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# The within-population variability of leaf spring and autumn phenology is influenced by temperature in temperate deciduous trees.

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# 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.

We considered as target phenological events the occurrence of 50% of leaf buds opened (for spring, Fig.1) or 50% of senesced (coloured or fallen) leaves (for autumn) in individual tree crowns. A leaf bud is considered open “once a green leaf tip is visible at the end of the bud, but before the first leaf from the bud has unfolded to expose the leaf stalk (petiole) or leaf base” (Denny et al., 2014). For leaf senescence, observations of both the individual tree crown percentages of coloured (i.e. yellow for the study species) and fallen leaves were combined in a single senescence metric (Vitasse et al., 2009). Continuous bud development and leaf senescence stages were calculated for each tree by linear interpolation of visual observations, assuming that bud development and leaf senescence trajectories are linear around 50% opened buds or 50% senesced leaves, respectively. For each individual tree, the date of the target stage (hereafter $BB_i$ for spring and $LS_i$ for autumn, expressed as a day of year, DoY) was estimated by the intersection between the phenological stages and the straight line passing through the two phenological observations bounding the stage (Fig. 1).

## Quantification of the within-population variability of leaf phenology.

We used the standard deviation of $BB_i$ and $LS_i$ ($SD_{BBi}$ and $SD_{LSi}$, respectively, expressed as a number of days) as a measurement of the within-population variability of spring and autumn phenology for a population-year. Standard deviation is a measure of the average duration between each individual $BB_i$ or $LS_i$ date and the average date established over all individuals. In other words, it is a metric of the dispersion of data values in a distribution. A low standard deviation indicates that individual phenological dates are close to each other, while a high standard deviation indicates that phenological dates are spread out.

*<Expected location of Figure 1>*

## Quantification of the speed of phenological events.

In order to further describe the spread of phenological events among individuals, we calculated the speed of the budburst or leaf senescence sequence within population-years. The phenological development speed for each population-year is as follows:

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

where $Speed_{py}$ is the speed of the phenological sequence for the population-year $py$ of interest, expressed in percentage of phenological development per day; $\Delta_{\text{stage}}$ is the difference (in percentage points of phenological development) between the occurrence of two stages of the within-population phenological sequence (e.g. from 10% to 90% trees reaching $BB_i$, we calculate $\Delta_{\text{stage}} = 90\text{-}10 = 80$ points); and $\Delta_{t_{py}}$ is the duration in day between the two stages of interest for the population-year considered. We calculated the speed of spring and autumn phenological sequences over the intervals from 10% to 90% trees reaching $BB_i$ (resp. $LS_i$) in a given population-year, as we observed that this stage interval resulted in the highest Pearson correlation coefficient with $SD_{BBi}$ (resp. $SD_{LSi}$) (Suppl. Mat. 4).

## Statistical methods

Before conducting a detailed statistical analyses, and because we know of no paper describing such data, we plotted for illustrative purposes the $SD_{BBi}$ and $SD_{LSi}$ data against the absolute minimum and average temperature calculated over the spring / autumn phenological sequences (from the first to the last tree reaching budburst / leaf senescence) of each population-year (in relation with our hypothesis n°1) and against the species-specific site-year average date of the considered phenological event (in relation with our hypothesis n°2). We further computed the rank (Spearman's) correlation between $SD_{BBi}$ or $SD_{LSi}$ and these variables. Then, in order to test our hypotheses (i.e. hypothesis n°1: warm springs or cold autumns would decrease $SD_{BBi}$ or $SD_{LSi}$, respectively; hypothesis n°2: a late budburst or senescence date would also decrease $SD_{BBi}$ or $SD_{LSi}$, respectively) we fitted our data with a linear model of the form (in the case of spring phenology):

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

Where $SD_{\text{BB}_{j,k}}$ (days) is the standard deviation of budburst dates among individuals of population-year $j$ of species $k$; $Tavg_{\text{BB}_{j,k}}$ (°C) is the temperature averaged throughout the BB sequence of population-year $j$ of species $k$; $Date_{\text{BB}_{j,k}}$(DoY) is the observed average BB date for population-year $j$ of species $k$; and $Species_k$ accounts for a possible *species* effect on the intercept of the relation (i.e. the average $SD_{BBi}$ may differ among species). For autumn 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), and $Species_k$. More complex model forms (including interaction terms temperature*species, date*species and date*species*temperature) were tested for both BB and LS but were not significantly different from zero and are consequently not reported. $SD_{BBi}$ and $SD_{LSi}$ data were log-transformed (eq. 2) for satisfying the linear model hypothesis of residuals homoscedasticity. In order to compare the average values of $SD_{BBi}$ or $SD_{LSi}$ we used Wilcoxon's rank sum test.

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

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

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

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

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

*<Expected location of Figure 2>*

# 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 $R^2=0.59$, $F=6.11$, $p<10^{-4}$). 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 significantly higher than $SD_{BBi}$ (Wilcoxon rank sum test, p<1e-11). When considered independently, neither the average date of senescence (Fig. 5a), nor the average temperatures (Fig. 5b), nor the minimum temperatures during the senescence period (Fig. 5c), were significantly correlated with $SD_{LSi}$.

*<Expected location of Figure 5>*

A linear model considering simultaneously the influence of temperatures, of the leaf senescence date, and of the species described a fair amount of the variability of log($SD_{LSi}$) (Adjusted $R^2=0.36$, F=5.96, p<0.0003). In this model, both $T_{avg}$ and the leaf senescence date increased $SD_{LSi}$ (Table 3). We observed a significant influence of the "species" factor on the intercept of the relation, meaning that the general trend to an increase of log($SD_{LSi}$) with increasing $T_{avg}$ and senescence date was translated upward or downward depending on the species considered.

*<Expected location of Table 3>*

The speed of leaf senescence was not related with the average temperatures during the LS period (Fig. 6a). The within-population variability of LS was strongly negatively correlated with the speed of leaf senescence (Fig. 6b).

*<Expected location of Figure 6>*

# Discussion

## Determining robust estimates of the within-population variability of leaf phenology

The within-population variability of leaf phenology affects the estimation of the statistical parameters of a tree population (e.g. average date, within-population variability calculated as the SD of the distribution etc.). This is all the more true that population sample sizes used in most phenological studies are usually low (the median number of observed individuals is 15, established across 132 tree populations reported in 22 papers; Liu et al., in prep.). Our study revealed that given the natural variability of phenological traits within tree populations, 28 and 23 individuals are required to estimate the standard deviation of spring and leaf senescence 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 the within-population standard deviation of budburst (respectively leaf senescence). Most phenological studies concern a lower number of individuals per population. If similar studies are to be conducted in the future, this will require an increase in the population sampling effort.

We have demonstrated that the within-population individual variability of budburst ($SD_{BBi}$) in temperate tree populations decreases with increasing temperature during budburst. Beyond the single effect of temperature, we showed that the population average budburst date and the species identity affect $SD_{BBi}$. The relation of the within-population individual variability of leaf senescence ($SD_{LSi}$) with autumn temperatures, the average date of leaf senescence and species identity was weaker than the one established for spring. Contrary to our hypothesis, we observed no strong link between $SD_{LSi}$ and temperature conditions during leaf senescence. However, in line with recent advances in the study of leaf senescence, we evidenced a clear relation of $SD_{LSi}$ with summer temperatures.

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## 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.

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**Table 1. Characteristics of the phenological sites.** The sites were sorted according to longitude. Asl= 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) |

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

| 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** |

**Table 3. Outputs from a linear model testing the impact of average temperature, leaf senescence average date and species on log($SD_{LSi}$).** The model is described by eq. 2. Bold lines highlight significant ($p<0.05$) coefficients. *Carpinus betulus* was used as a reference for calculating the intercept, so all other species effect are expressed as a difference to the *Carpinus* coefficient (illustrated with Δ).

| 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** |

## 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.