(\min(SFV(i), 1), 0\right) \end{cases} \quad \textbf{Eq. 7}$$

In these equations, T_{vern} is the temperature to reach an optimal vernalization value during a given day, $Ampli_{vern}$ is the amplitude of the vernalizing effect, D_{emer} and D_{harv} are respectively the day of emergence (during the IWG establishment year) or the day of the last harvest (for any other year), VV_{min} is the minimum number of vernalizing days (fixed at 1 for this analysis) and VV_{req} is the total number of required vernalizing day . As for Eq.5, the second term of Eq.7 ensures that SFV (i) is mathematically bounded between 0 and 1.

Therefore, once initiated ($\Sigma VV(i) > VV_{min}$), the vernalization routine proposed in STICS considers that the "resting state" during winter time is not total and allows for a partial accumulation of development units. Furthermore, in this formalism, incomplete vernalization requirements ($\Sigma VV(i) < VV_{req}$) would slow the development of crops but would thus allow evolving in the phenology, leading eventually to flowering and maturity at a slower rate, without stopping it and preventing ears to be fertile.

2.3.5. Snow cover correction

Due to their climatic conditions (climate type Dfb), Canadian sites are prone to significant snowfalls and snow cover during winter. As suggested by Jégo et al., (2014) using crop models in northern areas of Canada, Scandinavia or Russia requires accurately simulating the impacts of snow cover and soil freezing on soil processes, survival and growth of (perennial) crops. Snow cover indeed changes

the energy budget of the soil surface by increasing the albedo, reducing the soil heat flux and the surface roughness, and modifying the soil temperature and water content profiles (Jégo et al., 2014). In their paper, previous authors compared three snow modules, more or less complex in their representation of snow accumulation and melting. As we did not require the same level of complexity, we considered a simpler approach based on a simple temperature threshold (Eq. 8). Based on records obtained at Winnipeg, Canada, experimental sites regarding air temperature and soil temperature (Fig. 1), a bilinear model was adjusted (Eq. 8).

$$\begin{cases} T_{corr}(i) = T_{mean}(i) & if \quad T_{mean}(i) > 0°C \\ T_{corr}(i) = 0.165.T_{mean}(i) & if \quad T_{mean}(i) < 0°C \end{cases} \qquad \textbf{Eq. 8}$$

Within climate type Dfb, this correction (R^2=0.369) was considered sufficient to mimic the impact of snow insulation, which in turn allowed proper estimates of the effective temperature sensed by the crop during the effective period of vernalization. Based on existing snow model (Jego et al., 2014) and the recorded data (Fig. 1), "0°C" was considered a robust and coherent threshold. It was furthermore to constrain the regressions through the origins [0,0]. The slope of the trend on records reported in the upper right quadrant of Fig. S1 was quite logically forced to 1, while the slope of the trend on records reported in the lower left quadrant was fit through automatic regression, resulting in a coefficient of 0.165.

2.4. Crop model inversion

2.4.1. The DREAM sampling algorithm

Since the works of Metropolis (Metropolis et al., 1953) and later Hastings (1970), Bayesian approaches have greatly improved to sample the most relevant parameter posterior distribution, notably through the use of Markov Chain Monte Carlo (MCMC) simulations (Metropolis et al., 1953). While a lot of research was devoted to improve Metropolis-Hastings approach up to the late 1990's,

299 algorithms remained long inefficient when confronted with very heavy tails posterior distribution and
300 with posterior model output prediction surfaces that contained multiple local optima. Based on Ter
301 Braak's work (2006), research was conducted that successively lifted the different limitations and
302 enhanced considerably the efficiency of Bayesian MCMC genetic sampling procedures. The
303 Differential Evolution Adaptive Metropolis (DREAM) algorithm developed by Vrugt et al. (2009) is a
304 follow-up of the DE-MC method (Ter Braak, 2006), and integrates the advantages of the Shuffled
305 Complex Evolution Metropolis (SCEM-UA) global optimization algorithm (Vrugt et al., 2003).
306 The DREAM algorithm is probably one of the most advanced MCMC algorithms. Detailed descriptions
307 of the DREAM algorithm have been published, e.g. in Vrugt et al. (2009) and Vrugt (2016). Recently,
308 Dumont et al. (2014) coupled for the first time the DREAM algorithm with a complex crop model
309 (STICS in this case). This section presents a summary of the algorithm but we refer to papers for a
310 detailed description.
311
312 The advantages of DREAM are summarized here:
313 - DREAM incorporates a self-adaptive randomized subspace sampling routine;
314 - It can maintain a detailed balance and ergodicity that has proven effective to accommodate a
315 heavy-tailed and multimodal target;
316 - It solves limitations such as the need to choose the starting values and the unlimited number
317 of parameters that could be optimized at the same time;
318 - By integrating a formal approach to specify the likelihood function and explicitly consider the
319 residual errors statistical model, DREAM allows separation of behavioural solutions from
320 non-behavioural ones.
321 The last characteristic has been proven particularly effective in the case of crop model parameter
322 sampling (Dumont et al., 2014). Indeed, in agricultural research, the (model) errors are most of the
323 time correlated, non-stationary and non-Gaussian. As stated by Wallach et al. (2006), site-year
324 characteristics have a strong influence on observations and observations/model errors. When several

measurements are performed at different dates in a given site-year, observations and (model) residuals will most often be auto-correlated.

2.4.2. Sampling procedure

With regard to the DREAM options, the toolbox ran a maximum of 5,000 evaluation functions multiplied by the number of sampled parameters. Preliminary tests concluded that convergence was easily ensured with such a rule. The number of Markov chains was fixed at two times the number of parameters to be sampled, following Vrugt et al. (2009). Following the observation made by Dumont et al. (2014), to improve the convergence of the algorithm when coupled with a crop model, a standard error was considered on recorded data to compute the likelihood function. It was decided to use a fixed sigma of 5 days, which is among the greatest standard error generally observed at BBCH 65 due to the temporal sprawl of the flowering stage. Other options of the DREAM toolbox were kept as the original release.

The initial values and the prior distribution were determined as specified in Table 1, based on parameters as defined within the STICS model, literature review (Table S1) or expert knowledge. Other parameters of the phenology model were kept at a fixed value: DT_{opt} and DT_{max} were respectively fixed at 35 and 45°C, and VV_{min} was fixed at 1 equivalent-day

Table 1 : Table of the parameter being optimised

Parameter	*Initial value*	*A priori*	Origin of the initial value
DT_{min}	0	[0 - 15]	Grassland / Wheat STICS parameter
VV_{req}	35	[20 - 100]	Grassland STICS parameter
T_{vern}	5	[-5 - 15]	Ryegrass STICS parameter
$Ampli_{vern}$	7.5	[1 - 20]	Ryegrass STICS parameter
$PhotoP_{base}$	8	[1 - 12]	Grassland / Wheat STICS parameter
$PhotoP_{sat}$	20	[13 - 24]	Grassland / Wheat STICS parameter
$\Sigma UPVT_{BBCH30}$	215	[0 - 600]	Preliminary test
$\Sigma UPVT_{BBCH39}$	345	[200 - 1000]	Preliminary test
$\Sigma UPVT_{BBCH65}$	700	[400 - 1200]	Preliminary test
$\Sigma UPVT_{BBCH89}$	1500	[800 - 2000]	Preliminary test

2.4.3. Data analysis and parameter uncertainty

Assessing the posterior distribution of the model parameters using MCMC simulations, as performed with DREAM, lead to several chains that contained all the necessary information about model parameters.

We first analyzed the marginal posterior distribution function (PDF) to retrieve the main information regarding sampled parameters, i.e. the posterior means, medians, the main percentiles. We furthermore looked at the correlation coefficients between the generated parameter samples. To do so, the last 500 values of each chain, where stationarity had been achieved, were kept to process data.

To further use the crop model as research or decision-support tools, it is necessary to summarize the marginal posterior probability distribution function (PDF) in one parameter estimate. A first solution would be to select, among the chains, the parameter set that offers the optimal solution, i.e. the one that optimizes the convergence criterion. However, provided convergence has achieved a stationary distribution, from a statistical/methodological point of view, the information contained in each chain

has statistically the same relevance. It was therefore decided to use the medians of the distributions to evaluate the overall model performance.

2.4.4. Assessment of model performance

There is a need to define criteria that will help determine whether or not a model is 'acceptable', in pursuit of set objectives and its ability to represent reality (Loague and Green, 1991). Three main statistical criteria were used to assess model performance namely the root mean square error (RMSE), the model efficiency (EF) and the normalized deviation (ND). These criteria are defined in equations 9, 10 and 11.

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2} \quad \textbf{Eq. 9}$$

$$EF = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y})^2} \quad \textbf{Eq. 10}$$

$$ND = \frac{\sum_{i=1}^{n}(\hat{y}_i) - \sum_{i=1}^{n}(y_i)}{\sum_{i=1}^{n}(y_i)} \quad \textbf{Eq. 11}$$

In these equations, n is the number of observations, y_i is the ith observation, $\bar{y}$ is the average of observation and $\hat{y}_i$ is the simulated value corresponding to the ith observation.

RMSE, EF and ND are rarely used alone for evaluating model quality. Different authors (Beaudoin et al., 2008; Brisson et al., 2002; Dumont et al., 2014) used RMSE, EF and ND jointly, on the basis that model calibration or validation is accurate if the RMSE is relatively low compared with the mean of the observations, and if EF >0.5 and |ND|<0.1

2.4.5. Iterative process-based modelling approach

The crop model-based approach was used to pursue a two-fold objective

- First, following the literature regarding IWG (Mitchell et al., 1998, Ivancic et al, under review), the added-value of improving the temperature-driven phenological model with vernalization and photoperiod processes was assessed. Each process was activated sequentially. At each step, all model parameters related to the respectively activated formalisms were optimized on all site-year combinations (Table S2), including the data sets

dedicated to validation. However, the data treatment was only focused on the global model performance. The idea driving this phase was to determine whether or not IWG phenological modelling demonstrated sensitivity to these processes, which would in turn corroborate the findings of field and controlled experiments.

- In a second phase, once the sensitivity of IWG phenological modelling to vernalization and photoperiod was determined, an actual calibration/validation process was launched. All relevant parameters were considered for sampling. In this second phase, data sets were respectively dedicated to either calibration or validation, as per Table S2. The objective of this phase was to create additional knowledge on IWG phenological development, by retrieving the most probable value of the parameters controlling the developmental processes.

2.5. Software availability

The software programs (this phenological model and DREAM) are libraries of Matlab® functions. The full version of the current release of the STICS soil-crop model is accessible at https://www6.paca.inrae.fr/stics_eng/. The functions of the phenological model presented in this paper, which shares similarities with the STICS model, can be obtained by contacting the authors (benjamin.dumont@uliege.be). The DREAM source codes were obtained from the developer (jasper@uci.edu). Interested users should contact him directly.

405 # 3. Results

406 ## 3.1. Growing-degree day accumulation to flowering from February 1 base 0°C

407 **Table 2.** Growing degree day accumulation from February 1 to flowering (base 0)

Regions and climate type	GDD accumulation range	Mean (different letters denote statistical differences across means)
Europe, Cfb climate	1527-1885	1628.9c
Canada, Dfb climate	952-1379	1160.2a
USA, Dfa climate	1234-1610	1436.5b

408

409 Computing GDD accumulation from Feb 01 to flowering (using the simpler formalization of eq. 1 and
410 2) demonstrates a large variability (from 952 to 1885) between fields and years. These values cover
411 most of the GDD range proposed by Cruz et al. (2010), hence belonging either to *early, medium,* or
412 *late forage grass species.* Meanwhile, values are however clustered by growth regions. European
413 conditions (Cfb Koppen climate classification) show the highest GDD values, while Canadian
414 conditions (Dfb) represent the lowest and USA (Dfa) provides intermediate values. Therefore, GDD
415 values are more likely relevant at a given regional scale to identify a plant growth pattern within the
416 region, rather than useful to characterize the overall plant phenological drivers. This latter
417 consideration highlights the need for more refined tools to simulate and evaluate IWG phenological
418 growth.

419

420 ## 3.2. IWG sensitivity to vernalization and photoperiod induction processes

421

422 First, the crop model approach (including an intermediate step of parameter sampling) was used to
423 determine whether or not the temperature-driven phenological model would benefit from the
424 vernalization and photoperiod response processes to reproduce the observations. Table 3 reports
425 the overall model performances. The poor performance of the sole GDD_t formalization confirms

results presented at previous section. Adding the sole photoperiodic effect (SFP) did not improve sufficiently the model performance; RMSE was marginally decreased and model efficiency remained below the 0.5 threshold. The greatest improvement to model performance appeared when the vernalization process was activated (SFV). As observed, RMSE reached 10.06 days and model efficiency increased up to 0.97. Finally activating the photoperiod response function in addition to the SFV provided an additional improvement in model performance, with the RMSE dropping to 7.5 days and model efficiency increasing slightly (0.98). At each step, a value of ND close to 0 is showing the algorithm tendency to avoid any under or overestimation (minimization of RMSE).

Table 3. Overall model performances considering the two induction processes

Model formalism	Model Performance		
	RMSE	EF	ND
GDD_t	57.49	-0.06	0.00
$GDD_t \times SFP$	48.95	0.23	0.00
$GDD_t \times SFV$	10.06	0.97	0.00
$GDD_t \times SFV \times SFP$	7.68	0.98	0.00

3.3. Posterior distribution of crop parameters and model validation

Table 4 summarizes the main descriptor of the posterior distribution function of the different parameters, namely the best parameter set, the median parameter set and its 10%-90% confidence interval. Table S3 presents the correlation matrix between the parameters.

Table 4. Descriptor of the posterior distribution function

Parameter	*Best*	*Median*	*CI [10%-90%]*
DT_{min}	0.35	0.49	[0.059 - 1.002]
VV_{req}	71.90	66.97	[36.116 - 79.378]
T_{vern}	4.64	4.49	[2.94 - 5.387]
$Ampli_{vern}$	7.43	7.09	[5.296 - 8.452]
$PhotoP_{base}$	9.65	9.99	[9.369 - 10.821]
$PhotoP_{sat}$	17.90	17.33	[15.687 - 22.336]
$\Sigma UPVT_{BBCH30}$	212.26	191.26	[127.534 - 260.885]
$\Sigma UPVT_{BBCH39}$	392.14	413.15	[282.854 - 537.153]
$\Sigma UPVT_{BBCH65}$	859.03	877.51	[601.251 - 1112.863]
$\Sigma UPVT_{BBCH89}$	1585.56	1622.31	[1354.823 - 1865.226]

Among the parameters optimized, DT_{min} tends towards "0" indicating that no growth is achieved below this value, as found in other crops and grasses. T_{vern} indicates the optimal vernalization temperature is reached around 4.6°C, which tends to be similar or lower than other temperate forage grasses or annual grain crops. $Ampli_{vern}$ indicated that vernalizing conditions are (partially) met between ~-2.8 and ~+12°C. The total cold requirements (VV_{req}) were found to be equal to 58 days, which would be a more grass-like type (Table S1), since most annual grain crops are capable of vernalization with shorter cold periods. However, it is worth mentioning that some annual cultivars of winter wheat might require a similar amount of vernalizing days (Gate, 1995). Finally, we found that photoperiod was unlocked starting at 9.7 hours and would not be limiting anymore over 17.9 hours of daylength. This daylength range implies that the SFP formalism takes a value of 0.5 around 11.8h daylength, and 1 at 13.8h daylength. Overall, the optimized parameters confirm the relevance of a temperature-daylength coupled formalism to represent IWG phenological development under various growing conditions.

The correlation matrix (Table S3) indicates the level of correlation between parameters during the optimization process. A strong interdependency is observed between the sums of UPVT, which are also strongly correlated to $PhotoP_{sat}$. The limited contrast on upper photoperiod values in the dataset

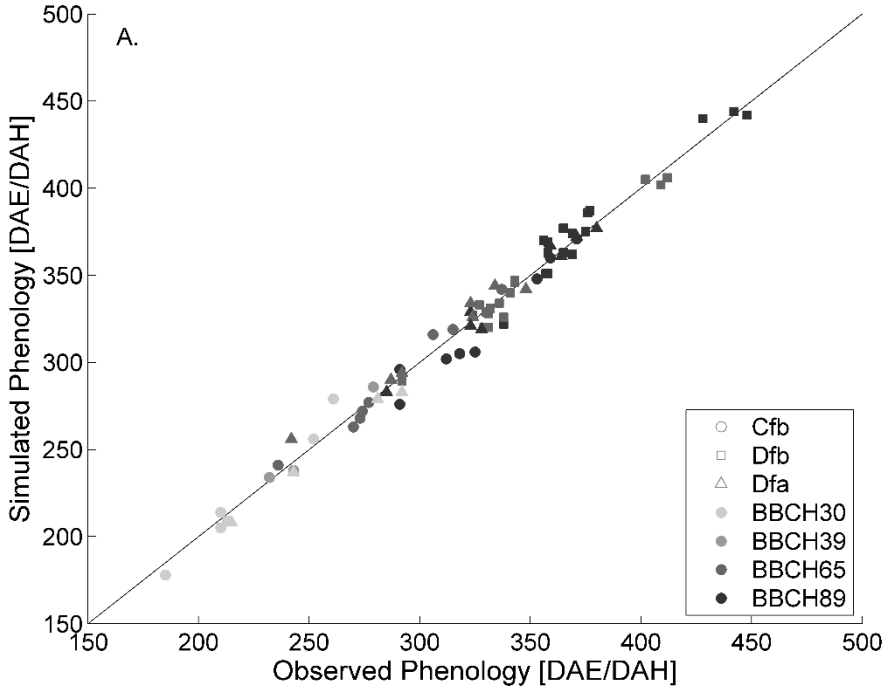
462 generates uncertainty on the parameter $PhotoP_{sat}$, that leads to lower reliability on the different
463 ΣUPVT due to the high correlation of both parameters. This might be solved by integrating new
464 observations gathered at Northern sites (e.g. Sweden), to precisely determine the saturation upper
465 limit of the photoperiod effect.
466 The model exhibited high performance both under calibration and validation datasets (Fig. 1 and
467 Table 5). The RMSE were respectively of 7.7 and 7.8 days, which respectively corresponded to a 2.4%
468 and 2.5% RRMSE (RMSE relative to the average of respective observations) in both cases. Model
469 efficiencies were close to 1, which is the upper theoretical threshold, indicative of a near perfect fit
470 of the model against observations. Finally, the normalized deviations, which indicate the tendency to
471 over- or underestimate observations, were very close to "0" and far below the 0.1 acceptance
472 threshold. As can be seen in Fig. 3, the simulated phenology (DAE/DAH at which the stage is
473 supposed to occur) is almost perfectly aligned on the 1:1 line with the observed phenology.

474 **Table 5:** Model performances under the calibration and validation steps

Criteria	*Calibration*	*Validation*
RMSE	7.562	8.401
EF	0.982	0.978
ND	-0.001	0.010

475

476



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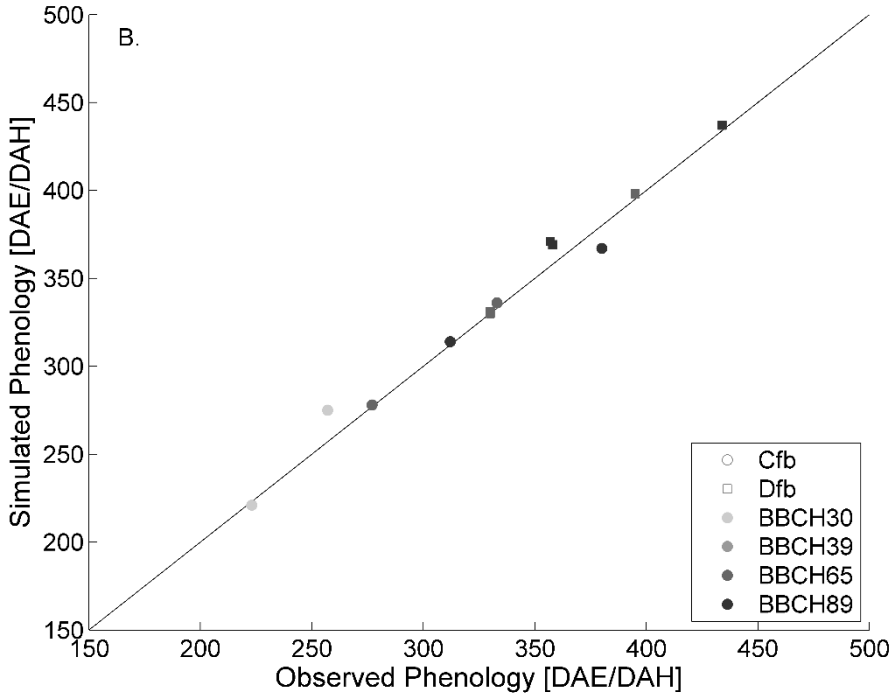


478

479 **Figure 1:** Observed and simulated phenology for the calibration (A) and validation (B) datasets. Climate type Cfb is
480 represented by circles (o), climate type Dfb is represented by squares (□) and climate type Dfa is represented by triangle
481 (Δ). Intensity of grey varies with simulated crop stage in BBCH scale, with lighter grey being stem extension (BBCH 30) and
482 darker grey being maturity (BBCH 89).

483

3.4. Development dynamics from different sites and limiting environmental conditions

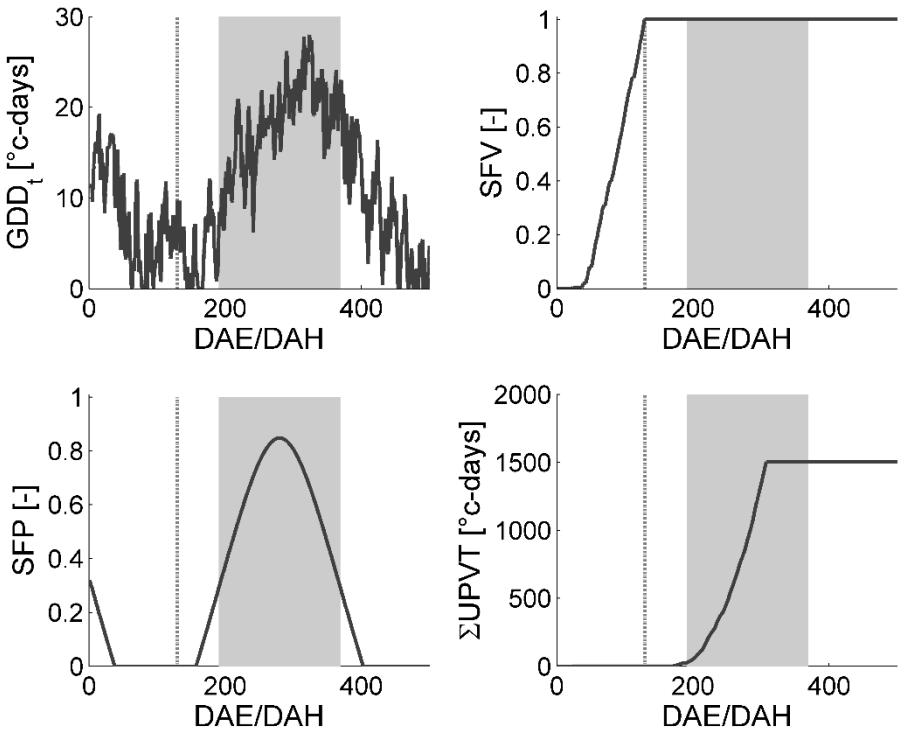
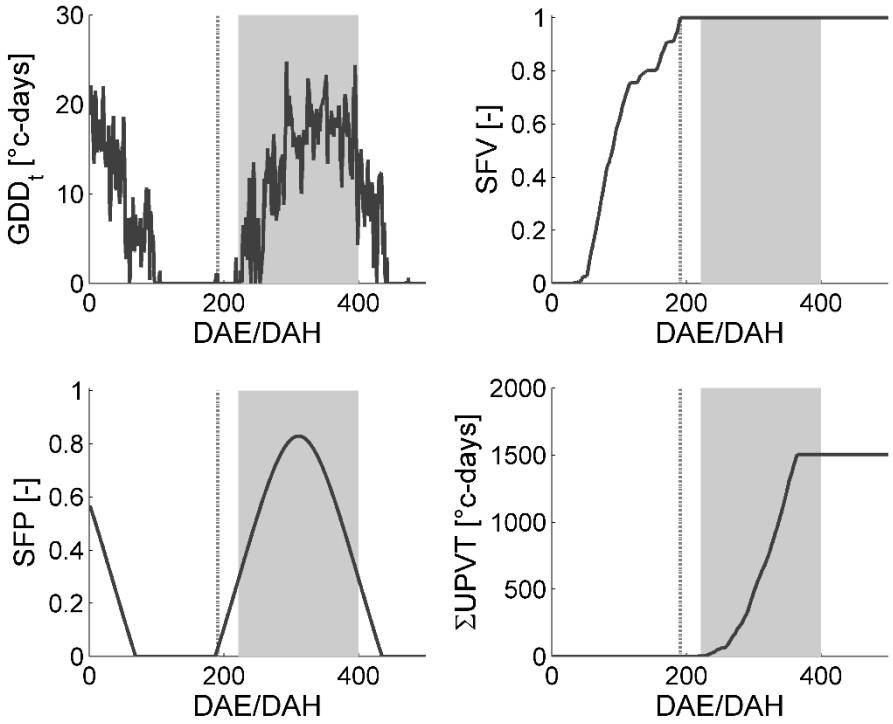


Figure 2: Simulated GDD_t (Growing-Degree-Day), SFV (Slowdown Factor accounting for Vernalization), SFP (Slowdown Factor accounting for Photoperiod) and UPVT (Photo-Vernalo-Thermic Units) for the Maubec French site (validation site) over the season 2018 (establishment year). Light grey dashed line represents the day where cold requirement is fully met. Light grey shaded area represents the period for which SFP is greater than 0.3 (>11h daylength). UPVT accumulation was stopped when maturity was reached.



491

492 **Figure 3:** Simulated GDD_t (Growing-Degree-Day), SFV (Slowdown Factor accounting for Vernalization), SFP (Slowdown
493 Factor accounting for Photoperiod) and UPVT (Photo-Vernalo-Thermic Units) for the Carman-LN Canadian site (validation
494 site) over the season 2017 (second growing year). Light grey dashed line represent the day where cold requirement is fully
495 met. Light grey shaded area represent period for which SFP is greater than 0.3 (>11h daylength). UPVT accumulation was
496 stopped when maturity was reached.

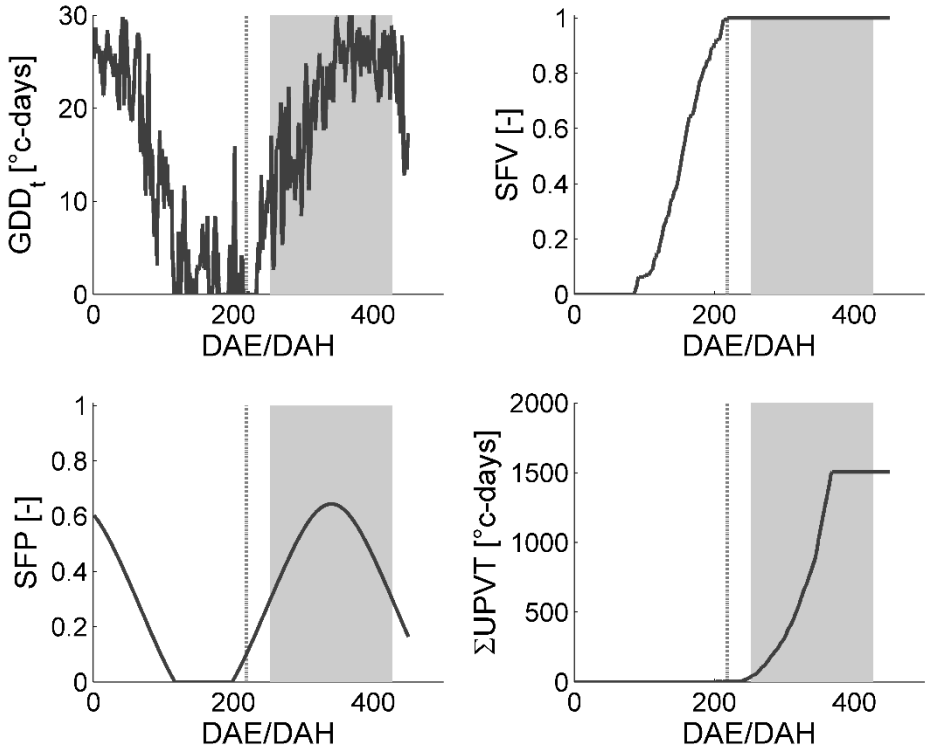


Figure 4: Simulated GDD_t (Growing-Degree-Day), SFV (Slowdown Factor accounting for Vernalization), SFP (Slowdown Factor accounting for Photoperiod) and UPVT (Photo-Vernalo-Thermic Units) for the Salina US site (calibration site) over the season 2017 (second growing year). Light grey dashed line represents the day where cold requirements is fully met. Light grey shaded area represents the period for which SFP is greater than 0.3 (>11h daylength). UPVT accumulation was stopped when maturity was reached.

Comparing the two validation sites (Maubec-18: Cfb climate, and Carman-LN-17: Dfb climate) and one calibration site (Salina: Dfa climate), the dynamic of UPVT accumulation is expressing the combined status of the SFV, SFP and GDD parameters. The period of UPVT accumulation between sites indicates the development of reproductive growth of *Th. intermedium,* which correspond to the progression from BBCH30 to BBCH89 stages.

- Under Cfb climate (temperate European conditions, e.g. Maubec-18, Fig. 2), fulfillment of vernalization requirements was reached in early January (~140 DAE) after around 90 days of SFV accumulation. However, UPVT accumulation encompasses a period of about 110 days corresponding to the period between March and July. Despite early GDD accumulation, the

SFP coefficient was below 0.3 (<11h daylength) until 200 DAE (mid-March), strongly limiting UPVT accumulation. This would represent a period of about two months between vernalization achievement and significant reproductive growth, which means early development and secondary induction of *Th. intermedium* was limited by the photoperiod mediation and short daylength.

- Under Dfb climate (Canadian conditions, e.g. Carman-LN-17, Fig. 3), fulfillment of vernalization requirements was reached in March (~190 DAH) after around 140 days of SFV accumulation. UPVT accumulation encompasses a period of about 150 days corresponding to the period between April and September. This start of reproductive growth corresponds to both the start of GDD accumulation and the increased daylength (>11h, grey zones in the figure 6.) In other words, *Th. intermedium* early development (prior to April) would have been limited by both GDD and short daylength, indicating a notable temperature-daylength coupling.
- Under Dfa climate (continental US conditions, e.g. Salina-19, Fig. 4): fulfillment of vernalization requirements was also reached in March (~210 DAH) after around 120 days of SFV accumulation. UPVT accumulation encompasses a period of about 130 days corresponding to the period between April and July. The start of reproductive growth corresponds to the increased daylength (>11h, grey zones in Fig 7.), while GDD was never the limiting factor. In other words, *Th. intermedium* early development would have been mostly limited by short daylengths.

4. Discussion

4.1. Tiller primordia induction (primary induction)

Th. intermedium appears to be highly dependent on the vernalizing process. The requirements for low temperatures (LT) is almost mandatory for tiller induction, but our study was not calibrated to uncover the potential influence of contrasted daylength (SD-LD) on these requirements. With

538 vernalizing temperatures between -2.8 and 12 °C (optimum at 4.6°C ; in keeping with Ivancic et al.,
539 *under review* ; Table 4), LT requirements are similar to winter cereal grain crops and other
540 vernalizing cool-season grasses (*Lolium perenne, Festuca pratensis, Poa pratensis, Agrostis capillaris)*
541 (Table S1), although certain species would have greater vernalizing success than IWG under cooler
542 temperatures (e.g. *Dactylis glomerata, Bromus inermis),* shorter periods of exposure (annual grains),
543 or longer periods of exposure (other perennial grasses). Depending on climatic conditions, earliness
544 of vernalization fulfillment might differ significantly and substantially influence dormancy break.
545 Considering the large and general trend where LD increase LT requirements (if not inhibiting) in
546 various vernalizing grasses, we can hypothesize that *Th. intermedium* would behave similarly (Heide,
547 1987, 1984) and might require an increased vernalization treatment under longer daylengths.
548
549 Interestingly, no significant discrepancy was observed at the sward level in the phenology model
550 between the different germplasm origins (TLI, UMN) and breeding cycles tested (TLI-C3, C4, C5).
551 Among the populations considered, it is notable that the Canadian sites grew experimental
552 populations that were *de facto* selected for increased winter survival capacity (Cattani, 2017; Cattani
553 and Asselin, 2018b). Therefore, their similar fitness with respect to the phenology model indicates
554 that either: i) cold tolerance of *Th. intermedium* may not be tightly linked to the vernalization
555 process (Seppänen et al., 2013); and/or ii) differences in vernalizing requirements were too subtle to
556 be detected; and/or iii) the integration of winter snow-cover into the model, and the induced air
557 temperature corrections, masks a potential discrepancy.
558
559 ### 4.2. Tiller growth and flowering (secondary induction)
560 Following vernalization achievement, the accumulation of heat units (GDD base 0 ; Table 4) that
561 triggers break of dormancy, plant growth and flowering were strongly associated with a photoperiod-
562 mediated process (Fig. 5). Such daylength induction confirms that primary induction must be
563 followed by a secondary induction - including daylength responsiveness - that starts the reproductive

564 growth period (stem elongation and flowering). Across all sites and years, initiation of anthesis was
565 observed between June 14 and July 2. In spite of the contrasted growing conditions and accumulated
566 GDD reported in Table 2, this relatively synchronized flowering period, would confirm the influence
567 of photoperiod regulation on growth rate and demonstrate the misrepresentation of GDD concept
568 alone to explain *Th. intermedium* phenological development in the various growing regions.
569 Such a photoperiod mediation process is widely known and observed in forage grasses and cereal
570 grains, but the degree of sensitivity varies. The proposed phenological model indicates the potential
571 for reproductive growth between 9.7 and 17.9h daylength (Table 4), but we noted that new
572 observations on Northern regions would likely lower the saturation upper limit of the photoperiod
573 effect. According to the demonstration of UPVT accumulation (Fig 2, 3, 4), plant phenological
574 development from BBCH30 generally began around 11h of daylength. Earlier development was
575 however possible with temperatures above 0°C, but was strongly limited due to the combination of
576 low GDD and SFPI coefficient <0.3, or may have resulted in vegetative growth rather than
577 reproductive tiller development. Between 13 and 14h daylengths, plant development was not
578 limited by the photoperiodic response and was fully associated with GDD accumulation.
579

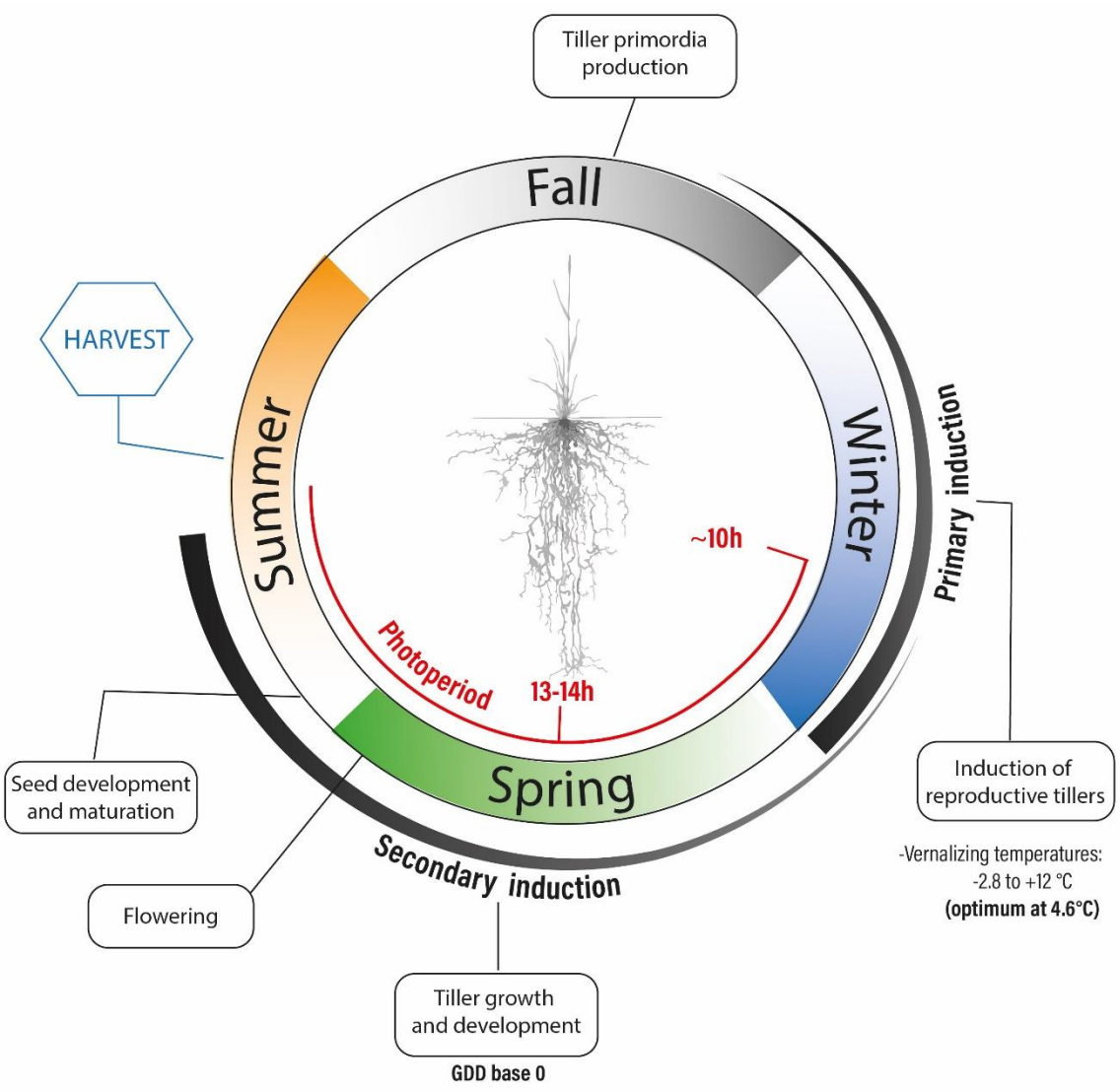


Figure 5: *Thinopyrum intermedium* phenological development milestones and environmental drivers. (with colors)

4.3. Tiller elongation: a crucial context-dependent trait to manage production

In production fields, flowering earliness is a critical factor since it provides a good representation of the whole growth cycle timing and stages (Ansquer et al., 2009a), driving the field operations agenda (e.g. fertilization). In spite of the variability of flowering earliness due to different growth rates and stem elongation, particularly influenced by N availability, the calculation of GDD under similar climatic and daylength contexts has been demonstrated as a robust method to predict flowering periods of different cool-season forage grasses (Ansquer et al., 2009a). Therefore, it has been

590 accepted as one of the main criteria that distinguish different plant growth strategies under similar
591 situations and low-input systems (Ansquer et al., 2009a; Cruz et al., 2010; Duru et al., 2009).
592
593 Under French and Belgium temperate conditions, GDD calculation until flowering (Table 2) indicate
594 that *Th. intermedium* belongs to the slow-growing and more 'conservative' plants commonly found in
595 these regions (e.g. *Brachypodium sp., Agropyron sp., Deschampsia cespitosa, Phleum pratense)*
596 compared to earlier plants (*e.g. Alopecurus pratense, Lolium perenne, Festuca pratense).* These later
597 flowering species are generally characterized by taller stands, longer leaf lifespan, lower leaf area per
598 mass unit, lower leaf nitrogen concentration and relative growth rate (Ansquer et al., 2009b; Cruz et
599 al., 2010; Duru et al., 2005, 1995; Ryser and Lambers, 1995). In low input fields, slow establishment
600 and a slow growing canopy can result in weed infestations and poor grain filling in dry conditions in
601 late summer. As a result, slow-growing species like IWG may be better suited to higher altitude fields
602 or higher latitude situations often characterized by delayed growth season.
603
604 On the other hand, the *Th. intermedium* flowering period in the North American continental context
605 might be seen as relatively early (lower GDD accumulation) compared to warm-season grasses
606 *Panicum virgatum*, *Andropogon gerardii* and *Sorghastrum nutans* commonly found under harsh
607 growing conditions of the *Northern Great Plains Tallgrass Prairie*. Those species are described as very
608 conservative, capable of high biomass production and very efficient in nitrogen recycling and use
609 (Friesen and Cattani, 2017). Conversely, *Th. intermedium* would require higher nitrogen
610 concentration and require more nitrogen availability to ensure optimal reproductive growth under
611 similar conditions. Compared to warm-season grasses, the more acquisitive traits of *Th. intermedium*
612 would be favorable to quicker plant growth and establishment in fields in situations of suitable
613 resource availability.
614

If vernalization is more quickly achieved under Cfb climate, the timing of secondary induction relative to the loss of cold hardiness in the spring could be the difference in observed response between Western Europe and the Northern Great Plains of North America and its continental climate. If a plant loses its cold acclimation and the plant has yet to reach the inductive day length (or gdd accumulation combination), nutrients and water may be used for new vegetative tiller recruitment. Internode elongation will be both energy and water demanding. When induction conditions are met, nutrients (including water) may be diverted from reproductive growth to support excessive vegetative growth, reducing seed yield. Thus, timing of secondary induction and spring regrowth will be critical to optimizing the response to fertilization. For instance, if dormancy is broken and growth begins potentially in February (in France) and the flowering response is primarily to longer days (>13hr daylength), the pre-reproductive growth will be much longer duration than in Manitoba, Canada, where cold tolerance and dormancy will still be intact at that time of year. Therefore, growth will appear to be quicker in Manitoba as less time, if any, elapses between the resumption of growth in the spring and the onset of reproductive growth.

Under situations with prolonged non-reproductive growth after winter time, as observed in western European conditions, the ability of other species to respond to early fertility boost and grow reproductively may provide an advantage to weed species, e.g. perennial ryegrass (*Lolium perenne*). Selection for earlier flowering in these growth environments, potentially achieved though different and possibly interrelated methods (e.g. reducing phyllochron through reduced leaf length and appearance rate, or by altering daylength requirements) would then alter this timing relationship, and should move anthesis earlier in the growing season and potentially reduce the stressful influences from a later secondary induction timing. Extreme heat during anthesis, as experienced in France in 2019, is an excellent example of the risks of later flowering that can exacerbate already reduced grain yields of this new perennial crop.

640 The flowering induction process is critical to understanding environmental requirements that support
641 *Th. intermedium* reproductive growth, however it is primarily relevant when linked to flowering and
642 reproductive growth rate traits within a specific growth situation. The understanding of the
643 phenology will therefore inform agronomic practices.
644

645 ### 4.4. Scaling up the use of *Th. intermedium* grain production by designing and pairing
646 ecotypes with geographies for optimized flowering induction

647 Model compliance is based on IWG overall sward growth, without taking inter- and intra-individual
648 heterogeneity into account. However, individual discrepancy in flowering period has been observed
649 within fields. The observation of slower tillers, with delayed heading and flowering, calls for further
650 research on axillary bud production and induction, linked to vegetative growth periods and resource
651 availability dynamics. Also, with spring seedings, flowering in summer has been observed without
652 previous winter vernalization, although seed harvest would not be profitable due to the timing and
653 the limited amount of flowering observed. Such heterogeneity is regularly observed in perennial
654 grasses, and might indicate a potential breeding opportunity to develop ideotypes with favorable
655 phenology for specific target populations of environments. In the meantime, the effect of reducing
656 population diversity must be taken into account in order to define appropriate thresholds that
657 maintain the benefits of population diversity in fields (e.g. resilience, longevity). Breeding for a more
658 uniform ideotype may alter plant growth and might expose the crop to other issues not historically
659 associated with the species. For example, greater *Th. intermedium* earliness in breaking in dormancy
660 in the spring carries the risk of injury under later occurring adverse climatic conditions or seed
661 productivity decline (Cattani, 2017). Likewise, breeding toward more acquisitive plant traits
662 associated with quicker growth may also bring new drawbacks such as increased disease problems
663 (increased leaf moisture), reduced longevity or increased susceptibility to drought. More
664 conservative plants typically have higher water use efficiency (De Oliveira et al., 2019, 2018), while
665 acquisitive plants utilize water quickly to grow rapidly.

Influence of management practices such as fertilization illustrates the plasticity of acquisitive-conservative plant functional types in managed growth environments, which potentially can be very different in terms of resource availability, competitive interactions and climatic effects as compared to the native growth habitat of the plant. Among the most studied practices, nitrogen fertilization of forage grasses, was shown to be responsible for improving leaf elongation rate and leaf area (Gastal and Durand, 2000) thus potentially impacting the overall plant growth rate, assimilation, and tillering (Mitchell et al., 1998; Poorter and Remkes, 1990; Shipley, 2006; Simon and Lemaire, 1987). Similarly, the management of defoliation practices might widely influence plant growth, notably due to influence on carbon and nitrogen fluxes and reserves (Ferraro and Oesterheld, 2002; Gastal et al., 2010; Gastal and Lemaire, 2015; Hunter et al., 2020; Medina-Roldán and Bardgett, 2011). The usually large ontogenic plasticity of forage grasses also reinforces the influence of defoliation, which result in disturbed phytomers. According to Nelson (2000), most cool-season grasses demonstrate interrelated vegetative (leaf) growth and tillering, whereas vegetative growth improvement (biomass) generally reduces tillering and lengthens the phyllochron, likely due to increased light interception and competition to the detriment of axillary (tiller) bud activation (Simon and Lemaire, 1987). Thus, significant non-reproductive growth under favorable environmental conditions might ultimately lead to fewer tillers. This would be similar to observed situations under aging (three-four years old), or "sod-bound" *Th. intermedium* stands, where tillering activity is strongly reduced (Hunter et al., 2020; Tautges et al., 2018), and may require strategic canopy disturbance to maintain reproductive tillers. Thus, a large field of research remains open to determine the interactions between agronomic management and directed breeding, with plant plasticity, including reproductive growth rate, timing and intensity, to optimize its reproductive potential.

5. Conclusion

This study shows that introducing a new grain crops from new genotype and ecotype pools requires a broader assessment than only attention towards its yield potential. Here we show that vernalization, followed by GDD-daylength coupled dynamics in spring, drives IWG sward functional changes,

potentially resulting in variable agronomic performances depending on growth environment and cropping system management. Our results highlight the need to develop an integrative research approach combining crop genetics, ecology and agronomy to improve our understanding of our cropping systems as a whole.

6. Acknowledgement

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