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1 Process-based analysis of *Thinopyrum intermedium* phenological development  
2 highlights the importance of dual induction for reproductive growth and agronomic  
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4

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16 **Keywords**

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

18 **Highlights**

- 19
- IWG reproductive growth requires a vernalization treatment
- 20
- In spring, IWG reproductive growth is associated with GDD accumulation and photoperiodic
- 21 response
- 22
- GDD-daylength coupled dynamics drive IWG sward functional changes during reproductive
- 23 growth
- 24
- GDD-daylength coupled dynamics can inform and improve agronomic management.

## 25 Abstract

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

## 40 1. Introduction

41 The wheat-relative intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R.  
42 Dewey) (IWG) is a winter-hardy cool-season perennial grass, which has recently undergone  
43 development as a perennial grain by several breeding programs (Bajgain et al., 2020). Improved IWG  
44 populations have been released by *The Land Institute* (Salina, Kansas, USA) under the trade name  
45 Kernza® (DeHaan et al., 2018). Intermediate wheatgrass can support the transition to agroecological  
46 systems because this perennial crop produces forage and grain for several years with minimal soil  
47 disturbance and associated environmental issues (Duchene et al., 2019; Ryan et al., 2018). Featuring  
48 large and deep roots, year-round soil cover, increased resource use efficiency and an extended  
49 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).

76

77 In winter grain crops and forage grasses, the achievement of primary induction (vernalization) needs  
78 either LT or SD, but sometimes requires both (e.g. *Bromus inermis*), or has a preferential  
79 temperature/photoperiod inductive pathway (e.g. *Phleum nodosum*, *Agrostis canina*; Cooper and  
80 Calder, 1964; Halevy, 1989). Temperature and photoperiod are interactive factors since a change in  
81 one parameter can modify inductive requirements of the other (Halevy, 1989; Heide, 1994; Limin and  
82 Fowler, 2006; Mahfoozi et al., 2000; Ritchie, 1991). However, warm-season perennial grasses (e.g.  
83 *Panicum virgatum*, *Andropogon gerardii*), and certain cool-season species (e.g. *Phleum pratense*) do  
84 not require vernalization to achieve flowering (Table S1). Moreover, population diversity, breeding,  
85 and plant life-history in fields leads to a certain variability or heterogeneity of inductive requirements  
86 among the same species, with the potential formation of cultivars or local ecotypes (Dubcovsky et al.,  
87 2006 Cooper and Calder, 1964; Jokela et al., 2015; Palit et al., 2014). Considering IWG, the need of  
88 primary induction (vernalization treatment) to ensure proper reproductive growth has been shown  
89 previously (Frischknecht, 1959) and has been recently confirmed by field observations and results  
90 from controlled experiments (Ivancic et al, *under review*).

91

92 The transition from winter dormancy to spring growth and flowering (secondary induction) vary  
93 greatly among perennial grasses in terms of timing and environmental requirements (Ansquer et al.,  
94 2009). Flowering earliness generally differentiates fast growing species with generally lower  
95 requirements. Conversely, late maturing species generally require greater heat unit accumulation,  
96 associated with higher phyllochrons, to achieve flowering (Duru et al., 1993, 2008b; Frank and Bauer,  
97 1995). Photoperiod mediation of the growth period is observable in many species, with different  
98 degrees of importance, late flowering and single induction grasses would depend solely on  
99 photoperiod responsiveness (Castro et al., 2011; Esbroeck et al., 2003; Mitchell et al., 1997).  
100 Considering IWG, the role of photoperiod in reproductive growth has been suggested before and

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

103

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

110

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

119

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

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

131

## 132 2. Materials and methods

133 To characterize IWG phenological responses to contrasted growing environments, and compare its  
134 behavior to known perennial grasses or annual grain crops characterized in the literature (section  
135 2.1), a database was constructed with experiments conducted across Western Europe and North  
136 America (section 2.2). In an attempt to better understand crop response to those conditions, field  
137 result analysis was coupled with crop modeling approaches. Classic field result analysis, consisting of  
138 comparing phenological stages and degree-day accumulation starting February 01 (shown to  
139 minimize GDD accumulation variability and corresponding to plant changes in assimilate allocation;  
140 Ansquer et al., 2009; Peacock, 1976), was first conducted (section 2.3). Crop modeling approaches  
141 were then deployed to further ascertain the impacts of vernalization and photoperiod on the  
142 phenological development (section 2.4).

### 143 **2.1. Experimental sites and data collection**

#### 144 [2.1.1. Site description and experimental conditions](#)

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

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

### 153 2.1.2. Data collection

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

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

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

167

## 168 2.2. Growing-degree-day calculation

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

171

$$172 \quad T_{mean}(i) = \frac{T_{max}(i) - T_{min}(i)}{2} \quad \text{Eq. 1}$$

$$173 \quad GDD(i) = T_{mean}(i) - T_{base} \quad \text{Eq. 2}$$

174

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



177 As in Ansquer et al. (2009), and as usually done for perennial crops, the sum of GDD is usually  
178 computed starting Feb. 01 in France. In this paper, the sum of GDD was computed from February, 01  
179 and accumulated up to flowering (BBCH 65). This approach has demonstrated its relevance to  
180 determine grass development milestones (Ansquer et al. 2009 ; Bartholomew and Williams, 2005 ;  
181 Brown et al., 1986 ; Chauvel et al., 2000 ; Frank and Hofmann, 1989 ; Mitchell et al., 1997). Using a  
182 constant base temperature over which any additional degree is accumulated as a temperature  
183 enabling developmental unit is largely used (e.g. Ansquer et al., 2004 ; Cruz et al., 2010 ; Duru et al.,  
184 2008c ; Luo et al. 2011 ; Parthasarathi et al., 2013). Such an approach has been integrated in most  
185 plant growth models (Wang et al., 2017).

186

### 187 **2.3. Crop modelling**

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

#### 191 **2.3.1. Phenological development**

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

197

$$198 \quad UPVT(i) = GDD_t(i) \cdot SFP(i) \cdot SFV(i) \quad \text{Eq. 3}$$

199

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

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

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

### 217 2.3.2. Effect of temperature

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

219

$$\left\{ \begin{array}{ll} GDD_t(i) = 0 & \text{if } T_{mean}(i) \leq DT_{min} \text{ or } T_{mean}(i) \geq DT_{max} \\ GDD_t(i) = T_{mean}(i) - DT_{min} & \text{if } DT_{min} < T_{mean}(i) \leq DT_{opt} \\ GDD_t(i) = \frac{DT_{opt} - DT_{min}}{DT_{opt} - DT_{max}} \cdot (T_{mean}(i) - DT_{max}) & \text{if } DT_{opt} < T_{mean}(i) < DT_{max} \end{array} \right.$$

220 **Eq. 4**

221

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

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

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

### 228 2.3.3. Photoperiod factor

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

232

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

234

235 In which PhotoP<sub>base</sub> is the photoperiod below which there is no development and PhotoP<sub>sat</sub> is the  
236 saturation photoperiod, above which there is no limitation. The second term of Eq.5 ensures that  
237 SFP(i) is mathematically bounded between 0 and 1.

238

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

### 243 2.3.4. Cold requirements

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

249

250 
$$VV(i) = \max\left(1 - \left[\frac{T_{vern} - T_{mean}(i)}{Ampli_{vern}}\right]^2, 0\right) \quad \text{Eq. 6}$$

251

252 
$$\begin{cases} SFV(i) = \frac{[\sum_{j=D_{emer} \text{ or } D_{harv}}^i VV(j)] - VV_{min}}{VV_{req} - VV_{min}} \\ SFV(i) = \max(\min(SFV(i), 1), 0) \end{cases} \quad \text{Eq. 7}$$

253

254

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

261

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

268

269 [2.3.5. Snow cover correction](#)

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

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

281

$$282 \quad \begin{cases} T_{corr}(i) = T_{mean}(i) & \text{if } T_{mean}(i) > 0^{\circ}C \\ T_{corr}(i) = 0.165 \cdot T_{mean}(i) & \text{if } T_{mean}(i) < 0^{\circ}C \end{cases} \quad \text{Eq. 8}$$

283

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

292

## 293 **2.4. Crop model inversion**

### 294 **2.4.1. The DREAM sampling algorithm**

295 Since the works of Metropolis (Metropolis et al., 1953) and later Hastings (1970), Bayesian  
296 approaches have greatly improved to sample the most relevant parameter posterior distribution,  
297 notably through the use of Markov Chain Monte Carlo (MCMC) simulations (Metropolis et al., 1953).  
298 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

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

#### 327 2.4.2. Sampling procedure

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

337

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

342

343 **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

344

345

### 346 2.4.3. Data analysis and parameter uncertainty

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

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

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



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

#### 362 2.4.4. Assessment of model performance

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

$$368 \quad RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2} \quad \text{Eq. 9}$$

$$369 \quad EF = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad \text{Eq. 10}$$

$$370 \quad ND = \frac{\sum_{i=1}^n (\hat{y}_i) - \sum_{i=1}^n (y_i)}{\sum_{i=1}^n (y_i)} \quad \text{Eq. 11}$$

371

372 In these equations,  $n$  is the number of observations,  $y_i$  is the  $i^{\text{th}}$  observation,  $\bar{y}$  is the average of  
373 observation and  $\hat{y}_i$  is the simulated value corresponding to the  $i^{\text{th}}$  observation.

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

#### 378 2.4.5. Iterative process-based modelling approach

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

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

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

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

396

## 397 **2.5. Software availability**

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

404

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

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

434

435 **Table 3.** Overall model performances considering the two induction processes

Model formalism	Model Performance		
	RMSE	EF	ND
GDD <sub>t</sub>	57.49	-0.06	0.00
GDD <sub>t</sub> × SFP	48.95	0.23	0.00
GDD <sub>t</sub> × SFV	10.06	0.97	0.00
GDD <sub>t</sub> × SFV × SFP	7.68	0.98	0.00

436

437

438

### 439 **3.3. Posterior distribution of crop parameters and model validation**

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

443

444 **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]

445

446 Among the parameters optimized,  $DT_{min}$  tends towards “0” indicating that no growth is achieved  
447 below this value, as found in other crops and grasses.  $T_{vern}$  indicates the optimal vernalization  
448 temperature is reached around 4.6°C, which tends to be similar or lower than other temperate  
449 forage grasses or annual grain crops.  $Ampli_{vern}$  indicated that vernalizing conditions are (partially) met  
450 between  $\sim -2.8$  and  $\sim +12^\circ\text{C}$ . The total cold requirements ( $VV_{req}$ ) were found to be equal to 58 days,  
451 which would be a more grass-like type (Table S1), since most annual grain crops are capable of  
452 vernalization with shorter cold periods. However, it is worth mentioning that some annual cultivars  
453 of winter wheat might require a similar amount of vernalizing days (Gate, 1995). Finally, we found  
454 that photoperiod was unlocked starting at 9.7 hours and would not be limiting anymore over 17.9  
455 hours of daylength. This daylength range implies that the SFP formalism takes a value of 0.5 around  
456 11.8h daylength, and 1 at 13.8h daylength. Overall, the optimized parameters confirm the relevance  
457 of a temperature-daylength coupled formalism to represent IWG phenological development under  
458 various growing conditions.

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

462 generates uncertainty on the parameter  $\text{PhotoP}_{\text{sat}}$ , that leads to lower reliability on the different  
463  $\Sigma\text{PVT}$  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.

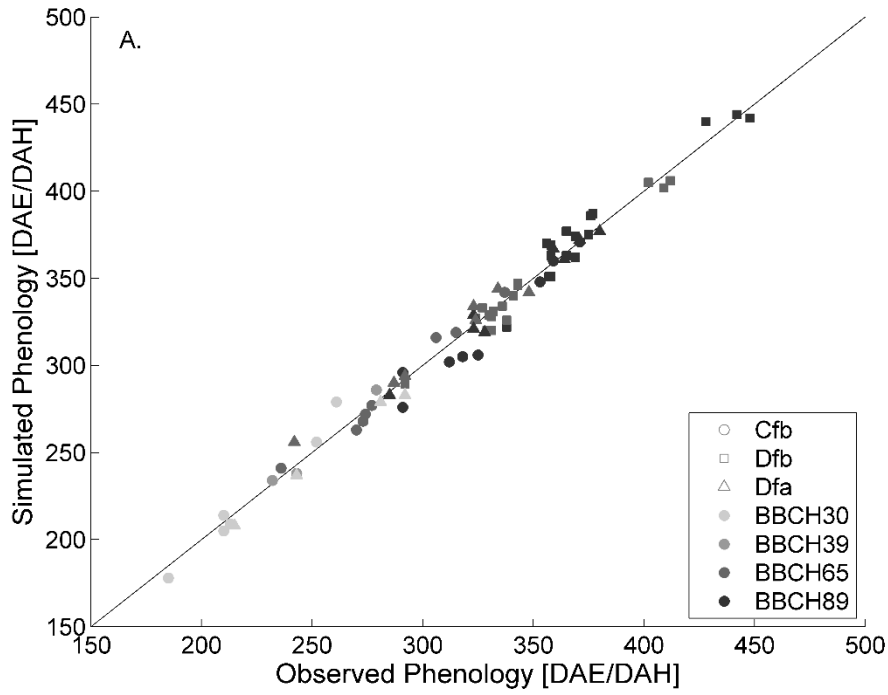
466 The model exhibited high performance both under calibration and validation datasets (Fig. 1 and  
467 Table 5). The RMSE were respectively of 7.7 and 7.8 days, which respectively corresponded to a 2.4%  
468 and 2.5% RRMSE (RMSE relative to the average of respective observations) in both cases. Model  
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

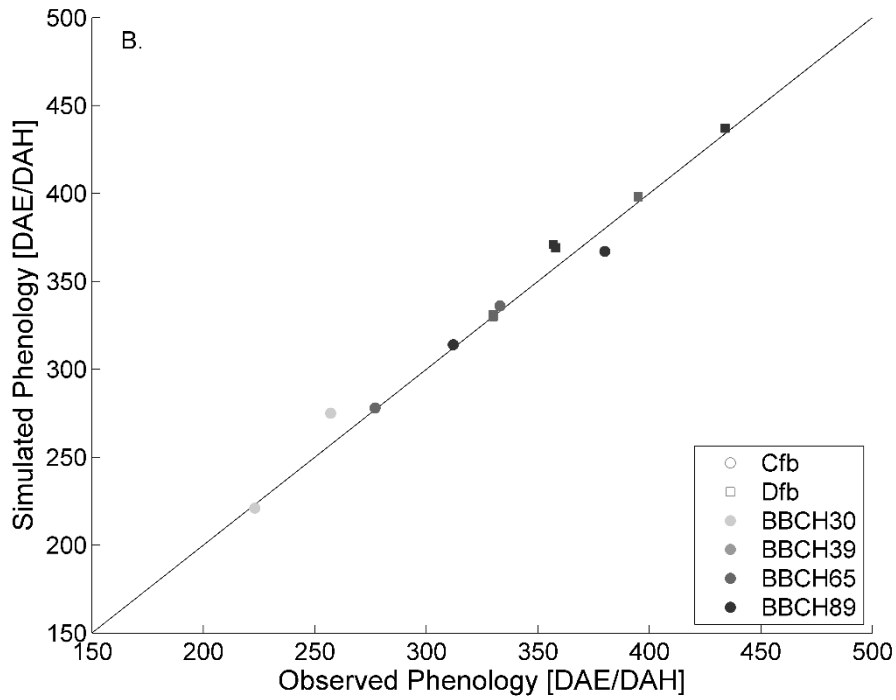
Criteria	<i>Calibration</i>	<i>Validation</i>
RMSE	7.562	8.401
EF	0.982	0.978
ND	-0.001	0.010

475

476



477

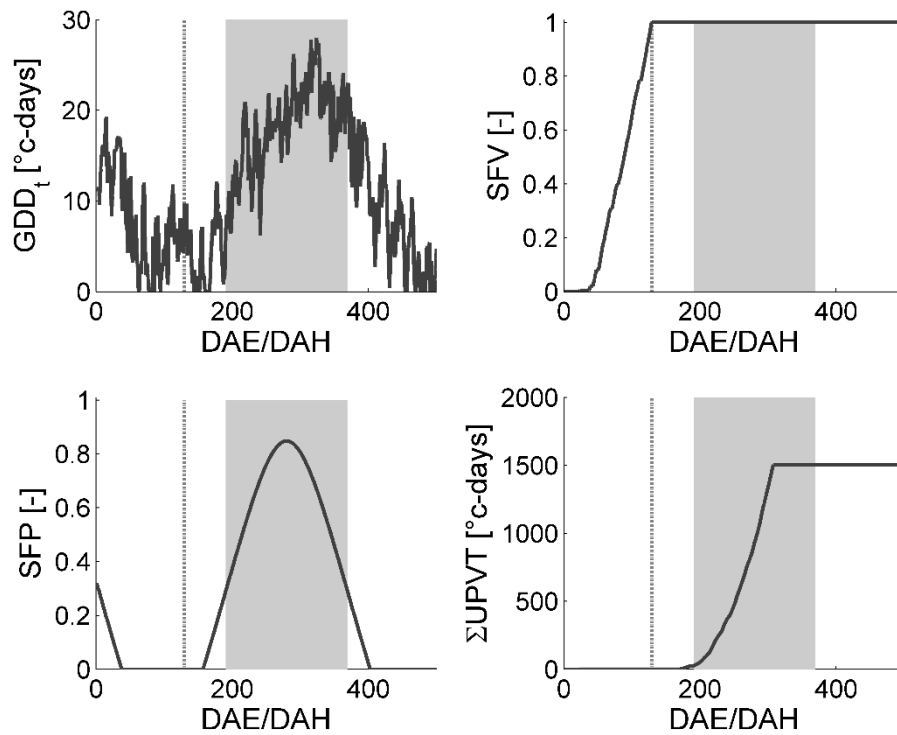


478

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

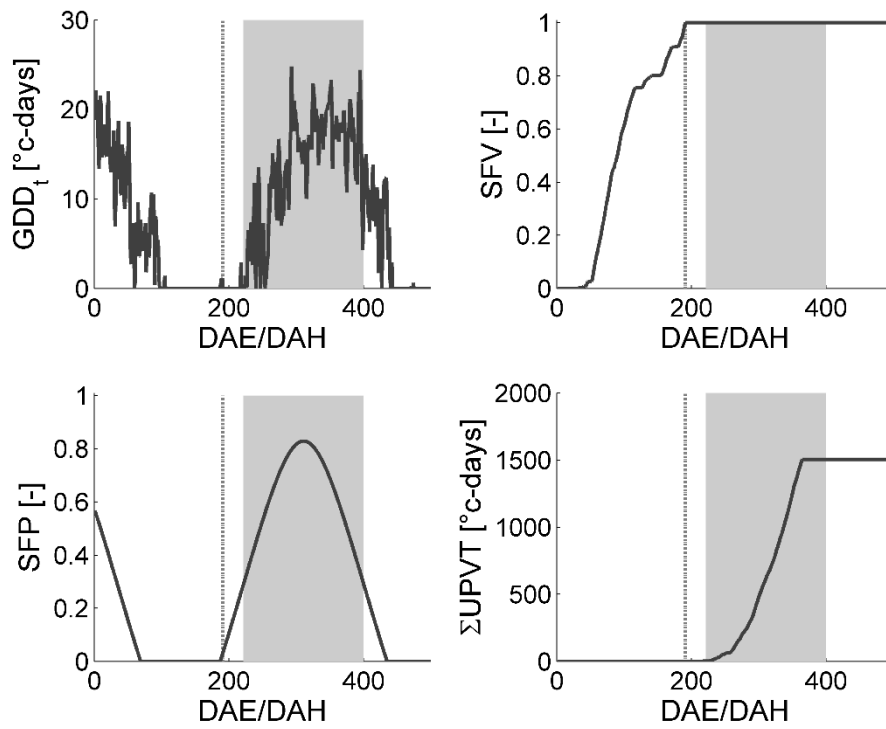
### 3.4. Development dynamics from different sites and limiting environmental conditions



485

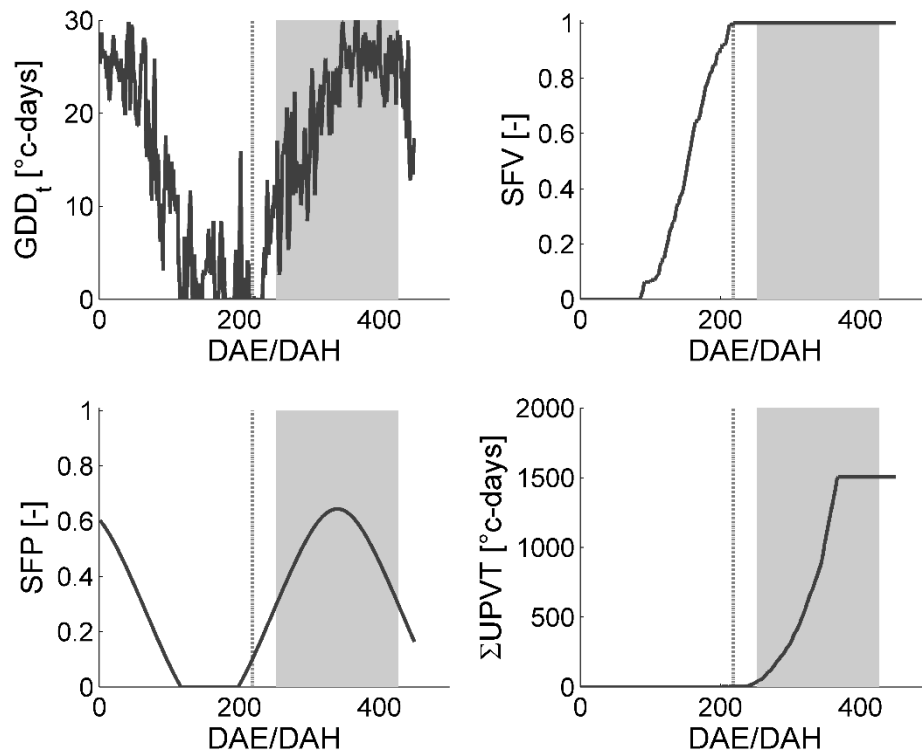
486 **Figure 2:** Simulated  $GDD_t$  (Growing-Degree-Day), SFV (Slowdown Factor accounting for Vernalization), SFP (Slowdown  
 487 Factor accounting for Photoperiod) and UPVT (Photo-Vernalo-Thermic Units) for the Maubec French site (validation site)  
 488 over the season 2018 (establishment year).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



497

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

503

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

509

510

511

512

- 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

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

518 • Under Dfb climate (Canadian conditions, e.g. Carman-LN-17, Fig. 3), fulfillment of  
519 vernalization requirements was reached in March (~190 DAH) after around 140 days of SFV  
520 accumulation. UPVT accumulation encompasses a period of about 150 days corresponding to  
521 the period between April and September. This start of reproductive growth corresponds to  
522 both the start of GDD accumulation and the increased daylength (>11h, grey zones in the  
523 figure 6.) In other words, *Th. intermedium* early development (prior to April) would have  
524 been limited by both GDD and short daylength, indicating a notable temperature-daylength  
525 coupling.

526 • Under Dfa climate (continental US conditions, e.g. Salina-19, Fig. 4): fulfillment of  
527 vernalization requirements was also reached in March (~210 DAH) after around 120 days of  
528 SFV accumulation. UPVT accumulation encompasses a period of about 130 days  
529 corresponding to the period between April and July. The start of reproductive growth  
530 corresponds to the increased daylength (>11h, grey zones in Fig 7.), while GDD was never the  
531 limiting factor. In other words, *Th. intermedium* early development would have been mostly  
532 limited by short daylengths.

## 533 4. Discussion

### 534 4.1. Tiller primordia induction (primary induction)

535 *Th. intermedium* appears to be highly dependent on the vernalizing process. The requirements for  
536 low temperatures (LT) is almost mandatory for tiller induction, but our study was not calibrated to  
537 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

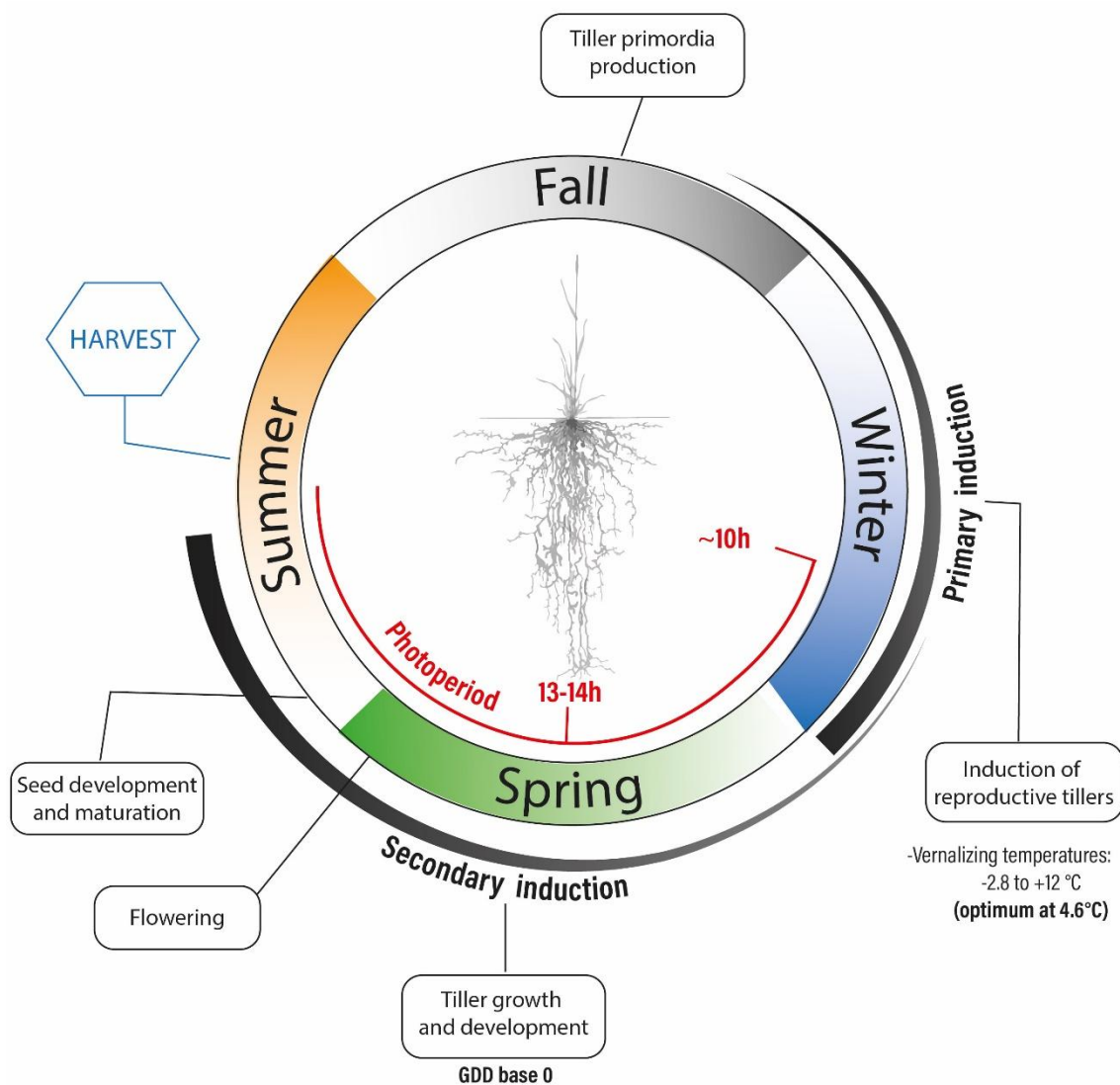
#### 559 4.2. Tiller growth and flowering (secondary induction)

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



580

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

582

583 4.3. Tiller elongation: a crucial context-dependent trait to manage production

584 In production fields, flowering earliness is a critical factor since it provides a good representation of  
 585 the whole growth cycle timing and stages (Ansquer et al., 2009a), driving the field operations agenda  
 586 (e.g. fertilization). In spite of the variability of flowering earliness due to different growth rates and  
 587 stem elongation, particularly influenced by N availability, the calculation of GDD under similar  
 588 climatic and daylength contexts has been demonstrated as a robust method to predict flowering  
 589 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

615 If vernalization is more quickly achieved under Cfb climate, the timing of secondary induction relative  
616 to the loss of cold hardiness in the spring could be the difference in observed response between  
617 Western Europe and the Northern Great Plains of North America and its continental climate. If a  
618 plant loses its cold acclimation and the plant has yet to reach the inductive day length (or gdd  
619 accumulation combination), nutrients and water may be used for new vegetative tiller recruitment.  
620 Internode elongation will be both energy and water demanding. When induction conditions are met,  
621 nutrients (including water) may be diverted from reproductive growth to support excessive  
622 vegetative growth, reducing seed yield. Thus, timing of secondary induction and spring regrowth will  
623 be critical to optimizing the response to fertilization. For instance, if dormancy is broken and growth  
624 begins potentially in February (in France) and the flowering response is primarily to longer days  
625 (>13hr daylength), the pre-reproductive growth will be much longer duration than in Manitoba,  
626 Canada, where cold tolerance and dormancy will still be intact at that time of year. Therefore, growth  
627 will appear to be quicker in Manitoba as less time, if any, elapses between the resumption of growth  
628 in the spring and the onset of reproductive growth.

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

639



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.

666 Influence of management practices such as fertilization illustrates the plasticity of acquisitive-  
667 conservative plant functional types in managed growth environments, which potentially can be very  
668 different in terms of resource availability, competitive interactions and climatic effects as compared  
669 to the native growth habitat of the plant. Among the most studied practices, nitrogen fertilization of  
670 forage grasses, was shown to be responsible for improving leaf elongation rate and leaf area (Gastal  
671 and Durand, 2000) thus potentially impacting the overall plant growth rate, assimilation, and tillering  
672 (Mitchell et al., 1998; Poorter and Remkes, 1990; Shipley, 2006; Simon and Lemaire, 1987). Similarly,  
673 the management of defoliation practices might widely influence plant growth, notably due to  
674 influence on carbon and nitrogen fluxes and reserves (Ferraro and Oesterheld, 2002; Gastal et al.,  
675 2010; Gastal and Lemaire, 2015; Hunter et al., 2020; Medina-Roldán and Bardgett, 2011). The usually  
676 large ontogenic plasticity of forage grasses also reinforces the influence of defoliation, which result in  
677 disturbed phytomers. According to Nelson (2000), most cool-season grasses demonstrate  
678 interrelated vegetative (leaf) growth and tillering, whereas vegetative growth improvement  
679 (biomass) generally reduces tillering and lengthens the phyllochron, likely due to increased light  
680 interception and competition to the detriment of axillary (tiller) bud activation (Simon and Lemaire,  
681 1987). Thus, significant non-reproductive growth under favorable environmental conditions might  
682 ultimately lead to fewer tillers. This would be similar to observed situations under aging (three-four  
683 years old), or “sod-bound” *Th. intermedium* stands, where tillering activity is strongly reduced  
684 (Hunter et al., 2020; Tautges et al., 2018), and may require strategic canopy disturbance to maintain  
685 reproductive tillers. Thus, a large field of research remains open to determine the interactions  
686 between agronomic management and directed breeding, with plant plasticity, including reproductive  
687 growth rate, timing and intensity, to optimize its reproductive potential.

## 688 5. Conclusion

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

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

696

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700

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