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HAL Id: hal-02735790
https://hal.inrae.fr/hal-02735790

Submitted on 7 Dec 2022

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Key words: Leaf phenology, budburst, leaf senescence, temperate forest, within-population variability, uncertainty quantification.

Abstract

Leaf phenology is a major driver of ecosystem functioning in temperate forests, and a robust indicator of climate change. Both the inter-annual and inter-population variability of leaf phenology have received much attention in the literature; in contrast, the within-population variability of leaf phenology has been far less studied. Beyond its impact on individual tree physiological processes, the within-population variability of leaf phenology can affect the estimation of the average budburst or leaf senescence dates at the population scale. Here, we monitored the progress of spring and autumn leaf phenology over 14 tree populations (9 tree species) in six European forests over the period of 2011 to 2018 (yielding 16 site-years of data for spring, 14 for autumn). We monitored 27 to 512 (with a median of 62) individuals per population. We quantified the within-population variability of leaf phenology as the standard deviation of the distribution of individual dates of budburst or leaf senescence (SD_{BBi} and SD_{LSi}, respectively). Given the natural variability of phenological dates occurring in our tree populations, we estimated from the data that a minimum sample size of 28 (resp. 23) individuals, are required to estimate SD_{BBi} (resp. SD_{LSi}) with a precision of 3 (resp. 7) days. The within-population of leaf senescence (average SD_{LSi}=8.5 days) was on average two times larger than for budburst (average SD_{BBi}=4.0 days). We evidenced that warmer temperature during the budburst period and a late average budburst date were associated with a lower SD_{BBi}, as a result of a quicker spread of budburst in tree populations, with a strong species effect. Regarding autumn phenology, we observed that later senescence and warm temperatures during the senescence period were linked with a high SD_{LSi}, with a strong species effect. The shares of variance explained by our models were modest suggesting that other factors likely influence the within-population variation in leaf phenology. For instance, a detailed analysis revealed that summer temperatures were negatively correlated with a lower SD_{LSi}.

Introduction

Phenology was defined by the International Biological Program (IBP) as "the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species" (Lieth, 1974). Leaf phenology has received substantial attention in the last decades mainly because it is a robust indicator of current climate change (Badeck et al., 2004; Donnelly and Yu, 2017; Donnelly et al., 2004). Observations, experiments and modelling have shown that the occurrence of leaf phenological events such as budburst and leaf senescence is mainly driven by both temperature (Delpierre et al., 2009a; Lim et al., 2007; Menzel et al., 2006; Vitasse et al., 2009; Walther et al., 2002) and photoperiod (Delpierre et al., 2016; Fu et al., 2019; Singh et al., 2017; Thakur et al., 2016; Vitasse and Basler, 2013; Way and Montgomery, 2015). In the Northern Hemisphere there is strong evidence that the global warming hastens the occurrence of spring phenological events (Menzel et al., 2006; Walther et al., 2002) and delays the occurrence of leaf senescence (Estrella and Menzel, 2006). The timing of spring and autumn phenological transitions could affect the ecosystem functioning. Indeed, the timing and duration of the leafy period impact the ecosystem carbon uptake (Delpierre et al., 2009b; Richardson et al., 2010; White et al., 1999). Moreover, leaf phenology, especially budburst, is strongly correlated with insect and insectivore phenology (Harrington et al., 1999) and could affect food webs within ecosystems.

To date, most phenological studies have addressed questions related to the inter-specific and the inter-annual variability of phenological events (see Ma et al., 2018 and Xie et al., 2018 for recent examples). However, the within-population variability of leaf phenology has received little attention in the literature (Cole and Sheldon, 2017; Crawley and Akhteruzzaman, 1988; Delpierre et al., 2017; Wesołowski and Rowiński, 2006). This is rather surprising since the within-population variability of leaf phenology can be large, averaging 19 days from the earliest to the latest tree leafing out, and 26 days from the earliest to the latest tree showing leaf senescence in a given population (as reviewed by Delpierre et al. (2017)). This is about 30% of the amplitude of the continental gradient of budburst or leaf senescence (Delpierre et al. 2017). Phenological studies conducted at the population scale have shown that individual trees can usually be grouped according to their phenological rank for both spring (Chesnoiu et al. 2009; Delpierre et al. 2017; Crawley and Akhteruzzaman, 1988) and autumn (Delpierre et al. 2017) phases: some are identified as "early-trees", others as "late-trees" and the majority are grouped

around the average (Chesnoiu et al., 2009). Moreover, individual tree phenology is often highly repeatable between years, suggesting that genetic factors and/or local micro-climatic variations would play a predominant role (Delpierre et al., 2017). Since the duration of the leafy period impacts the potential of resource acquisition of trees, one may assume that the phenological ranks of individual trees within a population affect their competitive status. For instance, individual European beeches (*Fagus sylvatica* L.) and deciduous oaks (*Quercus petraea* Matt. (Liebl) and *Quercus robur* L.) characterised by an earlier budburst or a later senescence than the population average, respectively, also showed a higher girth increment (Delpierre et al., 2017).

In this study, we explored how the within-population variability of leaf phenology varies with environmental predictors. Process-based models of leaf phenology (Chuine, 2000; Delpierre et al., 2009b, 2016; Vitasse et al., 2011) postulate that budburst or leaf senescence occur when a given accumulation of "warm" temperatures (i.e. above a temperature threshold, for spring phases) or "cold" temperatures (i.e. below a temperature threshold, for autumn) has been reached. Such models have been developed to predict the average date of occurrence of the phenophase of interest among trees in a population. We can go a step further and assume that the within-population variability of leaf phenology proceeds from the variability of an individual trait, such as the temperature sum required for triggering budburst (Kramer et al., 2008; Oddou-Muratorio and Davi, 2014) or leaf senescence. For example, as the accumulation of degree-days occurs faster during a warm spring, the time interval from the first to the last tree bursting buds in the population would be reduced as compared to a colder spring (see Suppl. Mat. 1). The same argument holds with the accumulation of cold temperature for the leaf senescence period. It follows that a warmer spring or a colder autumn would shorten the spread of budburst or leaf senescence dates in a tree population. On that basis, we hypothesize that warm temperatures during the budburst or cold temperatures during the senescence period would decrease the within-population variability of budburst or leaf senescence, respectively (hypothesis n°1). In addition to the impact of temperatures, photoperiod may act as a threshold signal triggering trees to burst buds in late spring (Vitasse and Basler, 2013) or to enter leaf senescence in late autumn (White et al., 1997). Hence, we formulate a second hypothesis stating that a late population-average date of budburst or leaf senescence would be associated with a reduced within-population variability of leaf phenology both for spring and autumn (hypothesis n°2).

Material and methods

Description of the phenological database

This study is based on phenological data collected from tree communities located across a longitudinal gradient spanning 2100 km in Europe (Table 1 and Suppl. Mat. 2). Budburst and leaf senescence observations were conducted at the individual tree scale for nine species: *Acer pseudoplatanus* L., *Betula pendula* Roth., *Carpinus betulus* L., *Castanea sativa* Mill., *Corylus avellana* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Quercus petraea* (Matt.) Liebl and *Quercus robur* L. These species are distributed in 12 populations representing 37 populations-years[1] for the budburst, and in 15 populations representing 46 populations-years for the leaf senescence (Suppl. Mat. 3). The tree populations were observed in their natural habitat, with the notable exception of the *Quercus petraea* populations observed in Toulenne (Table 1) which is a *common garden* experiment into which 10 populations from two altitudinal gradients are grown. This study took advantage of a high number of individual trees observed for each population-year: spring and autumn phenological observations were conducted over populations ranging from 27 to 249 (with a median of 62) individuals, and 27 to 512 (with a median of 61) individuals, respectively (Suppl. Mat. 3). Phenological observations were conducted at the individual-tree scale by local observers using binoculars at an interval of 3.7 days on average (from 2 to 7 days) from March to May for budburst (*BB*) and of 7.1 days on average (from 3 to 14 days) from September to November for leaf senescence (*LS*). The number of observers varies from one (Orsay) to five (Wytham Woods) for spring phenology. All autumn phenological observations were systematically conducted by the same local observers. Temperature data were in most cases acquired in the vicinity of the study sites, except for the Fundeanu site for which gridded meteorological data at a 0.5° spatial resolution were used (Haylock et al., 2008) (Table 1).

<Expected location of Table 1>

Individual estimation of budburst and leaf senescence date.

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[1] A « population-year » refers to one tree population being observed during one year. Thus, e.g. four population-years may refer to one population observed for four years, or two populations observed both for two years, or two populations observed for three and one year, respectively etc.

177 We considered as target phenological events the occurrence of 50% of leaf buds opened (for

178 spring, Fig.1) or 50% of senesced (coloured or fallen) leaves (for autumn) in individual tree

179 crowns. A leaf bud is considered open "once a green leaf tip is visible at the end of the bud, but

180 before the first leaf from the bud has unfolded to expose the leaf stalk (petiole) or leaf base"

181 (Denny et al., 2014). For leaf senescence, observations of both the individual tree crown

182 percentages of coloured (i.e. yellow for the study species) and fallen leaves were combined in

183 a single senescence metric (Vitasse et al., 2009). Continuous bud development and leaf

184 senescence stages were calculated for each tree by linear interpolation of visual observations,

185 assuming that bud development and leaf senescence trajectories are linear around 50% opened

186 buds or 50% senesced leaves, respectively. For each individual tree, the date of the target stage

187 (hereafter BB_i for spring and LS_i for autumn, expressed as a day of year, DoY) was estimated

188 by the intersection between the phenological stages and the straight line passing through the

189 two phenological observations bounding the stage (Fig. 1).

190

191 **Quantification of the within-population variability of leaf phenology.**

192

193 We used the standard deviation of BB_i and LS_i (SD_{BBi} and SD_{LSi}, respectively, expressed as a

194 number of days) as a measurement of the within-population variability of spring and autumn

195 phenology for a population-year. Standard deviation is a measure of the average duration

196 between each individual BB_i or LS_i date and the average date established over all individuals.

197 In other words, it is a metric of the dispersion of data values in a distribution. A low standard

198 deviation indicates that individual phenological dates are close to each other, while a high

199 standard deviation indicates that phenological dates are spread out.

200
201 *<Expected location of Figure 1>*

202
203 **Quantification of the speed of phenological events.**

204

205 In order to further describe the spread of phenological events among individuals, we calculated

206 the speed of the budburst or leaf senescence sequence within population-years. The

207 phenological development speed for each population-year is as follows:

208 $$Speed_{py} = \frac{\Delta_{stage}}{\Delta_{t_{py}}} \qquad \text{(eq. 1)}$$

209 where $Speed_{py}$ is the speed of the phenological sequence for the population-year *py* of interest,

210 expressed in percentage of phenological development per day; Δ_{stage} is the difference (in

211 percentage points of phenological development) between the occurrence of two stages of the

212   within-population phenological sequence (e.g. from 10% to 90% trees reaching BB$_i$, we

213   calculate Δ_{stage}= 90-10 = 80 points); and $\Delta_{t_{py}}$ is the duration in day between the two stages of

214   interest for the population-year considered. We calculated the speed of spring and autumn

215   phenological sequences over the intervals from 10% to 90% trees reaching BB$_i$ (resp. LS$_i$) in a

216   given population-year, as we observed that this stage interval resulted in the highest Pearson

217   correlation coefficient with SD$_{BBi}$ (resp. SD$_{LSi}$) (Suppl. Mat. 4).

218

219   **Statistical methods**

220

221   Before conducting a detailed statistical analyses, and because we know of no paper describing

222   such data, we plotted for illustrative purposes the SD$_{BBi}$ and SD$_{LSi}$ data against the absolute

223   minimum and average temperature calculated over the spring / autumn phenological sequences

224   (from the first to the last tree reaching budburst / leaf senescence) of each population-year (in

225   relation with our hypothesis n°1) and against the species-specific site-year average date of the

226   considered phenological event (in relation with our hypothesis n°2). We further computed the

227   rank (Spearman's) correlation between SD$_{BBi}$ or SD$_{LSi}$ and these variables. Then, in order to

228   test our hypotheses (i.e. hypothesis n°1: warm springs or cold autumns would decrease SD$_{BBi}$

229   or SD$_{LSi}$, respectively; hypothesis n°2: a late budburst or senescence date would also decrease

230   SD$_{BBi}$ or SD$_{LSi}$, respectively) we fitted our data with a linear model of the form (in the case of

231   spring phenology):

232    $$\log(SD_{\text{BB}_{j,k}}) \sim Tavg_{\text{BB}_{j,k}} + Date_{\text{BB}_{j,k}} + Species_k \quad \text{(eq. 2)}$$

233   Where $SD_{\text{BB}_{j,k}}$ (days) is the standard deviation of budburst dates among individuals of

234   population-year j of species k; $Tavg_{\text{BB}_{j,k}}$ (°C) is the temperature averaged throughout the BB

235   sequence of population-year j of species k; $Date_{\text{BB}_{j,k}}$(DoY) is the observed average BB date for

236   population-year j of species k; and $Species_k$ accounts for a possible *species* effect on the

237   intercept of the relation (i.e. the average SD$_{BBi}$ may differ among species). For autumn

238   phenology, we expressed $SD_{\text{LS}_{j,k}}$ under (eq. 2) as a function of $Tavg_{\text{LS}_{j,k}}$ (°C), $Date_{\text{LS}_{j,k}}$ (DoY),

239   and $Species_k$. More complex model forms (including interaction terms temperature*species,

240   date*species and date*species*temperature) were tested for both BB and LS but were not

241   significantly different from zero and are consequently not reported. SD$_{BBi}$ and SD$_{LSi}$ data were

242   log-transformed (eq. 2) for satisfying the linear model hypothesis of residuals homoscedasticity.

243   In order to compare the average values of SD$_{BBi}$ or SD$_{LSi}$ we used Wilcoxon's rank sum test.

244 All statistical analyses were conducted with R 3.4.0. Because the experimental plan was
245 unbalanced, we used the "Anova" function from the "car" library to test model parameters.
246

Quantification of the uncertainty of the within-population variability metric
248

249 Determining the average date or quantifying the within-population variance of a phenological
250 event is subject to a population sampling effect, for obvious statistical reasons (see Sokal &
251 Rohlf, 1995, p. 136). We used the standard deviation from the average (SD) as a metric to
252 quantify the within-population variability of spring and autumn phenology (see above). Since
253 SD is sensitive to the size of the sample for which it is established, we quantified its uncertainty
254 due to population subsampling.

255 In a given population, phenological observations were conducted over N individuals
256 (Suppl. Mat. 3) leading to standard deviation values of budburst (SD_{BBi}). When subsampling n
257 individuals within the population ($n < N$), we decrease the precision of our SD_{BBi} estimate. To
258 quantify this loss of precision, we calculated the SD of phenological event dates (i.e. SD_{BBi} and
259 SD_{LSi}) for subsample sizes n taking values from 2 to N individuals. For each n, we randomly
260 picked individuals in the population sample and calculated the associated SD. We repeated the
261 sub-sampling 5000 times for each n to obtain a robust estimate of the range of possible standard
262 deviation values associated with a subsample size of n individuals (SD_n) (Fig. 2). We used the
263 distribution of SD_n values to quantify the uncertainty of the within-population variability of the
264 considered phenological event (e.g. uncertainty of SD_{BBi}) at a given sample size n (e.g. $SD_{BBi,n}$).
265 By repeating this process over all the populations sampled, we created a conservative
266 uncertainty scale by reporting for each possible sample size n the largest uncertainty of SD_{BBi}
267 or SD_{LSi} calculated among all populations (i.e. maximum value of $SD_{BBi,n}$ or $SD_{LSi,n}$). In
268 subsequent analyses, we assigned to each SD_{BBi} or SD_{LSi} value its worst uncertainty estimate
269 for the sample size of the population-year considered, according to this scale.

270 We determined that a minimum sample size of 28 individuals is required to estimate
271 SD_{BBi} with an uncertainty of 3 days (compared with the time resolution of BB observations
272 which is 3.7 days), and a minimum sample size of 23 individuals is required to estimate SD_{LSi}
273 with an uncertainty of 7 days (compared with the time resolution of LS observations which is
274 7.1 days) (Suppl. Mat. 5).

275

276 *<Expected location of Figure 2>*

277

Results

Within-population variability of spring phenology

The average duration between each individual budburst date (BB_i) and the population-year average date, quantified as SD_{BBi}, was 4.0 days (ranging from 1.7 to 9.7 days). Considering all species and populations together, SD_{BBi} was not correlated with the average date of budburst (Fig. 3a). SD_{BBi} was significantly and negatively correlated with both the average and the absolute minimum temperatures during the budburst period (Fig. 3b,c). The relation of SD_{BBi} with average temperatures during the budburst period decreased from around 10 days at 9°C to 2.5 days at 12°C and then levelled off (Fig. 3b). The relation between SD_{BBi} and minimum temperatures during the budburst period decreased from 10 days at -1.8°C to 1.8 days at 3.7°C degrees (Fig. 3c).

<Expected location of Figure 3>

A linear model considering simultaneously the influence of temperatures, of the budburst date, and of the species described a good share of the variability of $\log(SD_{BBi})$ (Adjusted R²=0.59, F=6.11, p<10⁻⁴). In this model, both T_{avg} and the budburst date decreased SD_{BBi} (Table 2). We observed a significant influence of the "species" factor on the intercept of the relation, meaning that the general trend to a decrease of $\log(SD_{BBi})$ with increasing T_{avg} and budburst date was translated upward or downward depending on the species considered.

<Expected location of Table 2>

The speed of budburst was positively correlated with the average temperature during phenological development period (Fig. 4a). Moreover, the speed of budburst was related with the individual variability of budburst dates (Fig. 4b). Thus, the faster the bud development in the population, the lower the within-population variability of budburst.

<Expected location of Figure 4>

Within-population variability of leaf senescence

The average duration between each individual leaf senescence date (LS_i) and the population-year average date, quantified as SD_{LSi}, was 8.5 days (ranging from 4.2 to 15.7 days). This is

315   significantly higher than SD_{BBi} (Wilcoxon rank sum test, p<1e-11). When considered

316   independently, neither the average date of senescence (Fig. 5a), nor the average temperatures

317   (Fig. 5b), nor the minimum temperatures during the senescence period (Fig. 5c), were

318   significantly correlated with SD_{LSi}.

319

320   *<Expected location of Figure 5>*

321

322   A linear model considering simultaneously the influence of temperatures, of the leaf

323   senescence date, and of the species described a fair amount of the variability of $\log(SD_{LSi})$

324   (Adjusted R²=0.36, F=5.96, p<0.0003). In this model, both T_{avg} and the leaf senescence date

325   increased SD_{LSi} (Table 3). We observed a significant influence of the "species" factor on the

326   intercept of the relation, meaning that the general trend to an increase of $\log(SD_{LSi})$ with

327   increasing T_{avg} and senescence date was translated upward or downward depending on the

328   species considered.

329

330   *<Expected location of Table 3>*

331

332   The speed of leaf senescence was not related with the average temperatures during the

333   LS period (Fig. 6a). The within-population variability of LS was strongly negatively correlated

334   with the speed of leaf senescence (Fig. 6b).

335

336   *<Expected location of Figure 6>*

337

338

339

340   **Discussion**

341

342   **Determining robust estimates of the within-population variability of leaf phenology**

343

344   The within-population variability of leaf phenology affects the estimation of the statistical

345   parameters of a tree population (e.g. average date, within-population variability calculated as

346   the SD of the distribution etc.). This is all the more true that population sample sizes used in

347   most phenological studies are usually low (the median number of observed individuals is 15,

348   established across 132 tree populations reported in 22 papers; Liu et al., in prep.). Our study

349   revealed that given the natural variability of phenological traits within tree populations, 28 and

350   23 individuals are required to estimate the standard deviation of spring and leaf senescence

351   distribution with an accuracy of 3 and 7 days, respectively (Suppl. Mat. 5). Moreover, because

phenological observations are subjective, phenological parameter estimations are subject to an "observer uncertainty". Some protocols aim to reduce this uncertainty. For instance, Cole and Sheldon (2017) collected phenological observations using five observers, covering the same proportion of habitats and elevation. No quantification of the "observer effect" has been done yet (Liu et al., in prep).

Factors affecting the within-population variability of budburst

Our hypothesis n°1, which predicted that warmer spring would decrease the within-population variability, was validated (Fig. 3b,c; Table 2). Moreover, we observed positive correlations between the speed of phenological development within populations and temperature (Fig. 4a). The overall hastening of the budburst date by warm temperatures has been established for a long time (e.g. Delpierre et al. 2016). More recently, warm temperatures were demonstrated to affect the rate of bud development (Basler and Korner, 2014). Our results show that the impact of warm temperatures extend at higher integration scales: that of the individual tree crown (Suppl. Mat. 6), and that of the tree population (Fig. 4a). Overall, our results support the idea of considering phenological traits such as the required temperature sum for reaching budburst (Kramer et al., 2008; Oddou-Muratorio and Davi, 2014) as discriminant among tree individuals in a population. However, the interplay between tree individual sensitivities to photoperiod and exposure to chilling remains to be determined before being able to build robust models of the within-population variability of budburst. Indeed, our results showed that beyond the influence of average temperature conditions during budburst, the average date of budburst (or photoperiod, since both are almost equivalent in spring on the latitudinal range of our study, Table 1) influenced the within-population variability (Table 2). Later budburst dates are associated with a lower within-population variability of budburst (see negative coefficient associated to $Date_{BBi}$ in Table 2), and more generally with a faster development of leaves (Klosterman et al., 2018). Contrary to the influence of temperatures, the influence of budburst date on SD_{BBi} is probably of second order, since it is not significant (Fig. 3a) without simultaneously considering an effect of both temperatures and the species (as appears in Table 2). We tested our hypotheses over a set of populations from different species and locations, looking for general patterns. For some species (*Acer pseudoplatanus*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*), we could only gather data for two population-years, satisfying our criteria as regards the number of trees sampled (a minimum of 28 tree per population, see above) and the time resolution of phenological observations (twice a week for budburst). It is

clear that a detailed understanding of the within-population variability of budburst, and its stratification among species, will require more data.

Factors affecting the within-population variability of leaf senescence.

Our first hypothesis, which predicted that cold autumn would decrease the within-population variability of LS was partially validated. Individually, the three factors do not influence the SD_{LSi} (Fig. 5). However, when considered together, the average temperatures, the date of LS and the Species predict SD_{LSi} (Table 3). In agreement with our prediction, increasing temperatures is linked with higher SD_{LSi}. However, contrary to our expectations later senescence dates are linked with higher SD_{LSi}.

Overall, the linear model explains 36% of the variability of $\log(SD_{LSi})$, strongly suggesting that other factors are probably acting here. When considered as a single predictor, temperature is not a related to SD_{LSi} (Fig. 5b,c), nor is it related with the speed of LS (Fig. 6a) which is a powerful predictor of SD_{LSi} (Fig. 6b). More generally, the interplay of temperature with photoperiod and other drivers likely to affect leaf senescence (e.g. soil water stress or the date of budburst) remains unclear to date (Gill et al. 2014; Delpierre et al. 2016). Hence it is not surprising that we are not able to identify clear drivers explaining the within-population variability of leaf senescence. A recent study by Liu et al. (2018) revealed that temperature cues are related to leaf senescence in a complex way, with antagonistic influences of autumn (delaying) and summer (hastening) leaf senescence in several temperate trees species. In line with their work, and contrary to our hypothesis, we observed that SD_{LSi} were more strongly related with summer temperatures (Suppl. Mat. 7) than with autumn temperature (Fig. 5). The correlation is negative, meaning that warm summer temperatures are related with a low SD_{LSi}, while cold summer temperatures are related with a high SD_{LSi} (Suppl. Mat. 7). Since warm summer temperatures may reduce the cold-degree-days (CDD) requirement for leaf senescence in some species (Liu et al., 2018, 2019), a logical link would be that a warmer summer reduces the within-population variability of CDD requirement for leaf senescence, implying a narrower distribution of leaf senescence dates in the following autumn.

Conclusion

In this study, we took advantage of a high number of trees observed per population to evaluate the uncertainty of phenological metrics caused by population subsampling. We calculated that a minimum of 28 (23) trees is required to evaluate with an uncertainty of 3 (respectively 7) days

421 the within-population standard deviation of budburst (respectively leaf senescence). Most
422 phenological studies concern a lower number of individuals per population. If similar studies
423 are to be conducted in the future, this will require an increase in the population sampling effort.
424   We have demonstrated that the within-population individual variability of budburst
425 (SD_{BBi}) in temperate tree populations decreases with increasing temperature during budburst.
426 Beyond the single effect of temperature, we showed that the population average budburst date
427 and the species identity affect SD_{BBi}. The relation of the within-population individual variability
428 of leaf senescence (SD_{LSi}) with autumn temperatures, the average date of leaf senescence and
429 species identity was weaker than the one established for spring. Contrary to our hypothesis, we
430 observed no strong link between SD_{LSi} and temperature conditions during leaf senescence.
431 However, in line with recent advances in the study of leaf senescence, we evidenced a clear
432 relation of SD_{LSi} with summer temperatures.
433

Acknowledgements

Author's contributions

N.D. and R.D. designed the research. R.D. and N.D. performed the research and wrote the
manuscript. All authors contributed phenological data and commented on the manuscript.

References

Badeck F-W, Bondeau A, Bottcher K, Doktor D, Lucht W, Schaber J, and Sitch S (2004).
    Responses of spring phenology to climate change. New Phytol. 162, 295–309.

Basler D, and Korner C (2014). Photoperiod and temperature responses of bud swelling and
    bud burst in four temperate forest tree species. Tree Physiol. 34, 377–388.

Chesnoiu E, Şofletea N, Curtu A, Toader A, Radu R, & Enescu M (2009). Bud burst and flowering
    phenology in a mixed oak forest from Eastern Romania. Annals Of Forest Research, 52(1),
    199-206.

Chuine I (2000). A Unified Model for Budburst of Trees. J. Theor. Biol. 207, 337–347.

Cole EF, and Sheldon BC (2017). The shifting phenological landscape: Within- and between-
    species variation in leaf emergence in a mixed-deciduous woodland. Ecol. Evol. 7, 1135–
    1147.

Crawley MJ, and Akhteruzzaman M (1988). Individual Variation in the Phenology of Oak Trees
    and Its Consequences for Herbivorous Insects. Funct. Ecol. 2, 409.

Delpierre N, Dufrêne E, Soudani K, Ulrich E, Cecchini S, Boé J, and François C (2009a). Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. Agric. For. Meteorol. 149, 938–948.

Delpierre N, Soudani K, François C, KöStner B, Pontailler J-Y, Nikinmaa E, Misson L, Aubinet M, Bernhofer C, Granier A, et al. (2009b). Exceptional carbon uptake in European forests during the warm spring of 2007: a data-model analysis. Glob. Change Biol. 15, 1455–1474.

Delpierre N, Vitasse Y, Chuine I, Guillemot J, Bazot S, Rutishauser T, and Rathgeber CBK (2016). Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. Ann. For. Sci. 73, 5–25.

Delpierre N, Guillemot J, Dufrêne E, Cecchini S, and Nicolas M (2017). Tree phenological ranks repeat from year to year and correlate with growth in temperate deciduous forests. Agric. For. Meteorol. 234–235, 1–10.

Denny EG, Gerst KL, Miller-Rushing AJ, Tierney GL, Crimmins TM, Enquist CAF, Guertin P, Rosemartin AH, Schwartz MD, Thomas KA, et al. (2014). Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. Int. J. Biometeorol. 58, 591–601.

Donnelly A, and Yu R (2017). The rise of phenology with climate change: an evaluation of IJB publications. Int. J. Biometeorol. 61, 29–50.

Donnelly A, Jones M, and Sweeney J (2004). A review of indicators of climate change for use in Ireland. Int. J. Biometeorol. 49.

Estrella N, and Menzel A (2006). Responses of leaf colouring in four deciduous tree species to climate and weather in Germany. Clim. Res. 32, 253–267.

Firmat C, Delzon S, Louvet J-M, Parmentier J, and Kremer A (2017). Evolutionary dynamics of the leaf phenological cycle in an oak metapopulation along an elevation gradient. J. Evol. Biol. 30, 2116–2131.

Fu YH, Zhang X, Piao S, Hao F, Geng X, Vitasse Y, Zohner C, Peñuelas J, & Janssens IA (2019). Daylength helps temperate deciduous trees to leaf-out at the optimal time. Global Change Biology.

Gressler E, Jochner S, Capdevielle-Vargas RM, Morellato LPC, and Menzel A (2015). Vertical variation in autumn leaf phenology of Fagus sylvatica L. in southern Germany. Agric. For. Meteorol. 201, 176–186.

Harrington R, Woiwod I, and Sparks T (1999). Climate change and trophic interactions. 14, 5.

Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, & New M (2008). A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. Journal of Geophysical Research: Atmospheres, 113(D20).

Klosterman S, Hufkens K, and Richardson AD (2018). Later springs green-up faster: the relation between onset and completion of green-up in deciduous forests of North America. Int. J. Biometeorol.

Kramer K, Buiteveld J, Forstreuter M, Geburek T, Leonardi S, Menozzi P, Povillon F, Schelhaas MJ, Teissier du Cros E, Vendramin GG, et al. (2008). Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. Ecol. Model. 216, 333–353.

Lieth H, 1974. Phenology and Seasonality Modeling. Springer Verlag, Berlin, 444 pp.

Lim PO, Kim HJ, and Gil Nam H (2007). Leaf Senescence. Annu. Rev. Plant Biol. 58, 115–136.

505 Liu G, Chen X, Zhang Q, Lang W, and Delpierre N (2018). Antagonistic effects of growing season and autumn temperatures on the timing of leaf coloration in winter deciduous trees. Glob. Change Biol. 24, 3537–3545.

508 Liu G, Chen X, Fu Y, and Delpierre N (2019). Modelling leaf coloration dates over temperate China by considering effects of leafy season climate. Ecol. Model. 394, 34–43.

510 Ma Q, Huang J-G, Hänninen H, and Berninger F (2018). Reduced geographical variability in spring phenology of temperate trees with recent warming. Agric. For. Meteorol. 256–257, 526–533.

513 Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-KüBler K, Bissolli P, Braslavská O, Briede A, et al. (2006). European phenological response to climate change matches the warming pattern. Glob. Change Biol. 12, 1969–1976.

516 Oddou-Muratorio S, and Davi H (2014). Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. Evol. Appl. 7, 453–467.

518 Richardson AD, Black TA, Ciais P, Delbart N, Friedl MA, Gobron N, Hollinger DY, Kutsch WL, Longdoz B, Luyssaert S, et al. (2010). Influence of spring and autumn phenological transitions on forest ecosystem productivity. Philos. Trans. R. Soc. B Biol. Sci. 365, 3227–3246.

522 Singh RK, Svystun T, AlDahmash B, Jönsson AM, and Bhalerao RP (2017). Photoperiod- and temperature-mediated control of phenology in trees - a molecular perspective. New Phytol. 213, 511–524.

525 Sokal RR, and Rohlf FJ (1995) Biometry: The Principles and Practice of Statistics in Biological Research. 3rd Edition, W.H. Freeman and Co., New York.

527 Thakur N, Sharma V, and Kishor K (2016). Leaf senescence: an overview. Indian J. Plant Physiol. 21, 225–238.

529 Vilhar U, De Groot M, Zust A, Skudnik M, and Simončič P (2018). Predicting phenology of European beech in forest habitats. iForest - Biogeosciences For. 11, 41–47.

531 Vitasse Y, and Basler D (2013). What role for photoperiod in the bud burst phenology of European beech. Eur. J. For. Res. 132, 1–8.

533 Vitasse Y, Porté AJ, Kremer A, Michalet R, and Delzon S (2009). Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. Oecologia 161, 187–198.

536 Vitasse Y, François C, Delpierre N, Dufrêne E, Kremer A, Chuine I, and Delzon S (2011). Assessing the effects of climate change on the phenology of European temperate trees. Agric. For. Meteorol. 151, 969–980.

539 Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, and Bairlein F (2002). Ecological responses to recent climate change. Nature 416, 389–395.

542 Way DA, and Montgomery RA (2015). Photoperiod constraints on tree phenology, performance and migration in a warming world: Photoperiod limits on tree climate responses. Plant Cell Environ. 38, 1725–1736.

545 Wesołowski T, and Rowiński P (2006). Timing of bud burst and tree-leaf development in a multispecies temperate forest. For. Ecol. Manag. 237, 387–393.

547 White MA, Thornton PE, and Running SW (1997). A continental phenology model for monitoring vegetation responses to interannual climatic variability. Glob. Biogeochem. Cycles 11, 217–234.

550 White MA, Running SW, and Thornton PE (1999). The impact of growing-season length
551   variability on carbon assimilation and evapotranspiration over 88 years in the eastern US
552   deciduous forest. Int. J. Biometeorol. 42, 139–145.
553 Xie Y, Wang X, Wilson AM, & Silander JA (2018). Predicting autumn phenology: How deciduous
554   tree species respond to weather stressors. Agricultural and Forest Meteorology, 250, 127-
555   137.
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557 **Table 1. Characteristics of the phenological sites.** The sites were sorted according to longitude. Asl=
558 above sea level.

Sites	Site locations	Species	Years of spring observation	Years of autumn observation	Temperature data acquisition	Reference
Wytham Woods	51.8°N, 1.3°W, 60 m asl, England	*Fraxinus excelsior, Quercus robur, Acer pseudoplatanus, Fagus sylvatica, Corylus avellana, Betula pendula*	2013-2014	none	Local (0 km), below tree canopy	(Cole and Sheldon, 2017)
Toulenne	44.5°N, 0.25°W, 20 m asl, France	*Quercus petraea*	none	2014, 2016, 2017	Meteorological station (0.3 km), measured at 2-m height over grassland	(Firmat et al., 2017)
Orsay	48.7°N 2.2°E, 150 m asl, France	*Quercus petraea, Castanea sativa, Carpinus betulus*	2012-2015, 2018	2011-2015	Meteorological station (4 km), measured at 2-m height over grassland	(Delpierre et al., 2017)
Barbeau	48.5°N, 2.8°E, 90 m asl, France	*Quercus petraea, Carpinus betulus*	2013, 2015-2017	2015-2017	Flux tower (0 km), above tree canopy	(Delpierre et al., 2017)
Freising	48.2°N, 11.4°E, 450 m asl, Germany	*Fagus sylvatica*	none	2012	Local (0 km), below tree canopy	(Gressler et al., 2015)
Fundeanu	46.0°N, 26.7°E, 230 m asl, Romania	*Quercus robur*	2008, 2009, 2015-2017	none	Regional circulation model (spatial resolution 0.5°)	(Chesnoiu et al., 2009)

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561　**Table 2. Outputs from a linear model testing the impact of average temperature, budburst average**
562　**date and species on log(SD$_{BBi}$).** The model is described by eq. 2. Bold lines highlight significant
563　coefficients (p<0.05). *Acer pseudoplatanus* was used as a reference for calculating the intercept, so all
564　other species effect are expressed as a difference to the *Acer* coefficient (illustrated with Δ).
565

Model parameter	Estimate	SE	t-value	Pr(>|t|)
Tavg$_i$	**-0.10**	**0.03**	**-3.28**	**0.003**
Date$_{BBi}$	**-0.03**	**0.01**	**-4.86**	**<10^{-4}**
***Acer pseudoplatanus* (Intercept)**	**6.90**	**0.86**	**8.05**	**<10^{-7}**
Δ*Betula pendula*	-0.49	0.27	-1.79	0.085
Δ*Carpinus betulus*	**-1.30**	**0.26**	**-4.94**	**<10^{-4}**
Δ*Castanea sativa*	-0.44	0.23	-1.92	0.067
Δ*Corylus avellana*	**-0.84**	**0.28**	**-2.97**	**0.006**
Δ*Fagus sylvatica*	-0.26	0.27	-0.96	0.347
Δ*Fraxinus excelsior*	0.42	0.30	1.43	0.165
Δ*Quercus petraea*	**-0.68**	**0.23**	**-2.98**	**0.006**
Δ*Quercus robur*	**-0.59**	**0.22**	**-2.61**	**0.015**

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568 **Table 3. Outputs from a linear model testing the impact of average temperature, leaf senescence**
569 **average date and species on $\log(SD_{LSi})$.** The model is described by eq. 2. Bold lines highlight
570 significant (p<0.05) coefficients. *Carpinus betulus* was used as a reference for calculating the intercept,
571 so all other species effect are expressed as a difference to the *Carpinus* coefficient (illustrated with Δ).
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Model parameter	Estimate	SE	t-value	Pr(>|t|)
$Tavg_i$	**0.17**	**0.04**	**3.998**	**0.0003**
$Date_{LSi}$	**0.04**	**0.01**	**4.128**	**0.0002**
***Carpinus betulus* (Intercept)**	**-12.43**	**3.59**	**-3.47**	**0.001**
Δ*Castanea sativa*	0.23	0.19	1.207	0.23
Δ*Quercus petraea*	**-0.34**	**0.13**	**-2.579**	**0.014**
Δ*Fagus sylvatica*	**-0.002**	**0.31**	**-0.007**	**0.994**

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Figure Captions

Figure 1. **Individual budburst development for *Quercus petraea* in Orsay, 2018**. Phenological observations for a given tree are linked by gray lines. The within-population variability (red double arrow, n= 58 trees) and the average date of budburst (blue vertical line) are presented. An example tree (yellow line) has been artificially advanced in time to exemplify its estimated budburst date (green vertical line).

Figure 2. Example of the quantification of the SD_{BBi} uncertainty due to subsampling for the *Quercus robur* population of Wytham Woods, 2014. (A) The distribution of possible standard deviation values of individual budburst dates for each sample size (196 individuals were observed for this population in 2014). We considered that the minimum sample size required for estimating SD_{BBi} accurately was reached when 90% of the standard deviation values were within 3 days (see text), corresponding to 28 individuals in this case. (B) The distribution of the standard deviations values (SD_{BBi}) estimated by randomly picking 28 trees among 196 (indicated by the blue vertical line in plot A). The red lines in plots A and B indicate the best estimate of SD_{BBi}, calculated over 196 individuals.

Figure 3. Relation of SD_{BBi} with the population average date of budburst, and temperature conditions during budburst. SD_{BBi} (in days) is related to (a) the average date of budburst, (b) the average temperatures during the budburst period and (c) the absolute minimum temperature during the budburst period. *Rho*= Spearman's rank correlation established across population-years, with its p-value. Two values of Rho were calculated, including ("with Orsay 2012") or excluding ("without Orsay 2012") the maximum SD_{BBi} value of 9.7 days which was observed for the *Quercus petraea* population located in Orsay in 2012. Error bars indicate the subsampling uncertainties of standard deviation values.

Figure 4. The within-population speed of budburst depends on spring temperatures (a) and is related with SD_{BBi} (b). We calculated the speed of budburst over the interval stage of phenological development (from 10 to 90 % of BB_i in the population) best correlated with SD_{BBi}. The average temperatures were calculated between these two stages for each population-year.

Figure 5. Relation of SD_{LSi} with the population average date of leaf senescence, and temperature conditions during leaf senescence. SD_{LSi} (in days) is related to (a) the average date of leaf senescence, (b) the average temperatures during the leaf senescence period and (c) the lowest temperature during the leaf senescence period. *Rho*= Spearman's rank correlation established across population-years, with its p-value. The different species codes for *Quercus petraea* in the Toulenne common garden refer to the different altitudes where trees were collected before planting.

Figure 6. The within-population speed of leaf senescence does not depend on autumn temperatures (a) but is related with SD_{LSi} (b). We calculated the speed of leaf senescence over the interval stage of phenological development (from 10 to 90 % of LS_i in the population) best correlated with SD_{LSi}. The average temperatures were calculated between these two stages for each population-year. The different species codes for *Quercus petraea* tree populations observed in the Toulenne common garden refer to the different altitudes where trees were collected.