1   **Running Head:** Effects of day vs. night warming on phenology

2   **Title:** Three times greater weight of daytime than of nighttime temperature on leaf

3   unfolding phenology in temperate trees

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Abstract

- The phenology of spring leaf unfolding plays a key role in the structure and functioning of ecosystems. The classical concept of heat requirement (growing degree days) for leaf unfolding was developed hundreds of years ago, but this model does not include the recently reported greater importance of daytime than nighttime temperature.

- A manipulative experiment on daytime vs. nighttime warming with saplings of three species of temperate deciduous trees was conducted and a bayesian method was applied to explore the different effects of daytime and nighttime temperatures on spring phenology.

- We found that both daytime and nighttime warming significantly advanced leaf unfolding, but the sensitivities to increased daytime and nighttime temperatures differed significantly. Trees were most sensitive to daytime warming (7.4 ± 0.9, 4.8 ± 0.3 and 4.8 ± 0.2 days advancement per degree Celsius warming (days $°C^{-1}$) for birch, oak and beech, respectively) and least sensitive to nighttime warming (5.5 ± 0.9, 3.3 ± 0.3 and 2.1 ± 0.9 days $°C^{-1}$). Interestingly, a Bayesian analysis found that the impact of daytime temperature on leaf unfolding was approximately three times higher than nighttime temperatures.

- Nighttime global temperature is increasing faster than daytime temperature, so model projections of future spring phenology should incorporate the effects of these different temperatures.

Key words: leaf phenology; climatic warming; daytime and nighttime warming; growing degree days; growing degree hours; leaf unfolding; Bayesian analysis; deciduous trees

Introduction

Plant phenology is highly sensitive to climate change (Menzel *et al.*, 2006; Schwartz *et al.*, 2006; Jeong *et al.*, 2011; Fu *et al.*, 2014b). Warming-induced phenological changes can affect ecosystemic structure and functioning by extending the length of the growing season (Cleland *et al.*, 2007; Piao *et al.*, 2008), changing species composition (Chuine, 2010) or altering the interaction between plants and animals (Hunter, 1992; Memmott *et al.*, 2007), and even plants and climate (Peñuelas *et al.*, 2009). The underlying physiological mechanisms nevertheless remain unclear (Hänninen & Kramer, 2007; Chuine *et al.*, 2013; Fu *et al.*, 2013). A better understanding of plant phenological processes is required to predict the response of plants to future climate change (Richardson *et al.*, 2013; Fu *et al.*, 2015b).

Several centuries ago, Réaumur proposed that the date of leaf unfolding could be linked with the accumulated temperature in a preceding period, generally called heat requirement or growing degree days (GDD) (Réaumur, 1735). Other environmental factors have also recently been associated with leaf unfolding, such as winter chilling (Murray *et al.*, 1989; Fu *et al.*, 2013; Laube *et al.*, 2014a), photoperiod (Körner & Basler, 2010; Way & Montgomery, 2014), humidity (Laube *et al.*, 2014b), precipitation (Penuelas *et al.*, 2004; Fu *et al.*, 2014c) and conditions in the previous year (Fu *et al.*, 2014a). Taking advantage of these findings, models that include not only GDD but also chilling and photoperiod (Hänninen & Kramer, 2007; Chuine *et al.*, 2013) have been widely used to predict leaf unfolding and its response to climate change. Such predictions for leaf unfolding, however, still vary considerably and differ largely from in situ observations, resulting in substantial uncertainty when predicting ecosystemic responses of carbon and water balances to climate change (Levis & Bonan, 2004; Kucharik *et al.*, 2006; Piao *et al.*, 2007; Richardson *et al.*, 2012). Current phenological models may thus not capture all the

70   main mechanisms involved (Chuine *et al.*, 2013; Fu *et al.*, 2015a). A key weakness could be the

71   accuracy of estimation of the heat requirement, which has received less attention in previous

72   studies. The unit of heat requirement, i.e. daily GDD, is generally calculated by using the

73   average daily temperature in excess of a base temperature (Miller *et al.*, 2001). The weight of

74   daytime and nighttime temperatures in calculating GDD is thus the same. Recent studies,

75   however, have suggested that spring leaf phenology may be more dependent on daytime than

76   nighttime temperature (Hanes, 2014; Piao *et al.*, 2015). Specifically, both studies found that the

77   spring phenology, i.e. both in situ leaf unfolding (only maple trees in Hanes (2014)) and remote-

78   sensing based green-up onset over the Northern hemisphere (Piao *et al.*, 2015), are more related

79   to daily maximum temperate rather than minimum temperature. This implies an asymmetric

80   influence of daytime vs. nighttime temperatures on the heat requirement of leaf unfolding.

81   Spring phenology, especially of forest tree species, affects the global carbon and water balance

82   and climatic feedbacks (Pan *et al.*, 2011; Richardson *et al.*, 2013). To explore the different

83   effects of daytime and nighttime temperatures on spring phenology, well designed experiments

84   deliver increased process-understanding (De Boeck *et al.*, 2015). This, in turn, could be used to

85   improve the phenology models leading to more accurate projections of ecosystem responses

86   especially against a background of ongoing climate change. Indeed, the global minimum

87   temperature has increased about twice as fast as the maximum temperature since 1950 (IPCC.,

88   2014), rendering it even more pertinent to differentiate between daytime and nighttime

89   temperature changes. Only a few nighttime warming experiments have been conducted, focusing

90   on crops and grassland (Dhakhwa & Campbell, 1998; Peng *et al.*, 2004; Xia & Wan, 2012), but

91   (to our knowledge) the effects of daytime and nighttime warming on the tree phenology of leaf

92   unfolding have not been experimentally investigated.

93   We therefore designed a novel manipulative experiment to unveil potential differential effects of

94   daytime vs. nighttime warming on leaf phenology. We used saplings of three species of

95   temperate deciduous trees: birch (*Betula pendula* L.), oak (*Quercus robur* L.) and beech (*Fagus*

96   *sylvatica* L.), which are common species in Europe and characterized by different heat

97   requirements. The objectives of this study were to determine and quantify the different effects of

98   daytime and nighttime warming on leaf unfolding in these three temperate tree species.

99

Materials and Methods

Experimental design and phenological measurements

102   The experiment was conducted at the Drie Eiken campus of the University of Antwerp (Belgium,

103   51º19′N, 4º21′E). We transplanted local birch, oak and beech saplings 1 m in height into plastic

104   pots (diameter 25 cm, depth 40 cm) on 4 December 2014 and moved them into 12 outdoor

105   climate-controlled chambers on 1 January 2015. These saplings were bought from a nursery

106   close to our experimental site. Grown from seeds collected in a local forest, saplings had been

107   cultivated in the same field for one year prior to being transplanted into pots and used in our

108   experiment. The pots were filled with an organic substrate with a pH of 6.0 and 20% organic

109   matter (Universal potting soil, Viano, Aalst, Belgium). Seven saplings each of beech, oak and

110   birch were placed in each chamber, totaling 84 saplings per species. The chambers could be

111   artificially warmed in a controlled manner up to 9 °C above fluctuating ambient temperatures

112   using a centralized heating system (Fu *et al.*, 2013). They were sunlit, facing south, with a

113   transparent polycarbonate plate at the top 4 mm thick (light absorption =15% (Fu *et al.*, 2013).

114   The interior surface area was 200×150 cm, the height was 180 cm on the south side and 200 cm

5

115   on the north side (Fig. S1). Temperature sensors (Siemens, type QFA66, Berlin, Germany) were

116   used to continuously monitor the air temperature inside each chamber, logging every 30 minutes

117   and stored as hourly data. Over the experimental period (from 1 January 2015 until leaf

118   unfolding in spring 2015), the saplings were watered once or twice per week as soon as the

119   topsoil appeared dry.

120

121   Three replicate chambers were maintained at ambient temperature for the entire duration of the

122   experiment (control treatment), and the other nine chambers were used for three replicates of

123   three warming treatments: (1) whole-day warming, i.e. continuously warmed by 2 °C above

124   ambient over the entire experimental period, (2) daytime warming only and (3) nighttime

125   warming only. Daytime and nighttime were defined as the periods from sunrise to sunset and

126   sunset to sunrise, respectively (see Fig. 1A). A sample of the four treatments is shown in Fig. 1B.

127   The daily temperature settings of the daytime and nighttime warming treatments were changed

128   based on daily growing degree days (GDD) to ensure that the daily GDDs were identical among

129   the three warming treatments. Indeed, the mean temperature among the three warming treatments

130   were very similar, i.e. daytime warming (10.4 °C), nighttime warming (10.2 °C) and whole-day

131   warming (10.3 °C). The daily GDD was calculated as:

132
$$GDD = T_{mean} - T_{base} \qquad if \ T_{mean} > T_{base} \tag{1}$$

133
$$T_{mean} = (\sum_{hour=1}^{24} T_{hour})/24 \tag{2}$$

134   where T_{mean} is average daily temperature and T_{hour} is hourly temperature. T_{base} is the base

135   temperature, set at 0 °C in the present study as used by Sarvas (1972). Similar results were

136   observed using 5 °C as the base temperature (not shown). The chambers provided continuous

137   warming, with no significant differences in GDD accumulation among the three warming

138   treatments from 1 January to the end of May 2015, as programmed (Fig. 1C).

139   Phenological traits were observed on the terminal bud of each sapling. Leaf unfolding was

140   defined as the date when the entire leaf blade and stalk were visible (Fig. S1), following the

141   guidelines in Fu *et al.* (2013). Monitoring began on 1 February and was repeated every two days.

142

143   **Model description and calibration**

144   Three models of growing degree hours (GDH) were parameterized to predict the date of leaf

145   unfolding, i.e. (a) the classical GDH model (GDH$_{classical}$), which assumes that a certain number of

146   GDH (GDH$_{requirement}$) are needed to trigger leaf unfolding, and (b) an improved GDH model

147   (GDH$_{day-night}$), which weights daytime and nighttime temperatures differently for GDH

148   accumulation, and (c) GDD$_{nonlinear}$ model that assumes an exponential function to calculate GDH

149   accumulation. All models assume that leaves unfold when GDH$_{requirement}$ is reached.

150

151   The accumulation of GDH in the models starts on a fixed day t (1 January, as used by (Murray *et*

152   *al.*, 1989)) until the date of leaf unfolding (LU). During this period, GDH accumulate when the

153   hourly temperature (T_{hour}) exceeds a base temperature (T_{base}) by using a linear relationship:

$$GDH_{classical} = \sum_{t}^{LU} \left(\sum_{hour=1}^{24} \left(T_{hour} - T_{base} \right) \right) \quad if \quad T_{hour} > T_{base} \tag{3}$$

155   In the GDH$_{day-night}$ model, we defined the effect of daytime temperature on leaf unfolding has a

156   larger effect than nighttime temperature, and two new parameters are thus added to weight the

157   impact of daytime (K_a, prior parameter distribution: 0.5 - 1) and nighttime (K_b, prior parameter

158   distribution: 0 - 0.5) temperatures on GDH accumulation:

159 $$GDH_{day-night} = \sum_{t}^{LU} \left(\sum_{hour=1}^{24} \left(K_a * (T_{hour\_daytime} - T_{base}) + K_b * (T_{hour\_nighttime} - T_{base}) \right) \right) \quad if \quad T_{hour} > T_{base} \quad (4)$$

160 where $T_{hour\_daytime}$ and $T_{hour\_nighttime}$ are the hourly temperature (T_{hour}) during daytime and

161 nighttime, respectively.

162 The accumulation of GDH in the $GDH_{nonlinear}$ model starts on 1 January, as in the $GDH_{classical}$ and

163 $GDH_{day-night}$ models, until the date of leaf unfolding (LU). During this period, GDH accumulate

164 when the hourly temperature (T_{hour}) exceeds a base temperature (T_{base}) by using an exponential

165 function of hourly temperature:

166 $$GDH_{nonlinear} = \sum_{t}^{LU} \left(\sum_{hour=1}^{24} \left(K * T_{hour} * (T_{hour} - T_{base}) \right) \right) \quad if \quad T_{hour} > T_{base} \quad (5)$$

167 where K is the parameter range from 0 to 1.

168

169 The models were parameterized by a Bayesian Markov Chain Monte Carlo method. This

170 Bayesian calibration walks through the coefficient space of each parameter (prior distribution) in

171 such a way that the collection of visited points forms a set of parameter coefficients (posterior

172 distribution). The model was run 10^4 times with different parameter coefficients sampled from

173 the prior distribution of the coefficients. This method has previously been used to parameterize

174 phenological models; Fu *et al.* (2012) provides a detailed description. Information for the

175 parameters K_a and K_b was lacking, so flat distributions were defined as the prior parameter

176 distribution (Van Oijen *et al.*, 2005). We quantified the weights of daytime and nighttime

177 temperatures on daily GDH accumulation by calculating the K_a / K_b ratio for each run; the

178 distributions of the ratios are presented as histograms.

179

180   **Data analysis**

181   The mean date of leaf unfolding and the GDH requirement were analyzed using all saplings per

182   treatment, i.e. the mean values were averaged across all saplings of each treatment (in three

183   chambers). The differences between the mean date of leaf unfolding under warming treatments

184   and under controls were defined as the advancement of leaf unfolding under warming treatments.

185   Since chamber is a nested factor, we specified the nested effects of the chambers in the runs of

186   the linear mixed models, and found that the chambers did not significantly affect the results.

187   Tukey's post hoc HSD tests were applied to test pairwise comparisons of the advancement, GDH

188   requirement and temperature sensitivity of leaf unfolding among treatments. The temperature

189   sensitivity of leaf unfolding (S_T) was calculated using linear regression analyses (ordinary least

190   squares regressions) of the dates of leaf unfolding against mean air temperature from 1 January

191   to the day of leaf unfolding for each species and each warming treatment. All statistical analyses

192   were conducted using SPSS 16.0 (SPSS Inc., Chicago, USA). The effectiveness of the

193   phenological models was evaluated with the root mean square error (*RMSE*) of the difference

194   between the predicted and observed dates of leaf unfolding:

195
$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(Sim_i - Obs_i)^2}{n-1}} \qquad (6)$$

196   where *Obs*$_i$ and *Sim*$_i$ are the mean observed and simulated dates of leaf unfolding in chamber *i*,

197   respectively, and *n* is the number of dates.

198   **Results**

199   The three warming treatments significantly advanced the date of leaf unfolding for all three

200   species, but the amount of advancement differed significantly ($P<0.05$) among the treatments

201   (Fig. 2A), except for oak where the influence of nighttime and whole-day warming was the same.

202   Despite the similar GDDs among the treatments, daytime warming advanced the dates of leaf

203   unfolding most, with average advancements of 13.4 ± 4.1, 8.5 ± 2.5 and 8.3 ± 3.5 days for birch,

204   oak and beech, respectively. The advancement was shortest under nighttime warming but was

205   still significant (8.8 ± 3.0, 5.1 ± 3.8 and 2.9 ± 3.4 days for birch, oak and beech, respectively),

206   with whole-day warming eliciting an intermediate response (11.2 ± 5.2, 6.4 ± 4.4 and 5.6 ± 4.5

207   days, respectively).

208   The temperature sensitivity of leaf unfolding (change in days per degree Celsius warming,

209   days $°C^{-1}$) logically also differed significantly among the three warming treatments (Fig. 2B).

210   The trees of all three species were most sensitive to daytime warming (average rates of

211   advancement of 7.4 ± 0.9, 4.8 ± 0.3 and 4.8 ± 0.2 days $°C^{-1}$ for birch, oak and beech, respectively)

212   and least sensitive to nighttime warming (5.5 ± 0.9, 3.3 ± 0.3 and 2.1 ± 0.9 days $°C^{-1}$,

213   respectively), with whole-day warming intermediate (6.6 ± 0.7, 3.9 ± 0.4 and 3.5 ± 1.1 days $°C^{-1}$,

214   respectively).

215

216   Interestingly, the GDH calculated from 1 January 2014 to the day of leaf unfolding were

217   significantly larger for trees in the three warming treatments than for those in the control

218   treatments for all three species (Fig. 2C), even though the dates of leaf unfolding were

219   significantly advanced for the trees in the warming treatments (Fig. 2A). Among the three

220 warming treatments (i.e. daytime, nighttime and whole-day warming), we found that earlier leaf

221 unfolding was associated with less GDH accumulation, although the GDH accumulation did not

222 differ significantly among the three warming treatments. This suggests that the weight of

223 daytime and nighttime temperatures in calculating GDH should be different. Specifically,

224 daytime temperatures may play a more important role than nighttime temperatures in leaf

225 unfolding.

226

227 The modeling supported this finding. The performance of the $GDH_{day-night}$ model (which

228 incorporated the differential effects of daytime and nighttime temperatures) was a substantial

229 improvement over the $GDH_{classical}$ model. The RMSEs of the $GDH_{day-night}$ model were only one

230 day for all three species, compared to three days for the GDH model (Fig. 3A-C). The posterior

231 distribution of the K_a / K_b ratio was similar for the three species, with medians near three (Fig.

232 3D-F), indicating that the weight of daytime temperature on the accumulation of growing degree

233 hours was three times larger than the weight of nighttime temperature. The $GDH_{nonlinear}$ model

234 performed better than the classical GDD model, but still less well than the $GDH_{day-night}$ model

235 (Fig. 4).

236

237 **Discussion**

238 A trend toward earlier leaf unfolding with currently increasing temperatures has been widely

239 documented for plants in cold and temperate regions (Peñuelas *et al.*, 2002; Menzel *et al.*, 2006;

240 Schwartz *et al.*, 2006; Fu *et al.*, 2014b). The phenological response to climatic warming,

241 however, is nonlinear (Chuine *et al.*, 2010; Fu *et al.*, 2015b; Marchin *et al.*, 2015), and a

242   significant reduction in temperature sensitivity of leaf unfolding since the 1980s, attributed to

243   winter warming and potentially to photoperiod limitation, has recently been reported (Fu *et al.*,

244   2015b). Here, we provide experimental evidence of an additional mechanism contributing to the

245   non-linearity of the temperature response to warming: a threefold difference in the sensitivity of

246   leaf unfolding to increases in daytime vs. nighttime temperatures. Our result is consistent with

247   the main conclusion of a recent study by Piao *et al.* (2015), which demonstrated that spring leaf

248   phenological dates were mostly correlated with gridded daytime temperatures. Another finding,

249   however, differed between this large-scale analysis based on remote sensing and our analysis

250   based on saplings of three tree species: we found that nighttime warming also significantly

251   advanced the dates of leaf unfolding, albeit at a much lower rate compared to daytime warming.

252   The experimentally warmed nighttime temperatures in our experiment, though, were often higher

253   than the threshold temperature for heat accumulation, which was generally not the case in the

254   study by Piao et al (2015) that analyzed differences in ambient temperature.

255

256   The threefold greater impact of daytime compared to nighttime temperatures on leaf unfolding

257   suggests that weighted hourly temperatures are more appropriate for calculating heat

258   accumulation than daily mean temperatures. This implies that the GDD-based phenological

259   models currently used would not accurately predict leaf unfolding in future climates, as

260   nighttime temperatures are projected to increase faster than daytime temperatures (IPCC, 2014).

261   Better predictions of spring leaf-out timing could be achieved by acknowledging the nonlinear

262   relationship between diurnal temperature and heat accumulation for leaf unfolding we uncovered.

263

264   The asymmetric effect of daytime and nighttime temperature on the phenology of leaf unfolding

265   is clear. Why leaf unfolding is more dependent on daytime than nighttime temperature

266   nonetheless remains unclear. We propose two non-mutually exclusive hypotheses to explain

267   these results.

268   First, the response of heat accumulation to temperature may be non-linear, instead of linear as

269   assumed in the original GDD concept. Daytime temperatures are much higher and would thus

270   logically contribute more to heat accumulation if the temperature response was non-linear.

271   Indeed, we found that the $GDH_{nonlinear}$ model performed better than the classical GDD model,

272   but still less well than the $GDH_{day\text{-}night}$ model (Fig. 4), suggesting that the non-linear response of

273   heat accumulation to temperature may explain part of the asymmetric effect of daytime and

274   nighttime temperature on leaf unfolding, but this proposal is admittedly incomplete.

275   Second, daytime solar radiation warms meristems directly and more than air temperature,

276   especially under clear skies (Savvides *et al.*, 2014). Leaf unfolding is probably more directly

277   related to meristem temperature than to air temperature (Grace *et al.*, 1989). The difference

278   between meristem and air temperature is typically much smaller at night than during daytime,

279   and the sign of this temperature difference may even change. Calculating GDD using only the air

280   temperature may therefore introduce an error that underestimates the true temperature driving

281   phenology during daytime. The underlying mechanisms of how radiation and temperature affect

282   leaf unfolding by the accumulation of heat remain incompletely understood and require

283   additional manipulation experiments.

284

285   In addition to the heat requirement, a chilling requirement and photoperiod can contribute to the

286   timing of leaf unfolding in temperate tree species (Cannell & Smith, 1983; Murray *et al.*, 1989;

287   Körner & Basler, 2010; Fu *et al.*, 2014c; Laube *et al.*, 2014a; Way & Montgomery, 2014). The

288   saplings in our study were grown under the same photoperiodic conditions, eliminating any

289   effect of photoperiod. The concept of chilling assumes that a certain amount of low temperature

290   (the chilling requirement) is needed to end endodormancy, and sufficient warm temperatures

291   (heat requirement) are subsequently necessary to trigger leaf unfolding (Cannell & Smith, 1983;

292   Hänninen, 1990; Hänninen & Kramer, 2007; Chuine *et al.*, 2013). The chilling and heat

293   requirements are negatively correlated, with more chilling decreasing the heat requirements for

294   leaf unfolding (Murray *et al.*, 1989; Fu *et al.*, 2014c). The specifics of this correlation remain

295   unclear, which leads to differences among phenological models (Chuine, 2000). In the present

296   study, all warming treatments significantly reduced the amount of chilling hours compared to the

297   controls (Fig. 1D). The chilling hours under nighttime warming were significantly reduced

298   compared to those in the daytime warming treatment, but the heat requirement did not differ

299   significantly between these two treatments (Fig. 2C), suggesting that the chilling requirement

300   may have already been fulfilled in all saplings before the onset of all warming treatments. In

301   other words, no further chilling was likely needed after the release from endodormancy, even if

302   temperatures were suited to contributing to further chilling accumulation. Trees may therefore

303   sequentially accumulate chilling and heat during endodormancy and ecodormancy, respectively,

304   providing support for the sequential model of chilling and heating for predicting leaf unfolding.

305

306   In conclusion, this study demonstrated that leaf unfolding in temperate tree species advanced

307   with both daytime and nighttime warming, but the sensitivity to increased daytime or nighttime

308   temperatures differed significantly. The impact of increases in daytime temperature on leaf

309   unfolding via heat accumulation was approximately three times higher than that of increases in

310   nighttime temperatures. To our knowledge, this is the first time that direct experimental evidence

311   is provided for asymmetric daytime-nighttime warming effects. The nonlinear response of leaf

312   unfolding to climatic warming might be more pronounced due to a non-uniform diurnal

313   temperature warming with a faster increase in nighttime than daytime temperature (IPCC., 2014).

314   The asymmetric effect of daytime and nighttime warming on leaf unfolding should be

315   incorporated into models of leaf unfolding to improve phenological predictions and our

316   understanding of the responses of global carbon and water cycles to the ongoing climate change.

317   This requires more well-designed experiments to identify the generality of our results by

318   focusing on the underlying mechanisms.

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329

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Author contributions

332   Y.S.F, S.P and I.A.J designed the research. Y.S.F. and Y.P.H.L performed the experiments.

333   Y.S.F and I.A.J wrote the manuscript. Y.S.F, Y.P.H.L, H.J.B, A.M, I.N, M.P, J.P, S.P and I.A.J

334   contributed to the interpretation of the results and to the text.

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460

461   **Figure S1** The climate-controlled chambers used in the study at the University of Antwerp, Belgium.

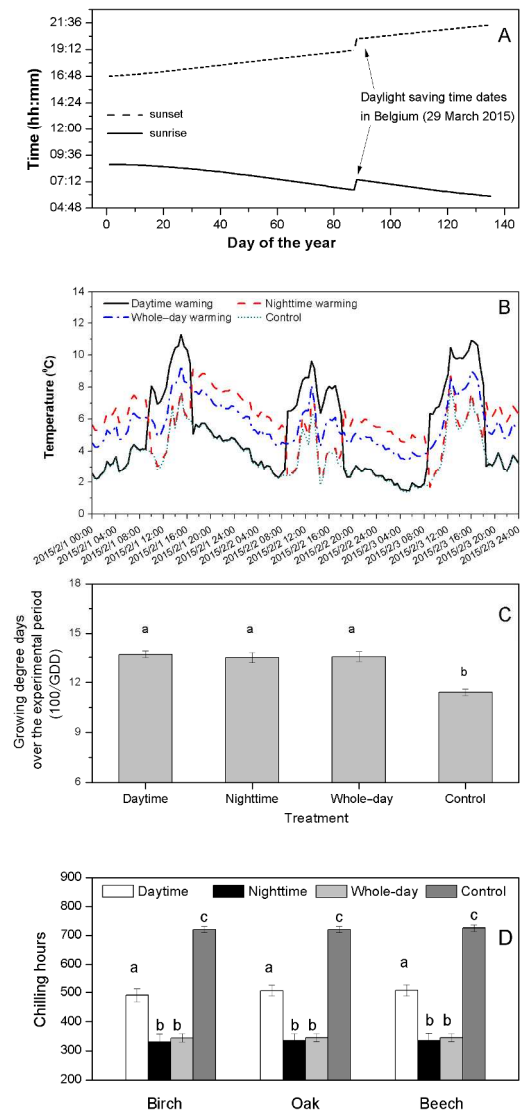462   **Figure legends**

463   Figure 1. (A) Timing of sunrise and sunset during the experimental period from 1 January to the

464   end date of leaf unfolding. (B) A sample of the variation in air temperature during three days

465   (year/month/day hh/mm) in all treatments, i.e. Whole-day warming. Daytime warming only,

466   Nighttime warming only and Control. (C) The mean growing degree days (GDD) and its one

467   standard deviation (error bar) in each treatment, accumulated from 1 January to the end of May

468   2015. (D) Changes of chilling and its one standard deviation (error bar) among the four

469   treatments during the experimental period from 1 January to the end date of leaf unfolding. The

470   chilling accumulation was calculated as chilling hours for hourly temperatures between 0 and

471   5 °C, as in a previous study (Fu *et al.,* 2015b). Different letters denote significant differences

472   (P<0.05).

473   Figure 2. Mean date of (A) leaf unfolding and its one standard deviation (error bar), (B)

474   temperature sensitivity (S_T) and its one standard deviation (error bar) and (C) mean accumulation

475   of growing degree hours (GDH) and its one standard deviation (error bar) calculated from 1

476   January to the date of leaf unfolding for each tree species. Different letters denote significant

477   differences (P<0.05) in the dates of leaf unfolding and growing degree hours among the four

478   treatments.

479   Figure 3. Comparison of observed and predicted dates of leaf unfolding for the models for

480   growing degree hours (GDH$_{classical}$ and GDH$_{day-night}$) for (A) beech, (B) oak and (C) birch.

481   Compared to the GDH$_{classical}$ model, two new parameters were added to GDH$_{day-night}$ to weight the

482   impacts of daytime (K_a) and nighttime (K_b) temperatures on GDH accumulation. The root mean

483   square errors (RMSEs) are provided for each model and species. The histograms show the

484   distributions of the Ka / Kb ratios of the $GDH_{day-night}$ model across all Markov Chain Monte

485   Carlo runs for (D) beech, (E) oak and (F) birch. The medians are provided for each species.

486   Figure 4. Comparison of observed and predicted dates of leaf unfolding with the nonlinear

487   growing degree hours model ($GDH_{nonlinear}$) for beech (A), oak (B) and birch (C). The root mean

488   square errors (RMSE) are provided for each species.

Figure 1. (A) Timing of sunrise and sunset during the experimental period from 1 January to the end date of leaf unfolding. (B) A sample of the variation in air temperature during three days (year/month/day hh/mm) in all treatments, i.e. Whole-day warming. Daytime warming only, Nighttime warming only and Control. (C) The mean growing degree days (GDD) and its one standard deviation (error bar) in each treatment, accumulated from 1 January to the end of May 2015. (D) Changes of chilling and its one standard deviation (error bar) among the four treatments during the experimental period from 1 January to the end date of leaf unfolding. The chilling accumulation was calculated as chilling hours for hourly temperatures between 0 and 5 °C, as in a previous study (Fu et al., 2015b). Different letters denote significant differences (P<0.05). 271x521mm (300 x 300 DPI)
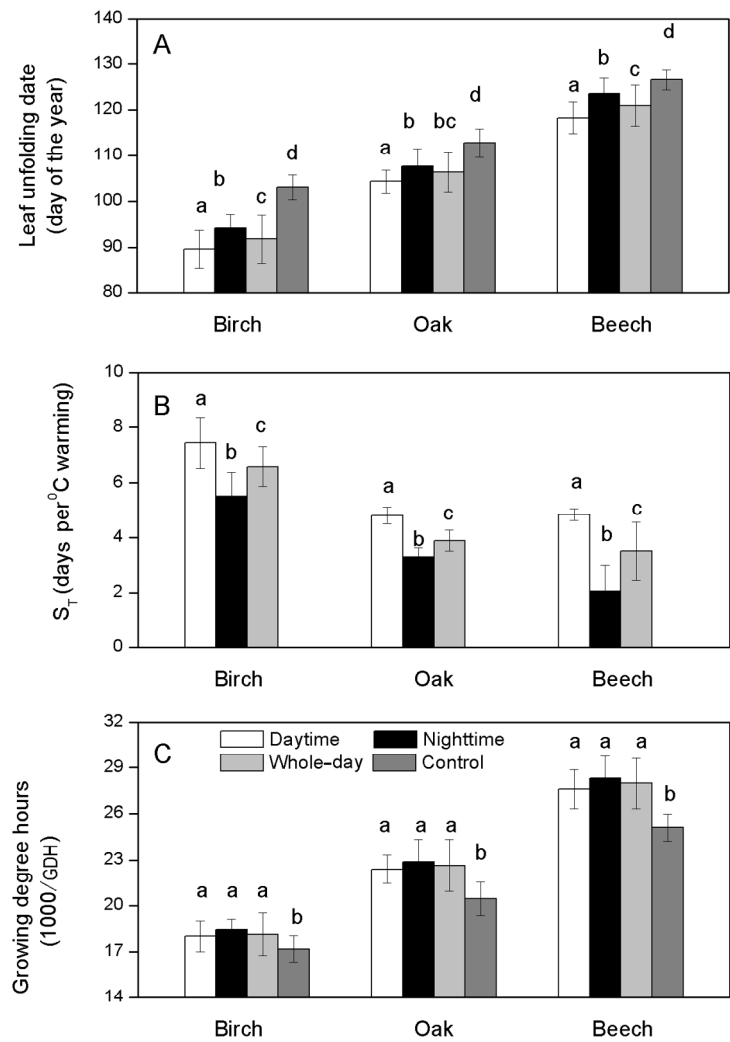
Figure 2. Mean date of (A) leaf unfolding and its one standard deviation (error bar), (B) temperature sensitivity (ST) and its one standard deviation (error bar) and (C) mean accumulation of growing degree hours (GDH) and its one standard deviation (error bar) calculated from 1 January to the date of leaf unfolding for each tree species. Different letters denote significant differences (P<0.05) in the dates of leaf unfolding and growing degree hours among the four treatments.
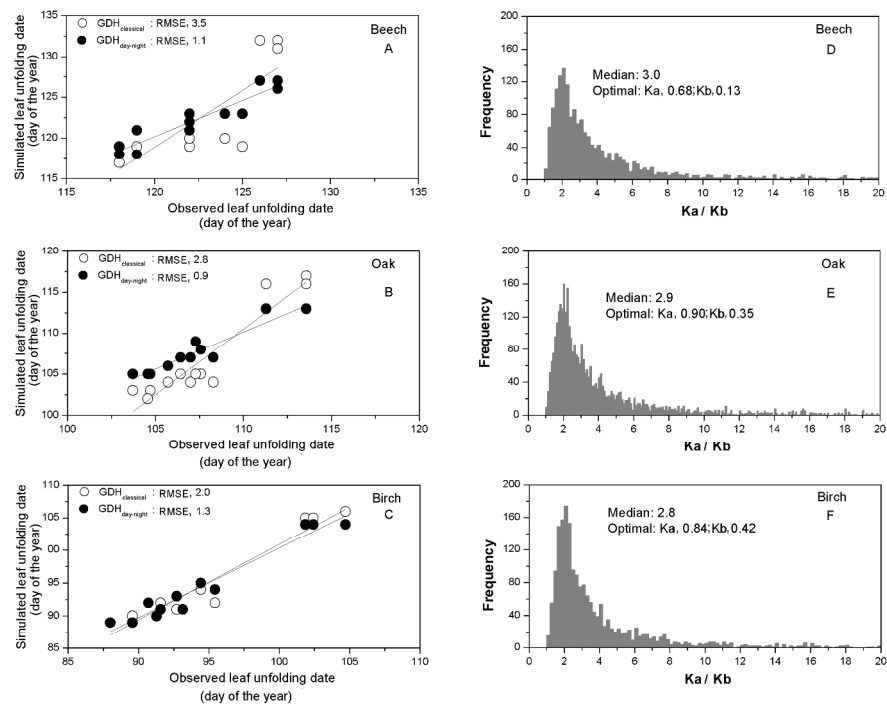
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Figure 3. Comparison of observed and predicted dates of leaf unfolding for the models for growing degree hours (GDHclassical and GDHday-night) for (A) beech, (B) oak and (C) birch. Compared to the GDHclassical model, two new parameters were added to GDHday-night to weight the impacts of daytime (Ka) and nighttime (Kb) temperatures on GDH accumulation. The root mean square errors (RMSEs) are provided for each model and species. The histograms show the distributions of the Ka / Kb ratios of the GDHday-night model across all Markov Chain Monte Carlo runs for (D) beech, (E) oak and (F) birch. The medians are provided for each species.
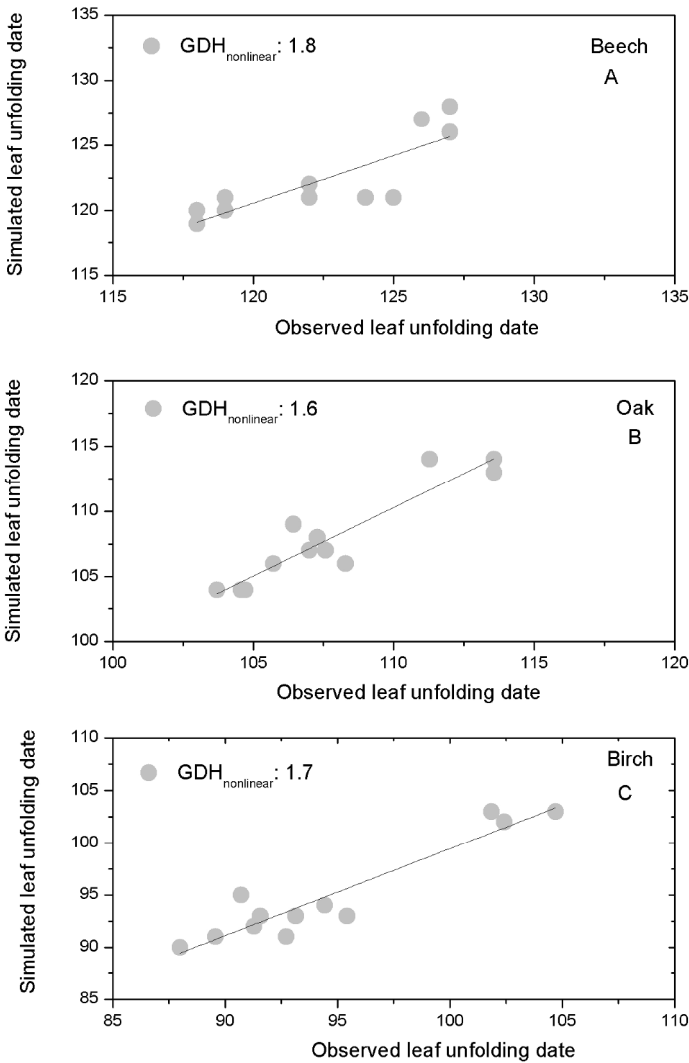527x403mm (300 x 300 DPI)

Figure 4. Comparison of observed and predicted dates of leaf unfolding with the nonlinear growing degree hours model (GDHnonlinear) for beech (A), oak (B) and birch (C). The root mean square errors (RMSE) are provided for each species.
271x396mm (300 x 300 DPI)