

# Tree phenological ranks repeat from year to year and correlate with growth in temperate deciduous forests



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## ABSTRACT

The timing of leaf phenophases greatly influences the functioning of trees. Phenological traits are thus considered major components of tree fitness, and are expected to be strongly selected under environmental or biotic pressures. To date, most phenological studies have been conducted at the population scale, with comparatively very few works at the scale of individuals. We take advantage of a unique phenological database, consisting of leaf unfolding (LU) and leaf senescence (LS) observations done at the individual scale for 5 years over 35 populations, representing >1200 dominant and co-dominant trees of three species (*Quercus robur*, *Quercus petraea* and *Fagus sylvatica*), to document the within-population variability of phenological traits in temperate deciduous forest trees. We show that individual phenological ranks mostly repeat from year to year among trees of a given population, though LU ranks tend to repeat more than LS ranks. Using simulated dynamics of soil water content, we suggest that inter-individual differences in the access to soil water may play a role in determining tree phenological ranks. The timing of leaf phenology is further correlated with individual growth in a given tree population. In Beech populations, early-leafers tend to grow more. On the other hand, Oak trees entering senescence later tend to grow more. The growth of Oak trees, being more prone to spring pathogenic attacks than Beech, may benefit less from a spring extension of leaf display.

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## 1. Introduction

The timing of leaf phenophases is a major fingerprint of climate change (Menzel, 2013; Parmesan and Yohe, 2003), which has received considerable attention over the past two decades. Huge efforts have been conducted to identify which environmental drivers are involved in determining the spatio-temporal variability of phenophases among forest tree populations. Experimental, observational and modelling results usually converge in identifying temperature and photoperiod as the most influential cues (Delpierre et al., 2016; Way and Montgomery, 2014). However, recent studies depict a more complex pattern in which (1) the soil water status can probably modulate the timing of both autumn (Archetti et al., 2013; Estrella and Menzel, 2006; Hwang et al., 2014; Xie et al., 2015) and possibly spring (Fu et al., 2014a; Schnull and

Thomas, 2000) phenophases, (2) the timing of leaf senescence may be partially dependent on the timing of spring (Fu et al., 2014b).

The timing and duration of leaf display has considerable impacts on ecosystem functioning and climate feedbacks (Richardson et al., 2013), as well as deep, and less well studied, ecological implications. It is for instance a key determinant of the carbon (Ahrends et al., 2009; Delpierre et al., 2009b; Richardson et al., 2010) and, probably, nutrient (Nord and Lynch, 2009) acquisitions of trees. Phenological traits are thus considered major components of tree fitness, and are expected to be strongly selected under environmental or biotic pressures. Considerable work has been done for describing and understanding the local adaptation of tree phenology to environmental conditions over large climate (latitudinal or altitudinal) gradients (Alberto et al., 2013; Savolainen et al., 2007), which is evidenced by the clinal responses often observed in so-called *common garden* experiments (Deans and Harvey, 1995; Vitasse et al., 2009a; Wuehlisch et al., 1995).

Comparatively to the knowledge gained at the population level, the within-population variability of adaptive traits received so far little consideration (Scotti et al., 2016). A survey of the literature dedicated to temperate Oaks and European Beech (Table 1)

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**Table 1**  
Within-population variability in the timing of budburst and leaf senescence in deciduous forest tree species, as reported in published papers. The number of years, populations, and individuals surveyed per population is indicated.

Phenological stage	Species	Reported range (days)	N years	N populations	N individuals	Latitude (°N)	Longitude (°E)	Reference
Bud burst	<i>Quercus petraea</i>	26	2	2	70	42.9–43.2	0.1–0.7	Dantec et al., 2015
	<i>Quercus petraea</i>	21 (13–32)	2	5	26	42.9–43.2	0.1–0.7	Vitasse, 2009
	<i>Quercus petraea</i>	11–12 <sup>b</sup>	2	1	31	48.5	2.8	Delpierre N, unpublished (FR-Fon forest <sup>c</sup> )
	<i>Quercus petraea</i>	14 (7–35)	5	15	36	see Fig. 1	see Fig. 1	this study
	<i>Quercus robur</i>	23	1	1	222	46	27.7	Chesnoiu et al., 2009
	<i>Quercus robur</i>	21	3	3	220	44.4	–0.5	Scotti-Saintagne et al., 2004
	<i>Quercus robur</i>	26 (25–27)	2	1	36	unknown	unknown	Crawley and Akterhuzaman, 1988
	<i>Quercus robur</i>	23 (18–26)	1–3	6	38	51.2	4.4	van Dongen et al., 1997
	<i>Quercus robur</i>	18	9	1	10	52.7	23.9	Wesołowski and Rowiński, 2006
	<i>Quercus robur</i>	20 (7–49)	5	8	36	see Fig. 1	see Fig. 1	this study
	<i>Quercus laevis</i>	17 (15–20)	2	3	98	34.7	–82.8	Fox et al., 1997
	<i>Fagus sylvatica</i>	14 (8–19)	3	1	19–30	48.4	11.6	Capdevielle-Vargas et al., 2015
	<i>Fagus sylvatica</i>	11 (4–29)	1–4	8	170	42.5–53.2	5.7 to 15.4	Kramer, 2004
	<i>Fagus sylvatica</i>	15 (7–28)	5	12	36	see Fig. 1	see Fig. 1	this study
Leaf senescence <sup>a</sup>	<i>Quercus petraea</i>	33	1	1	31	48.5	2.8	Delpierre N, unpublished (FR-Fon forest <sup>c</sup> )
	<i>Quercus petraea</i>	22 (7–56)	5	15	36	see Fig. 1	see Fig. 1	this study
	<i>Quercus robur</i>	19 (7–56)	5	8	36	see Fig. 1	see Fig. 1	this study
	<i>Fagus sylvatica</i>	28 (21–36)	3	1	19–30	48.4	11.6	Capdevielle-Vargas et al., 2015
	<i>Fagus sylvatica</i>	26 (7–56)	5	12	36	see Fig. 1	see Fig. 1	this study

<sup>a</sup> 50% colored or fallen leaves.

<sup>b</sup> data from years 2013 and 2015, with late, cold springs.

<sup>c</sup> the FR-Fon forest is member of the ICOS network ([www.barbeau.u-psud.fr](http://www.barbeau.u-psud.fr)).

yet highlights a large within-population variability in the timing of spring and autumn phenophases (mean within-population amplitude of 19 days and 26 days, respectively, Table 1). This within-population variability of tree phenology is remarkable, being for instance comparable with the among-population variability observed for spring (autumn) phases over a 560 (1300)-m elevation gradient (as calculated from Vitasse et al., 2009b for Oak populations). Noticeably more than 75% of the European tree populations of temperate Oaks and European Beech leaf out or enter senescence within these time ranges (Suppl. Notes S1).

Within a tree population, the inter-individual variability of phenological timing may partly be influenced by micro-environmental variations (*sensu lato*, i.e. considering both micro-meteorological and pedological conditions; Scotti et al., 2016). This influence is expected to be moderate if we focus on, e.g., the timing of budburst among dominant individuals. Indeed, those trees experience very similar conditions in terms of air temperature and photoperiod (the prominent drivers of the timing of budburst). In that case, a genetic/epigenetic component is also likely involved in the differentiation of phenological timings, since the variability in phenological traits is maintained among individuals experiencing very similar environmental conditions (Bontemps et al., 2015). However, the influence of micro-environmental variations is likely to be more prominent in other cases. For instance, in cases when soil moisture interacts with temperature in determining the timing of a phenophase (e.g. leaf senescence; Hwang et al., 2014; Parelle et al., 2006), one may expect a decrease in the year-to-year repetition of phenological ranks among individuals from a moist to a dry year. Indeed, changes in the spatial pattern of soil moisture associated with soil drying-rewetting cycles (Suppl. Notes S2 see also Ma et al., 2010; Ngao et al., 2012) are likely to differentially affect trees sharing the same social status (hence similar temperature and photoperiod) in the timing of their phenological phases.

Most studies documenting the within-population variability of phenological traits have so far been conducted over short time intervals and for a limited number of tree populations (Table 1). Noticeably, most of these studies did not consider identified individuals, so that the variability of phenological traits remains principally described at the population scale. Hence we still lack an in-depth description of the within-population variability of phenological traits. Here, we take advantage of an extensive phenological dataset collected at the individual scale over 35 tree populations for 5 years, in order to document the within-population variability of phenological traits in temperate deciduous forests. We specifically address three hypotheses: (1) we hypothesize that among dominant individuals of a tree population, the genetic/epigenetic differentiation among individuals determines most of the phenological phenotype, with micro-environmental variations having a second-order role. Hence we expect to observe consistent individual phenological ranks from year to year. (2) We hypothesize that the recently evidenced interdependence of leaf phenological stages (e.g. Fu et al., 2014b) holds at the individual scale, so that phenological ranking repeats among trees from leaf unfolding in spring to leaf senescence in autumn. (3) We hypothesize that the large phenological range observed within populations influences stem wood growth of individuals of the same social status, with higher growth being associated to a longer leaf display.

## 2. Material and methods

### 2.1. Description of the phenological database

In this work, we analyse two phenological datasets. (1) The RENECOFOR phenological database (Delpierre et al., 2009a; Lebourgeois et al., 2008) includes 51 deciduous forest populations over France, among which 34 were selected on the basis of the completeness of their phenological datasets over the 2009–2013 period.

**Table 2**

Characteristics of the study populations. LU = leaf unfolding, LS = leaf senescence, H = tree height, CBH = circumference at breast height. Values reported for H and CBH are the overall (i.e., across all populations) mean  $\pm$  standard deviation.

Species	Number of populations	Average number of observation years		total number of observations		H (m)	CBH (cm)
		LU	LS	LU	LS		
<i>Quercus robur</i>	8	4.4	4.1	1258	1182	23.5 $\pm$ 1.0	131 $\pm$ 23
<i>Quercus petraea</i> <sup>a</sup>	15	3.9	3.5	2146	1918	27.3 $\pm$ 0.9	139 $\pm$ 22
<i>Fagus sylvatica</i>	12	3.8	4.1	1551	1663	25.1 $\pm$ 1.0	125 $\pm$ 17

<sup>a</sup> composed of 14 RENECOFOR populations, plus the Orsay population (see text for details).

Three of the most representative deciduous species in Western Europe are represented: *Fagus sylvatica* L. (European Beech: 12 populations, FS hereafter), *Quercus petraea* (Matt.) Liebl. (Sessile Oak: 14 populations, QP) and *Quercus robur* L. (Common Oak: 8 populations, QR) (Table 2). The selected populations are located between 50 and 1400 m asl (average 365 m asl, Fig. 1), with mean annual temperature (MAT) ranging from 7.2 to 13.2 °C (average 10.8 °C). All RENECOFOR populations are even-aged. At each population, the timing of spring and autumn phenophases were observed on 36 dominant and co-dominant trees located in a 0.5-ha area. (2) In addition a population of 59 dominant sessile Oak trees was monitored in a high forest near the Orsay campus (48.7°N 2.2°E, 100 m ASL) over the 2011–2015 period (Fig. 1). The purpose of this second dataset was to assess the sensitivity of the results to the method used for the phenological observations.

## 2.2. Methodology of phenological observations

Individual trees were tagged at all observation sites, allowing continuous phenological surveys over the same individuals along the study period. At the RENECOFOR sites, the date of leaf unfolding (LU) of an individual tree is reported as the first day of the week (expressed as day of year, DoY) with open buds and emerging leaves over 20–50% of its crown (corresponding to the BBCH10 code, Finn et al., 2007; Ulrich and Cecchini, 2009). The day of leaf senescence (LS) of an individual tree is the first day of the week (DoY) with coloured or fallen leaves over 20–50% of its crown (corresponding to BBCH93 code). The RENECOFOR populations were monitored

weekly from March to June for LU and from September to November for LS. A refined protocol was used for the Orsay population, where the percentages of open buds (spring), coloured and fallen leaves (autumn) were monitored 2–3 times a week (spring) to once a week (autumn) on a 10%-step scale. In spring, individual tree LU was marked as the date when 50% buds were opened; in autumn, LS was marked as the date when 50% leaves were coloured or fallen. The timing of spring and autumn phenophases was comparable among the RENECOFOR and Orsay tree populations (Table 3).

## 2.3. Data filtering

The RENECOFOR dataset potentially included 170 site-years of observation for both LU and LS (i.e. 34 sites observed for 5 years). We excluded from the analysis 27 (26) site-years of LU (LS) on the basis of RENECOFOR meta-data reporting that the observations had been conducted (i) by more than 2 observers or (ii) most of the time without binoculars over the study period. We additionally excluded 6 (7) site-years for which all 36 trees of a population were given the same LU (LS) date. The application of these quality criteria conserved 75% (69%) of the LU (LS) site-years.

## 2.4. Ancillary tree measurements

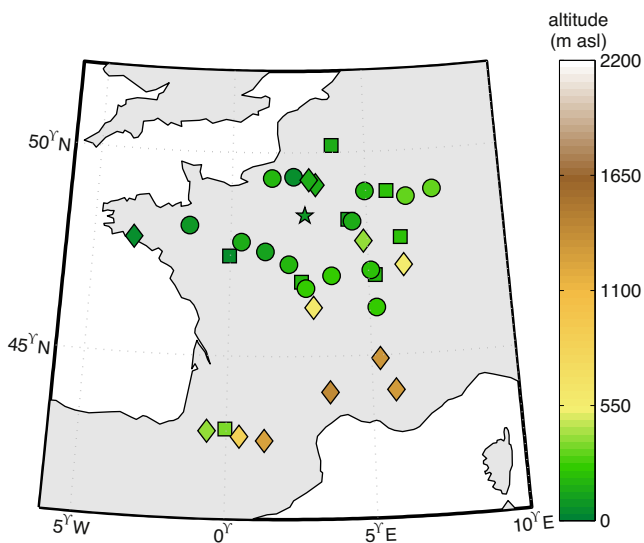
The height and circumference at breast height (CBH) of RENECOFOR trees were measured during forest inventory campaigns from 1991 to 2009 (Table 2), resulting in 2–5 surveys per plot with time intervals between two measurements ranging from 2 to 5 years. Tree basal area increments were calculated from the CBH data.

## 2.5. Soil water data

In order to evaluate the influence of soil water status on the repetition of phenological ranks, we used the CASTANEA process-based model to simulate the day-to-day variations of soil water content (SWC) at the RENECOFOR populations (see suppl. materials to (Guillemot et al., 2014) for a description of the parameters and simulation plan used on the RENECOFOR populations). To this aim, we correlated the population median phenological rank correlation coefficient (see below *Statistical analyses*) with the superficial soil water content (SWC, 0–30 cm depth) simulated by CASTANEA. SWC was integrated (i.e. averaged) over functionally meaningful time periods. We postulated that LU occurring on year  $y$  ( $LU_y$ ) could be influenced by SWC variations from the setting of buds in the preceding year (in July of  $y-1$ ) and that LS occurring on year  $y$  ( $LS_y$ ) could be influenced by SWC integrated over the current-year ( $y$ ) leafy season.

## 2.6. Statistical analyses

We used Spearman's rank correlation for evaluating (a) the repetition of tree phenological ranks within (a1) and across (a2) phenophases (referring to Hypothesis 1 and 2, resp.) and (b) the link between phenological rank and tree growth (Hypothesis 3). For



**Fig. 1.** Locations of the phenological stations. For the RENECOFOR stations, distinction is made among *Quercus petraea* (QP, circle), *Quercus robur* (QR, squares) and *Fagus sylvatica* (FS, diamond) populations. The Orsay QP population is indicated by a star. Colours denote the population altitudes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 3**  
Occurrence (day of year, DoY) of leaf unfolding (LU) and leaf senescence (LS) in the RENECOFOR and Orsay datasets. We report the average date of occurrence of LU and LS at the population scale across tree populations. For the RENECOFOR dataset, the standard deviation across populations appears between parentheses. In both datasets, we consider the phenological stage to occur at the population level when 50% of trees have reached the stage. QR = *Quercus robur*, QP = *Quercus petraea*, FS = *Fagus sylvatica*.

	Leaf unfolding (LU)				Leaf senescence (LS)			
	RENECOFOR		Orsay	RENECOFOR	RENECOFOR		Orsay	RENECOFOR
year	QR	QP	QP	FS	QR	QP	QP	FS
2009	105 (10)	103 (4)	–	116 (10)	287 (14)	297 (14)	–	283 (12)
2010	111 (9)	113 (4)	–	120 (10)	291 (9)	290 (13)	–	282 (14)
2011	100 (7)	96 (3)	–	107 (8)	287 (10)	289 (13)	286	284 (13)
2012	109 (12)	105 (10)	99	124 (8)	282 (16)	292 (18)	288	291 (11)
2013	116 (10)	116 (6)	112	119 (11)	289 (14)	291 (21)	295	290 (16)
2014	–	–	95	–	–	–	300	–
2015	–	–	104	–	–	–	286	–

(a1), individual phenological ranks were determined for each year of the study period, and correlated (Spearman rank correlation) across all possible year pairs (i.e. 10 pairs for a 5-year period). A representative estimate of the rank repetition for a given population was calculated as the median rank correlation coefficient, across all possible year pairs. The latter was calculated over a minimum number of two year pairs for each population. For (a2), phenological ranks were correlated within a given year (when assessing the repetition of ranks from  $LU_y$  to  $LS_y$ ) or across consecutive years (when assessing the repetition of ranks from  $LS_{y-1}$  to  $LU_y$ ). Again, a representative estimate of the rank repetition from one phenophase to the next for a given population was calculated as the median of the rank correlation coefficients calculated over the 5-year period, for the sole populations where at least two years of observations were available. For (b), we correlated the individual average (over 2009–2013) annual deviation from the population average phenological date (for LU, LS or GSL=green season length=LS-LU) with the individual tree basal area increment, established over 2004–2009.

For a given species, we aimed at deriving ensemble responses, established across populations. For that purpose, we used a meta-analytical approach, considering rank correlation coefficients (established at the population scale) as effect sizes using the random-effect DerSimonian-Laird framework as implemented in the *metacor* package in R (Laliberté, 2011). More precisely, this framework allowed us to test null hypotheses of the form: “the ensemble rank correlation coefficient, over all tree populations of a given species, is not significantly different from zero”. We report the p-value of those tests as  $p_{meta}$ . All statistical analyses were conducted in the R software (R Development Core Team, 2013). Statistical relationships were considered significant at  $p < 0.05$  unless indicated.

### 3. Results

#### 3.1. Do phenological ranks repeat among years?

The amplitude of individual phenological deviations observed within tree populations reached 14–26 days on average depending on the species and phenological stage considered (Table 1). In both QP and FS, the amplitude of the LS phase was significantly longer (by 8 and 11 days, respectively, Table 1) than the amplitude of the LU phase ( $p < 10^{-6}$ , Wilcoxon test of median differences). In QR, the amplitude of both LU and LS were comparable ( $p < 0.58$ ), reaching 20 days on average.

The distributions of phenological deviations were non-random (two sample Kolmogorov-Smirnov test against a random distribution,  $p < 10^{-10}$  in all cases), and overall positively correlated from one year to the next (Fig. 2). Trees classified in the first deciles on the basis of their average rank along the study period tended to show negative deviations across years, while trees from the last deciles

tended to show positive deviations (Fig. 3). Figs. 2 and 3 are hence illustrative of an overall repetition of the phenological ranks in individual trees along the period of interest. In other words, individual phenological ranks within a given tree population mostly repeated from year to year. This resulted in a significant positive average rank repetition for both LU and LS, in all three studied species (Fig. 4, all  $p_{meta} < 0.001$  (0.02) for LU (LS)).

Across QR populations, the site average April soil water content (SWC) was positively correlated with LU rank repetition (Fig. 5a). FS populations experiencing moister soils throughout the bud dormancy period (from preceding November to current April) also showed a higher consistency of spring phenological ranking from year to year (Fig. 5i). On the other hand, QP populations with drier soils in winter (January–February) showed more consistent spring phenological ranking (Fig. 5e). In FS, higher soil water content during autumn (November–December) was associated with a higher repetition of LS phenological ranks (Fig. 5j). On the other hand, QP populations experiencing moist summers (mid-August to mid-September) showed less consistent LS ranking (Fig. 5f).

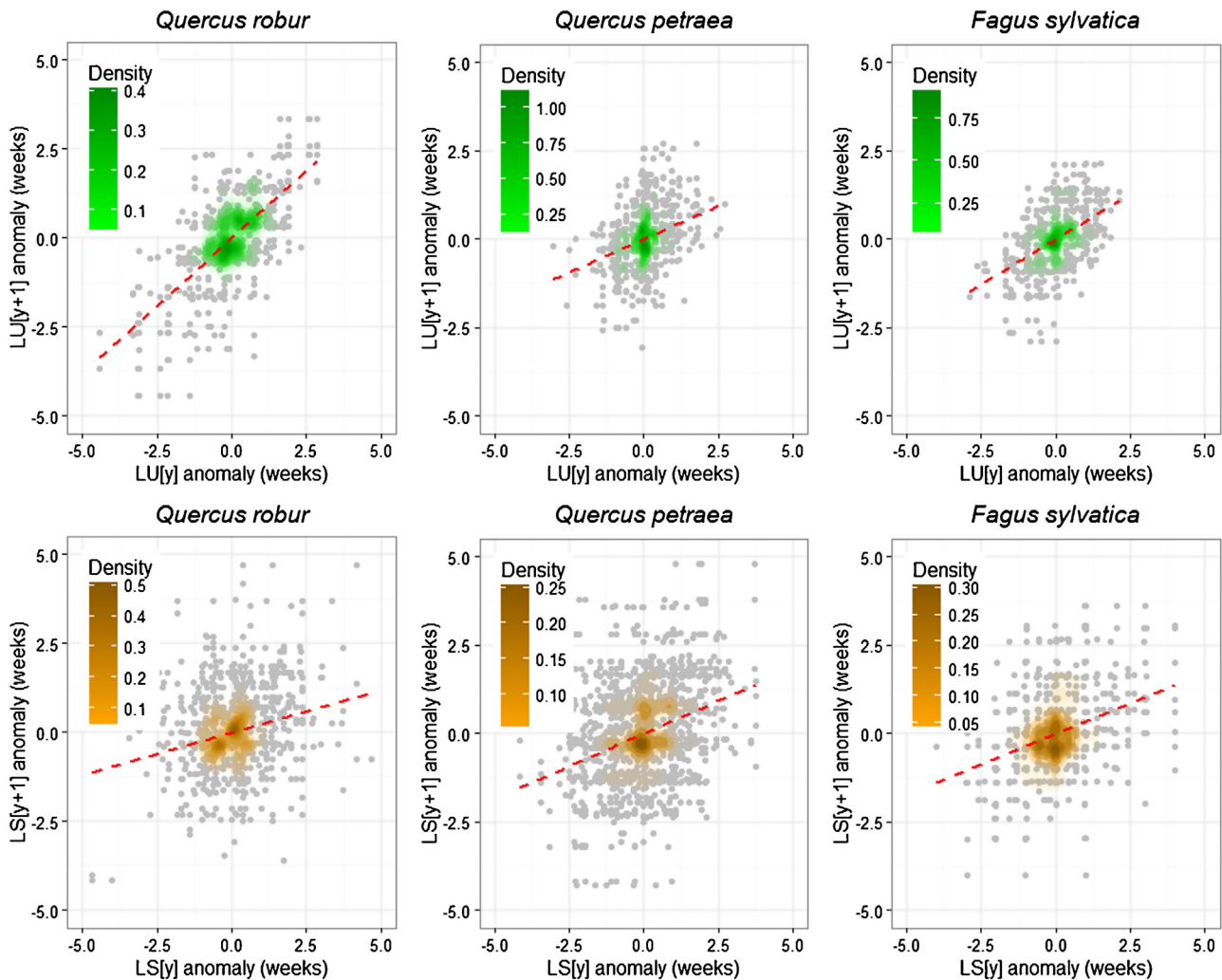
#### 3.2. Do phenological ranks repeat from one phenophase to the next?

For a given leafy season, phenological ranks usually repeated from LU to LS in QR populations ( $p_{meta} < 10^{-3}$ , Fig. 6a). A similar positive but non-significant ensemble response was observed for QP ( $p_{meta} < 0.11$ ) and FS ( $p_{meta} < 0.10$ ) populations. In FS, moister soils in summer (mid-August) were associated with higher rank repetition from LU to LS (Fig. 5k), while the opposite appeared in QP (Fig. 5g). Across the dormancy period (i.e. from one year to the next), we observed that trees entering senescence (LS) later during year  $y-1$  also unfolded leaves (LU) later during year  $y$  in QP populations ( $p_{meta} < 0.02$ , Fig. 6b). A similar positive but non-significant ensemble response was observed in QR populations ( $p_{meta} < 0.11$ ) but not in FS populations ( $p_{meta} < 0.34$ ). In QR, higher soil water content during bud dormancy (previous September to May) was associated with a higher rank repetition from  $LS_{y-1}$  to  $LU_y$  (Fig. 5d). A similar, weaker response was observed in FS (Fig. 5l).

#### 3.3. Is a longer leafy period beneficial for growth?

In FS populations, early-leafing trees tended to grow more than late-leafing trees ( $p_{meta} < 0.04$ , Fig. 7a). In both Oak species, trees entering senescence later tended to grow more than early-senescent trees ( $p_{meta} < 0.03$  for QR,  $p_{meta} < 0.02$  for QP, Fig. 7b). Compensating effects resulted in an ensemble null correlation between the length of the green season and tree individual growth in QR ( $p_{meta} < 0.44$ , Fig. 7c), while trees displaying leaves for a longer period tended to grow more in both QP ( $p_{meta} < 0.01$ , Fig. 7c) and FS ( $p_{meta} < 0.01$ , Fig. 7c) populations.





**Fig. 2.** Individual phenological deviations correlate positively across years. Each plot represents phenological deviations (i.e. deviations from the site-year population average, in days) observed at the tree scale, paired across all possible year combinations (from 2009 to 2013). For clarity, the 2D-kernel density of the data is superimposed as coloured areas. Linear regressions appear as red lines (all slopes significantly different from zero,  $p < 10^{-9}$ ). LU = leaf unfolding, LS = leaf senescence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

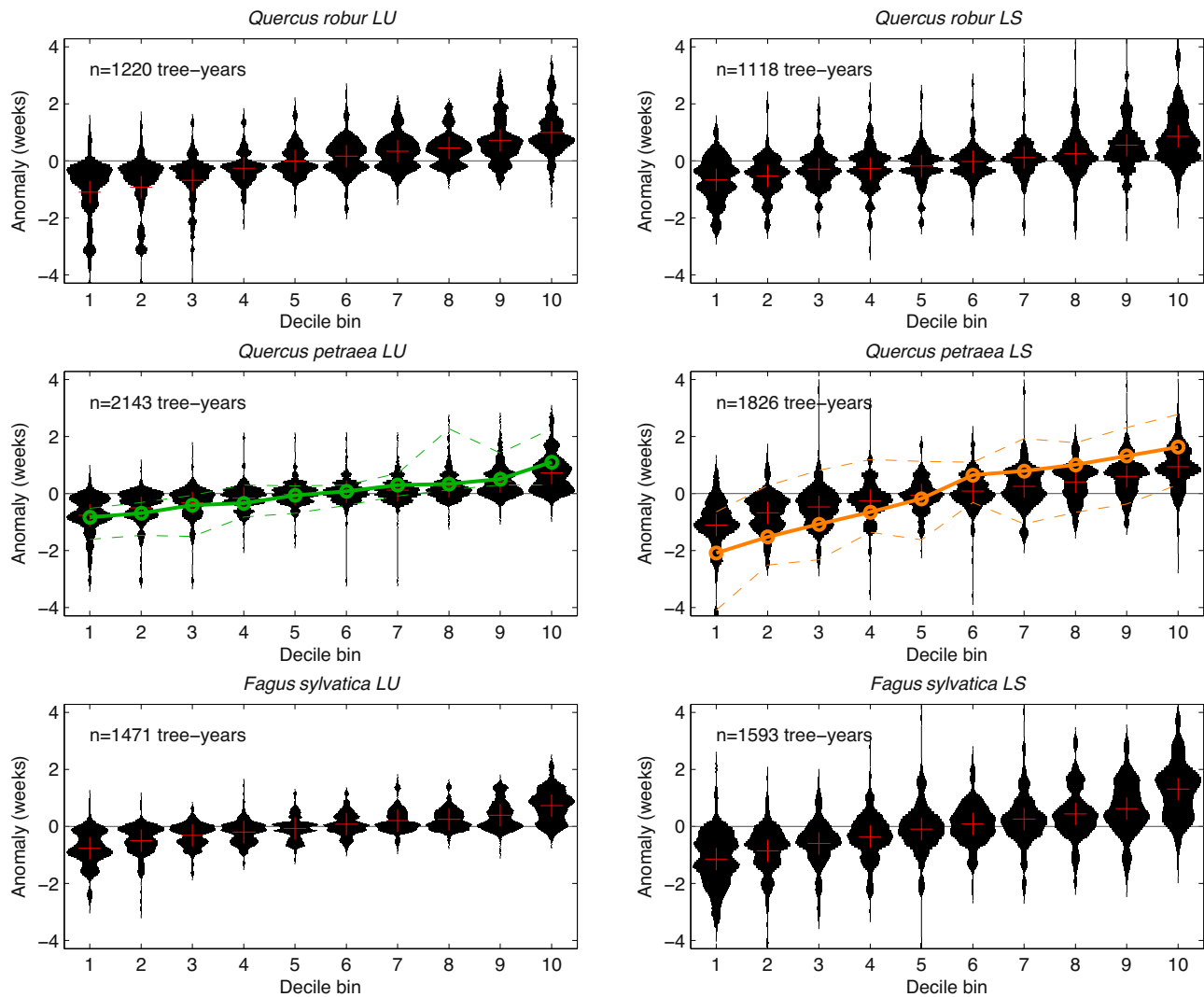
## 4. Discussion

### Hypothesis 1. Do phenological ranks repeat across years?

We hypothesized that, among dominant individuals of a tree population, the genetic/epigenetic differentiation determines most of the phenological phenotype, with micro-environmental variations having a second-order role. Under this hypothesis, the repetition of phenological ranks from year to year would be the rule, and would occasionally be disturbed when environmental determinants of the phenological phenotype do not apply equally to all individuals in a population. Within a tree population, all individuals experience the same photoperiod conditions, and (co-)dominant trees are mostly exposed to similar temperature conditions (e.g. we observed no ensemble dependence of the phenological rank on tree height, which determines its position in the canopy temperature profile, among the considered (co-) dominant trees, Fig. S4). Hence it is likely that the imperfect repetition of phenological ranks we observed among (co-)dominant trees (Figs. 2, 3) proceeds from the influence of environmental drivers varying at a fine (<10 m) spatial scale (e.g. influence of micro-meteorological, hydrological or pedological characteristics; Arend et al., 2016). In the absence of data characterising the micro-environmental conditions experienced by individual trees, we were not able to disentangle the role of these putative drivers. However, our analyses suggested that soil water content (SWC) may influence the among-population variations of phenological rank repetition (Fig. 5). We hypothesize that the positive correlations we observed between rank repetition and soil moisture in QR and FS populations (Fig. 5) proceeds from a more even access to soil water among individuals in populations experiencing moister soils (Notes S2). In QP, the negative correlations (Fig. 5) might reflect the sensitivity of the species to water-logging. It remains to be quantified on the field to which extent the actual variations of SWC may influence the repetition of phenological ranks within a given population.

Few published studies have so far documented the repetition of phenological ranks in forest tree populations, and comparisons among studies are complicated by the fact that those studies use different metrics and experimental protocols. We evaluated the impact of the observation protocol on the magnitude of rank repetition, and found that the use of the RENECOFOR protocol (see Material and methods section) tends to degrade the rank correlations achievable when using a refined protocol (Fig. 4, Suppl. Notes S3). Hence, it is likely that the correlation levels we report are under-estimated.

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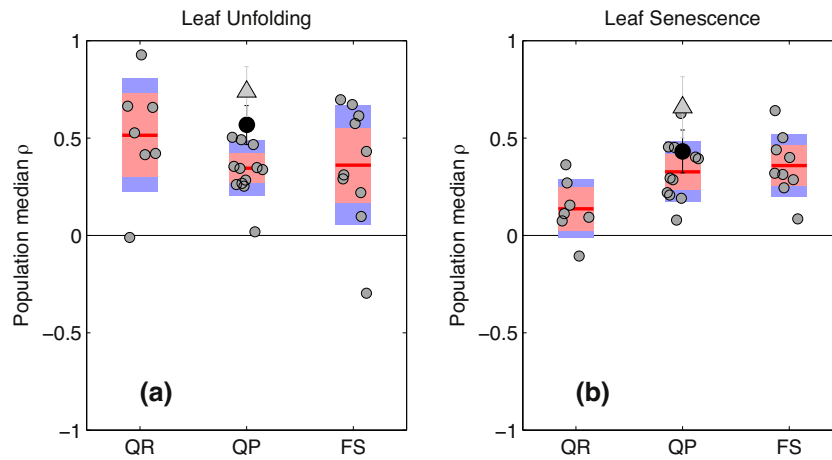


**Fig. 3.** Tree individual deviations of leaf unfolding (LU) and senescence (LS) in temperate deciduous trees. Deviations were calculated annually for each tree, as the individual deviation of phenological event with respect to the within-population annual average. Trees were then classified into decile bins according to their average rank along the study period. Red crosses mark the within-bin median deviation. In *Quercus petraea*, we highlight results from the Orsay population: bold (broken) lines indicate the average deviations ( $\pm$ SD) within each decile bins, calculated over 2011–2015. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

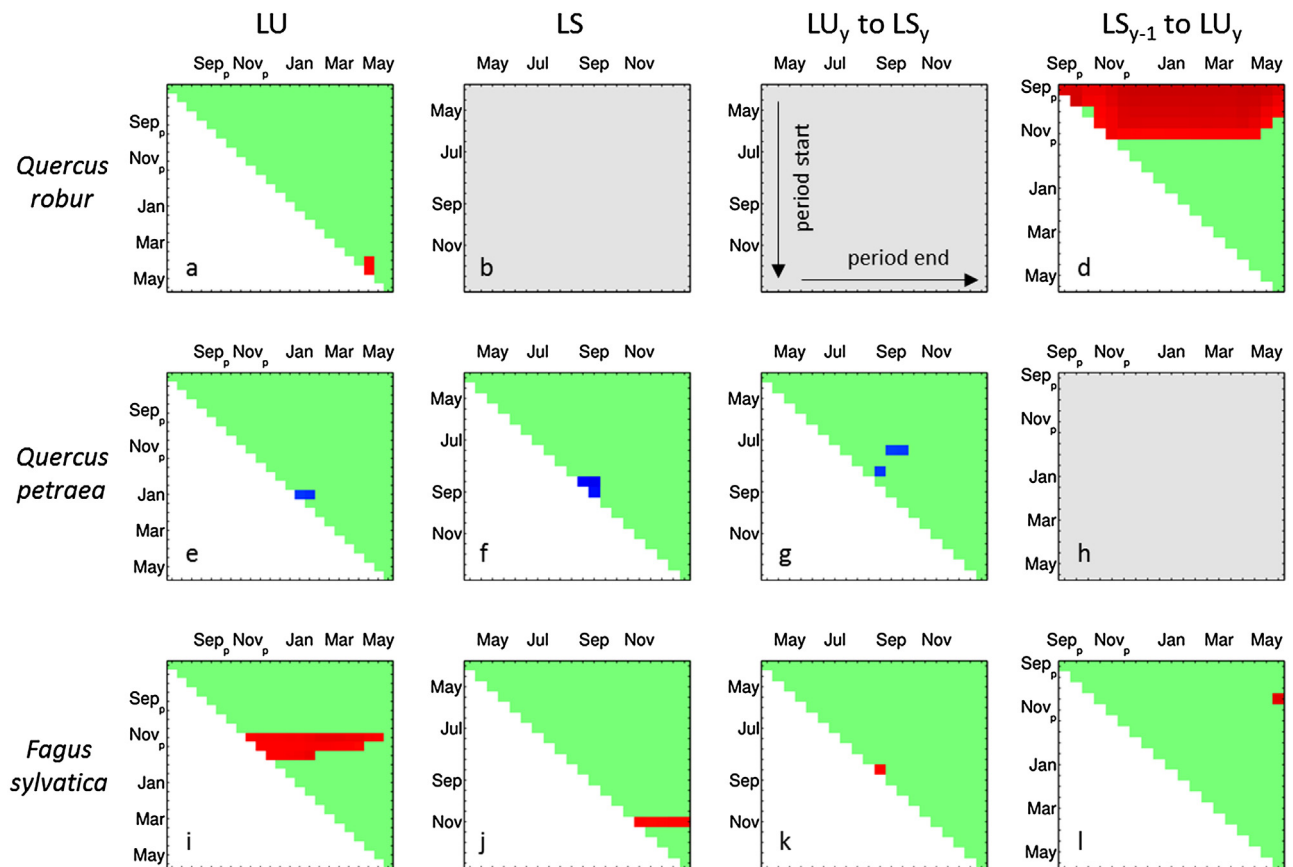
Overall, it appears that LU phenological ranks usually repeat from year to year in Oak and Beech populations (Crawley and Akhteruzzaman, 1988; Kramer, 2004; Wesołowski and Rowiński, 2006; this study). However, the magnitude of rank repetition varies across studies. Crawley and Akhteruzzaman (1988) and Fox et al. (1997) report for instance very high rank repetition in spring phenology (Spearman  $\rho > 0.8$ ) for two consecutive years in one *Quercus robur* and three *Quercus laevis* populations, respectively. Our analysis shows that although phenological ranks are overall significantly repeated in Oak and Beech populations, the degree of rank repetition considerably varies across populations of a given species (Fig. 4a). We were not able to identify a common site characteristic and/or environmental variable which would explain such inter-population variability for all the three species considered. Interestingly though, we noticed higher spring rank repetition for QR and FS populations experiencing higher spring soil water content (SWC, Fig. 5). Whether this observation is indicative of a particular sensitivity of QR and FS LU to water availability remains to be confirmed, in a context when very few papers have assessed the sensitivity of LU to soil water content (but see Angus and Moncur, 1977; Peñuelas et al., 2004; Schnull and Thomas, 2000).

Interestingly, the negative correlation observed for QP (Fig. 5e) could be related to the sensitivity of this species to soil water saturation (Becker and Lévy, 1990; Parelle et al., 2006).

There are very few published reports of the repetition of LS ranks. Our results demonstrate that, as observed for spring, the repetition of autumn phenological ranks is overall the rule in the study species (Fig. 4b). This ensemble result, obtained over a large number of tree populations, contradicts earlier reports mentioning, for instance, no repetition of the autumn phenological ranks among trees in one *Fagus sylvatica* population monitored over 3 years (Capdevielle-Vargas et al., 2015). We notice that the median rank correlation levels that we observe for autumn are slightly lower than those for spring in FS, and particularly in QR, but of the same order in QP (Fig. 4). As observed for spring, water availability variables correlate with the repetition of LS ranks (Fig. 5f, j). In FS, sites of higher autumn SWC are those with the highest LS rank repetition (Fig. 5j). These patterns may be indicative of a sensitivity of leaf senescence to individual tree water access, and echo recent reports on the partial dependence of leaf senescence on soil water availability (Archetti et al., 2013; Hwang et al., 2014; Xie et al., 2015). In QP, sites of moister summers show less repeatable



**Fig. 4.** Assessment of the conservation of phenological ranking in deciduous forest trees. For each tree population, we calculated the median phenological rank correlation ( $\rho$ ) coefficient across all 2009–2013 year pairs, for spring (a) and autumn (b) phases (grey dots = RENECOFOR populations, black dot = Orsay population observed with the RENECOFOR protocol, grey triangle = Orsay population observed with a refined protocol, see text for details). Boxes summarize the across-populations variability of rank conservation for the RENECOFOR populations (red lines = median  $\rho$ , red box = average  $\rho \pm 1.96$  standard error, blue box = average  $\rho \pm 1$  standard deviation). For the Orsay QP population, the error bar is the standard deviation of rank conservation across year pairs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** Assessing the link between soil water content and the conservation of phenological ranks. Each plot represents the correlation matrix between the population median phenological rank correlation coefficient and the soil water content (SWC) simulated by the CASTANEA model for each population along the study period. SWC was integrated (i.e. averaged) over different time periods (see text for details), with the start (end) of the integration period appearing on the y (x)-axis (see subplot c). For clarity, only significant ( $p \leq 0.05$ ) positive (negative) correlations appear in red (blue). Green denotes non-significant ( $p > 0.05$ ) correlations. Grey matrixes appear in case no significant correlation was observed whatever the integration period. The “p” indexed month are from the preceding year. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

autumn phenological ranks (Fig. 5f). Whether this result reflects the sensitivity of QP to soil moisture (Parelle et al., 2006) deserves further investigations.

**Hypothesis 2.** Do phenological ranks repeat from one phenophase to the next?

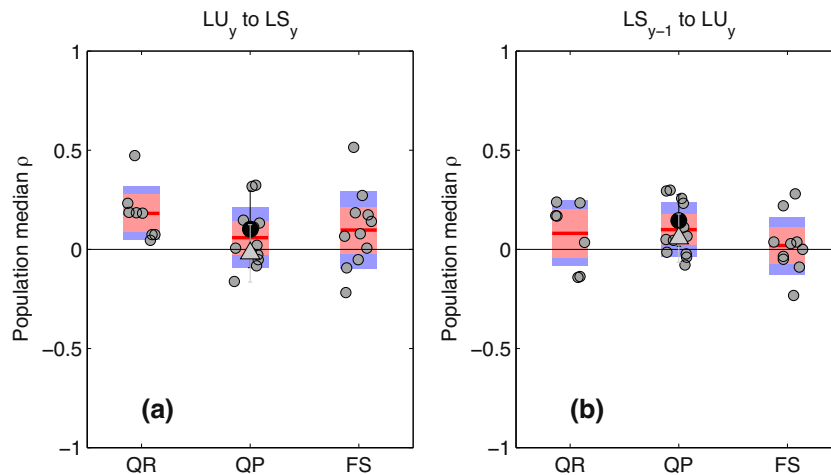
Within the annual phenological cycle, individual phenophases (e.g. spring and autumn) are usually considered and studied independently. An integrated framework of the phenological cycle needs to reconsider the question of a link between phenophases (Hänninen and Kramer, 2007). In QR, we observe that early-leaving individuals also entered senescence early (Fig. 6). This result confirms previous reports documenting rank repetition from spring to autumn in QR (Crawley and Akhteruzzaman, 1988), and an absence of in FS (Capdevielle-Vargas et al., 2015). The physiological and functional causes of this link, when it is observed, are not clear, and may be related to the hypotheses of pre-determined maximum leaf lifespan (Kikuzawa, 1995) or leaf carbon balance (Fu et al., 2014b). Our results further suggest a complementary role of the summer SWC status, as observed in FS (QP), in which populations experienc-

ing higher (lower) summer SWC had higher rank repetition from LU to LS (Fig. 5g and k) though overall (i.e. all populations considered) both species showed no significant ensemble repetition of ranks from spring to autumn (Fig. 6a).

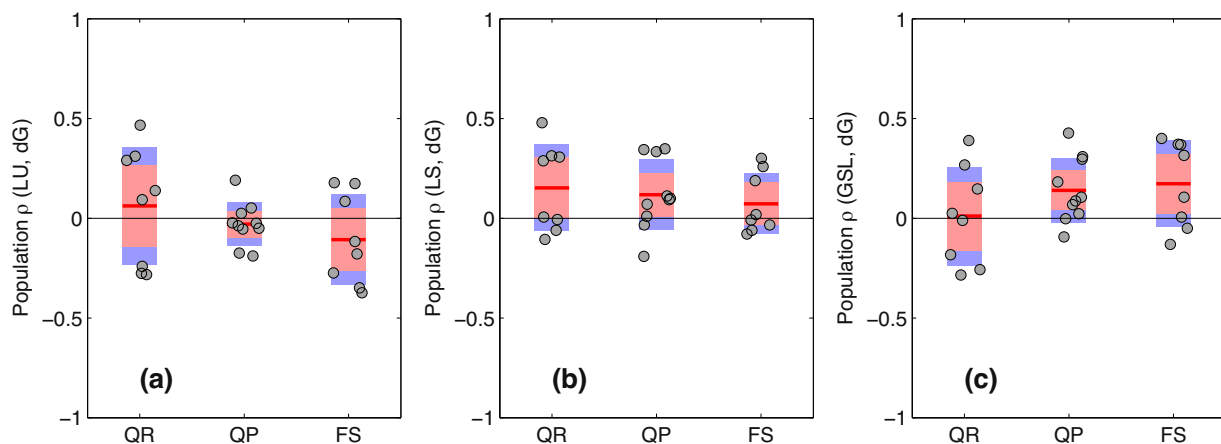
In QP, trees entering senescence (LS) later during year  $y-1$  also tended to unfold leaves (LU) later during year  $y$  (Fig. 6). The rank repetition from  $LS_{y-1}$  to  $LU_y$  was higher at sites of higher soil moisture during dormancy in both QR and FS (Fig. 5d, l). Again, this result points a likely impact of water availability on the timing of phenological events: our hypothesis is that water stress occurring during year  $y-1$  could both (i) alter the timing of LS during year  $y-1$  and/or (ii) impose conditions during bud dormancy that would modify the timing of LU during year  $y$  (Schiestl-Aalto et al., 2013).

**Hypothesis 3.** Does phenological ranking reflect tree growth?

The ecological implications of the within-population variability of phenology have to date been mostly studied under the angle of interspecific (Jolly et al., 2004; Richardson and O'Keefe, 2009) or tree social status comparisons (Gressler et al., 2015; Seiwa, 1999; Vitasse, 2013). These studies usually report a “phenologi-



**Fig. 6.** Assessment of the conservation of phenological ranks across phenophases. For each tree population, we calculated the median phenological rank correlation coefficient between (a) current year spring ( $LU_y$ ) and autumn ( $LS_y$ ) and (b) preceding autumn ( $LS_{y-1}$ ) and current spring ( $LU_y$ ), for each year of the 2009–2013 period (grey dots = RENECOFOR populations, black dot = Orsay population observed with the RENECOFOR protocol, grey triangle = Orsay population observed with a refined protocol, see text for details). Boxes summarize the across-populations variability of rank conservation of RENECOFOR populations (red lines = median  $\rho$ , red box = average  $\rho \pm 1.96$  standard error, blue box = average  $\rho \pm 1$  standard deviation). For the Orsay QP population, the error bar is the standard deviation of rank conservation across year pairs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 7.** Assessment of the correlation of phenological ranking and individual tree growth. We correlated the average individual deviation in (a) LU, (b) LS and (c) GSL (green season length =  $LS-LU$ ) with its basal area increment, established over the 2004–2009 period. Results were aggregated at the population level (grey dots). Boxes summarize the across-populations variability of rank conservation of RENECOFOR populations (red lines = median  $\rho$ , red box = average  $\rho \pm 1.96$  standard error, blue box = average  $\rho \pm 1$  standard deviation). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



cal avoidance” of younger or lower social status (i.e. smaller) trees, interpreted as indicative of a strategy to maximize light-harvesting and survival (Augspurger and Bartlett, 2003). Here we showed that phenological ranking is further correlated with tree growth among adult dominant conspecifics (Fig. 7). It is clearly established that early-flushing trees harvest more light (Jolly et al., 2004) and likely that they harvest more nutrients (Nord and Lynch, 2009) than late-flushing trees in spring, when soil water is not limiting. This may confer a competitive advantage to the early-flushing trees in the race toward light-harvest and growth that has partly shaped the evolution of forest trees (Falster and Westoby, 2003). The advantage of early-flushing trees could explain the pattern we report for FS populations (Fig. 7a), but appears less influential on the inter-individual variability of growth in Oak populations, which are also more prone to spring pathogenic attacks (data not shown). In the latter species, on average across the studied populations, late-senescent individuals are also those that grow most (Fig. 7b). Whether this link is causal is currently not known, and deserves further investigations related e.g. to the nutrient status (testing the hypothesis of a better nutrient resorption in late-senescent individuals), the carbon status (e.g. in ring-porous Oaks, do late-senescent individuals constitute higher C reserve pools allowing for higher growth in spring?, see e.g. Carbone et al., 2013) and the health status of individual trees (Suppl. Notes S4). If confirmed, such correlations between phenological traits and individual growth could illustrate the adaptive value of phenological traits within a mature tree population (under the hypothesis that tree growth is indeed related to fitness).

## 5. Conclusions

We evidenced in this paper that the repetition of phenological rank is a common, though not systematic, feature in deciduous forest tree populations. The repetition of phenological ranks is higher in spring (leaf unfolding) than in autumn (leaf senescence). In all three studied species, we observed correlations between individual tree growth and their phenological ranks. Our analyses suggest that the variations of phenological rank repetition observed across populations of a given species may be related to differences in the within-population variability of soil water access. We could not directly prove this hypothesis, lacking a systematic assessment of the within-population variations of soil water content. Hence we highlight the need for a proper characterisation of the role of water stress on the within-population variations of tree phenology.

We took advantage of a unique phenological database, gathering phenological observations done at the individual scale over 35 populations, representing >1200 trees, and >8000 individual phenological observations. We are confident that this unprecedented quantity of data allowed us to derive robust responses at the species scale. Yet, the observation of inter-individual phenological differences is a laborious task, requiring frequent (weekly is a minimum, notably for spring phases) and precise observations of a large number of trees. Beside field observation campaigns, we believe that the study of the within-population variability of leaf phenology will benefit from the analysis of digital images acquired by phenological cameras across large continental networks (Klosterman et al., 2014; Wingate et al., 2015). Altogether, such data on individual tree phenological traits are required to establish correspondences between those traits and phenological model parameters, with the aim to provide robust parameterisation of phenological modules to incorporate into physio-demo-genetic models (Kramer et al., 2008; Oddou-Muratorio and Davi, 2014) which aim at simulating microscale population evolution.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2016.12.008>.

## References

- Ahrends, H.E., Etzold, S., Kutsch, W.L., Stoeckli, R., Bruegger, R., Jeanneret, F., Wanner, H., Buchmann, N., Eugster, W., 2009. Tree phenology and carbon dioxide fluxes: use of digital photography for process-based interpretation at the ecosystem scale. *Clim. Res.* 39, 261–274. <http://dx.doi.org/10.3354/cr00811>.
- Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R., Savolainen, O., 2013. Potential for evolutionary responses to climate change – evidence from tree populations. *Glob. Chang. Biol.* 19, 1645–1661. <http://dx.doi.org/10.1111/gcb.12181>.
- Angus, J.F., Moncur, M.W., 1977. Water stress and phenology in wheat. *Crop Pasture Sci.* 28, 177–181.
- Archetti, M., Richardson, A.D., O’Keefe, J., Delpierre, N., 2013. Predicting climate change impacts on the amount and duration of autumn colors in a New England forest. *PLoS One* 8, e57373. <http://dx.doi.org/10.1371/journal.pone.0057373>.
- Arend, M., Geßler, A., Schaub, M., 2016. The influence of the soil on spring and autumn phenology in European beech. *Tree Physiol.* 36, 78–85. <http://dx.doi.org/10.1093/treephys/tpv087>.
- Augspurger, C.K., Bartlett, E.A., 2003. Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiol.* 23, 517–525. <http://dx.doi.org/10.1093/treephys/23.8.517>.
- Becker, G., Lévy, M., 1990. Le point sur l’écologie comparée du Chêne sessile et du Chêne pédonculé. *Rev. For. Française*, 148–154.
- Bontemps, A., Lefèvre, F., Davi, H., Oddou-Muratorio, S., 2015. In situ marker-based assessment of leaf trait evolutionary potential in a marginal European beech population. *J. Evol. Biol.* <http://dx.doi.org/10.1111/jeb.12801> (n/a–n/a).
- Capdevielle-Vargas, R., Estrella, N., Menzel, A., 2015. Multiple-year assessment of phenological plasticity within a beech (*Fagus sylvatica* L.) stand in southern Germany. *Agric. For. Meteorol.* 211 (–212), 13–22. <http://dx.doi.org/10.1016/j.agrformet.2015.03.019>.
- Carbone, M., Keenan, T., Czimczik, C., Murakami, P., Keefe, J.O., Schaberg, P., Xu, X., Richardson, A., 2013. Age, allocation, and availability of nonstructural carbohydrates in red maple. *New Phytol.* 200, 1145–1155.
- Chesnoiu, E.N., Sofletea, N., Curtu, A.L., Toader, A., Radu, R., Enescu, M., 2009. Bud burst and flowering phenology in a mixed oak forest from Eastern Romania. *Ann. For. Res.* 52, 199–206.
- Crawley, M.J., Akhteruzzaman, M., 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Funct. Ecol.* 2, 409–415.
- Dantec, C.F., Ducasse, H., Capdevielle, X., Fabreguettes, O., Delzon, S., Desprez-Loustau, M.L., 2015. Escape of spring frost and disease through phenological variations in oak populations along elevation gradients. *J. Ecol.* 103, 1044–1056. <http://dx.doi.org/10.1111/1365-2745.12403>.
- Deans, J.D., Harvey, F.J., 1995. Phenologies of sixteen European provenances of sessile oak growing in Scotland. *Forestry* 6, 265–273.
- Delpierre, N., Dufrêne, E., Soudani, K., Ulrich, E., Cecchini, S., Boé, J., François, C., 2009a. Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. *Agric. For. Meteorol.* 149, 938–948. <http://dx.doi.org/10.1016/j.agrformet.2008.11.014>.
- Delpierre, N., Soudani, K., François, C., Köstner, B., Pontailleur, J.-Y., Nikinmaa, E., Misson, L., Aubinet, M., Bernhofer, C., Granier, A., Grünwald, T., Heinesch, B., Longdoz, B., Ourcival, J.-M., Rambal, S., Vesala, T., Dufrêne, E., 2009b. Exceptional carbon uptake in European forests during the warm spring of 2007: a data-model analysis. *Glob. Change Biol.* 15, 1455–1474. <http://dx.doi.org/10.1111/j.1365-2486.2008.01835.x>.

- Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T., Rathgeber, C.B.K., 2016. Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. *Ann. For. Sci.* 73, 5–25, <http://dx.doi.org/10.1007/s13595-015-0477-6>.
- Estrella, N., Menzel, A., 2006. Responses of leaf colouring in four deciduous tree species to climate and weather in Germany. *Clim. Res.* 32, 253–267.
- Falster, D.S., Westoby, M., 2003. Plant height and evolutionary games. *Trends Ecol. Evol.* 18, 337–343, [http://dx.doi.org/10.1016/S0169-5347\(03\)00061-2](http://dx.doi.org/10.1016/S0169-5347(03)00061-2).
- Finn, G.A., Straszewski, A.E., Peterson, V., 2007. A general growth stage key for describing trees and woody plants. *Ann. Appl. Biol.* 151, 127–131, <http://dx.doi.org/10.1111/j.1744-7348.2007.00159.x>.
- Fox, C.W., Waddell, K.J., Groeters, F.R., Mousseau, T.A., 1997. Variation in budbreak phenology affects the distribution of leaf-mining beetle (*Brachys tessellatus*) on turkey oak (*Quercus laevis*). *Ecoscience* 4, 480–489.
- Fu, Y.H., Piao, S., Zhao, H., Jeong, S.J., Wang, X., Vitasse, Y., Ciais, P., Janssens, I.A., 2014a. Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at northern middle and high latitudes. *Glob. Change Biol.* 20, 3743–3755, <http://dx.doi.org/10.1111/gcb.12610>.
- Fu, Y.S.H., Campioli, M., Vitasse, Y., De Boeck, H.J., Van den Berge, J., Abd El Gawad, H., Asard, H., Piao, S., Deckmyn, G., Janssens, I., 2014b. Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proc. Natl. Acad. Sci. U. S. A.* 111, 7355–7360, <http://dx.doi.org/10.1073/pnas.1321727111>.
- Gressler, E., Jochner, S., Capdevielle-vargas, R.M., Patrícia, L., Morellato, C., Menzel, A., 2015. Vertical variation in autumn leaf phenology of *Fagus sylvatica* L. in southern Germany. *Agric. For. Meteorol.* 201, 176–186, <http://dx.doi.org/10.1016/j.agrformet.2014.10.013>.
- Guillemot, J., Delpierre, N., Vallet, P., François, C., Martin-Stpaul, N.K., Soudani, K., Nicolas, M., Badeau, V., Dufrene, E., 2014. Assessing the effects of management on forest growth across France: insights from a new functional-structural model. *Ann. Bot.* 114, 779–793, <http://dx.doi.org/10.1093/aob/mcu059>.
- Hänninen, H., Kramer, K., 2007. A framework for modelling the annual cycle of trees in boreal and temperate. *Silva Fenn.* 41, 167–205.
- Hwang, T., Band, L.E., Miniati, C.F., Song, C., Bolstad, P.V., Vose, J.M., Love, J.P., 2014. Divergent phenological response to hydroclimate variability in forested mountain watersheds. *Glob. Change Biol.* 20, 2580–2595, <http://dx.doi.org/10.1111/gcb.12556>.
- Jolly, W.M., Nemani, R., Running, S.W., 2004. Enhancement of understory productivity by asynchronous phenology with overstory competitors in a temperate deciduous forest. *Tree Physiol.* 24, 1069–1071, <http://dx.doi.org/10.1093/treephys/24.9.1069>.
- Kikuzawa, K., 1995. Leaf phenology as an optimal strategy for carbon gain in plants. *Can. J. Bot.* 73, 158–163.
- Klosterman, S.T., Hufkens, K., Gray, J.M., Melaas, E., Sonnentag, O., Lavine, I., Mitchell, L., Norman, R., Friedl, M.A., Richardson, A.D., 2014. Evaluating remote sensing of deciduous forest phenology at multiple spatial scales using PhenoCam imagery. *Biogeosciences* 11, 4305–4320, <http://dx.doi.org/10.5194/bg-11-4305-2014>.
- Kramer, K., Buitveld, J., Forstreute, M., Geburek, T., Leonardi, S., Menozzi, P., Povillon, F., Schelhaas, M.J., Teissier du Cros, E., Vendramin, G.G., van der Werf, D.C., 2008. Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. *Ecol. Modell.* 216, 333–353, <http://dx.doi.org/10.1016/j.ecolmodel.2008.05.004>.
- Kramer, K., 2004. Effects of silvicultural regimes on dynamics of genetic and ecological diversity of European Beech forests. Impact assessment and recommendations for sustainable forestry. Final report of the 5th framework project DynaBeech. Wageningen.
- Laliberté E., 2011. Package metacor (meta-analysis of correlation coefficients).
- Lebourgeois, F., Pierrat, J.-C., Perez, V., Piedallu, C., Cecchini, S., Ulrich, E., 2008. Déterminisme de la phénologie des forêts tempérées françaises: étude sur les peuplements du réseau RENECOFOR. *Rev. For. Française* 60, 323–343.
- Ma, S., Concilio, A., Oakley, B., North, M., Chen, J., 2010. Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. *For. Ecol. Manage.* 259, 904–915, <http://dx.doi.org/10.1016/j.foreco.2009.11.030>.
- Menzel, A., 2013. Plant phenological fingerprints. In: Schwartz, M.D. (Ed.), *Phenology: An Integrative Environmental Science*. Springer, Dordrecht, p. 610.
- Ngao, J., Epron, D., Delpierre, N., Bréda, N., Granier, A., Longdoz, B., 2012. Spatial variability of soil CO<sub>2</sub> efflux linked to soil parameters and ecosystem characteristics in a temperate beech forest. *Agric. For. Meteorol.* 154 (–155), 136–146, <http://dx.doi.org/10.1016/j.agrformet.2011.11.003>.
- Nord, E.A., Lynch, J.P., 2009. Plant phenology: a critical controller of soil resource acquisition. *J. Exp. Bot.* 60, 1927–1937, <http://dx.doi.org/10.1093/jxb/erp018>.
- Oddou-Muratorio, S., Davi, H., 2014. Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. *Evol. Appl.* 7, 453–467, <http://dx.doi.org/10.1111/eva.12143>.
- Parelle, J., Brendel, O., Bodenes, D., C.M.B. Dizengremel, P., Jolivet, Y., Dreyer, E., 2006. Differences in morphological and physiological responses to water-logging between two sympatric oak species. *Ann. For. Sci.* 63, 849–859.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42, <http://dx.doi.org/10.1038/nature01286>.
- Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradas, J., 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytol.* 1469 (161), 837–846, <http://dx.doi.org/10.1111/j.1469-8137.2003.01003.x>.
- Richardson, A.D., O'Keefe, J., 2009. Phenological differences between understory and overstory. In: Noormets, A. (Ed.), *Phenology of Ecosystem Processes*. Springer, New York, pp. 87–117.
- Richardson, A.D., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N., Hollinger, D.Y., Kutsch, W.L., Longdoz, B., Luyssaert, S., Migliavacca, M., Montagnani, L., Munger, J.W., Moors, E., Piao, S., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri, E., Vargas, R., Varlagin, A., 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 3227–3246, <http://dx.doi.org/10.1098/rstb.2010.0102>.
- Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O., Toomey, M., 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agric. For. Meteorol.* 169, 156–173, <http://dx.doi.org/10.1016/j.agrformet.2012.09.012>.
- Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene flow and local adaptation in trees. *Annu. Rev. Ecol. Syst.* 38, 595–619, <http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095646>.
- Schiestl-Aalto, P., Nikinmaa, E., Mäkelä, A., 2013. Duration of shoot elongation in Scots pine varies within the crown and between years. *Ann. Bot.* 112, 1181–1191, <http://dx.doi.org/10.1093/aob/mct180>.
- Schmull, M., Thomas, F.M., 2000. Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* Matt. Liebl., *Fagus sylvatica* L.) to waterlogging. *Plant Soil* 225, 227–242, <http://dx.doi.org/10.1023/a:1026516027096>.
- Scotti, I., González-Martínez, S.C., Budde, K.B., Lalagüe, H., 2016. Fifty years of genetic studies: what to make of the large amounts of variation found within populations? *Ann. For. Sci.* 73, 69–75, <http://dx.doi.org/10.1007/s13595-015-0471-z>.
- Scotti-Saintagne, C., Bodénès, C., Barreneche, T., Bertocchi, E., Plomion, C., Kremer, A., 2004. Detection of quantitative trait loci controlling bud burst and height growth in *Quercus robur* L. *Theor. Appl. Genet.* 109, 1648–1659, <http://dx.doi.org/10.1007/s00122-004-1789-3>.
- Seiwa, K., 1999. Changes in leaf phenology are dependent on tree height in *acer mono*, a deciduous broad-leaved tree. *Ann. Bot.* 83, 355–361.
- Ulrich, E., Cecchini, S., 2009. Manuel De référence No 12 Pour Les Observations Phénologiques Du réseau. RENECOFOR.
- Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R., Kremer, A., 2009a. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Can. J. For. Res.* 39, 1259–1269, <http://dx.doi.org/10.1139/X09-054>.
- Vitasse, Y., Porté, A.J., Kremer, A., Michalet, R., Delzon, S., 2009b. Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia* 161, 187–198, <http://dx.doi.org/10.1007/s00442-009-1363-4>.
- Vitasse, Y., 2009. Déterminismes environnemental et génétique de la Phénologie des Arbres de Climat tempéré : Suivi des Dates de Débourrement et de Sénescence le long d'un Gradient altitudinal et en Tests de Provenances. Université Bordeaux 1.
- Vitasse, Y., 2013. Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytol.* 198, 149–155, <http://dx.doi.org/10.1111/nph.12130>.
- Way, D.A., Montgomery, R.A., 2014. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant Cell Environ.* 38, 1725–1736, <http://dx.doi.org/10.1111/pce.12431>.
- Wesołowski, T., Rowiński, P., 2006. Timing of bud burst and tree-leaf development in a multispecies temperate forest. *For. Ecol. Manage.* 237, 387–393, <http://dx.doi.org/10.1016/j.foreco.2006.09.061>.
- Wingate, L., Ogeé, J., Cremonese, E., Filipa, G., Mizunuma, T., Migliavacca, M., Moisy, C., Wilkinson, M., Moureaux, C., Wohlfahrt, G., Hammerle, A., Hörtnagl, L., Gimeno, C., Porcar-Castell, A., Galvagno, M., Nakaji, T., Morison, J., Kolle, O., Knohl, A., Kutsch, W., Kolari, P., Nikinmaa, E., Ibrom, A., Gielen, B., Eugster, W., Balzarolo, M., Papale, D., Klumpp, K., Köstner, B., Grünwald, T., Joffre, R., Ourcival, J.M., Hellstrom, M., Lindroth, A., George, C., Longdoz, B., Genty, B., Levula, J., Heinesch, B., Sprints, M., Yakir, D., Manise, T., Guyon, D., Ahrends, H., Plaza-Aguilar, A., Guan, J.H., Grace, J., 2015. Interpreting canopy development and physiology using a European phenology camera network at flux sites. *Biogeosciences* 12, 5995–6015, <http://dx.doi.org/10.5194/bg-12-5995-2015>.
- Wuehlisch, G., von Krusche, D., Muhs, H.J., 1995. Variation in Temperature Sum Requirement for Flushing of Beech Provenances. *Silvae Genet.*
- Xie, Y., Wang, X., Silander, J.A., 2015. Deciduous forest responses to temperature, precipitation, and drought imply complex climate change impacts. *Proc. Natl. Acad. Sci. U. S. A.* 112, 13585–13590, <http://dx.doi.org/10.1073/pnas.1509991112>.
- van Dongen, S., Backeljau, T., Matthysen, E., Dhondt, A.A., 1997. Synchronization of hatching with budburst of individual host trees (*Quercus robur*) in the winter moth (*Operophtera brumata*) and its fitness consequences. *J. Anim. Ecol.* 66, 113–121, <http://dx.doi.org/10.2307/5969>.