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

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## ARTICLE INFO

## 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; Schmull 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)

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| | Quercus petraea | 11–12[b] | 2 | 1 | 31 | 48.5 | 2.8 | Delpierre N, unpublished (FR-Fon forest[c]) |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| Leaf senescence[a] | Quercus petraea | 33 | 1 | 1 | 31 | 48.5 | 2.8 | Delpierre N, unpublished (FR-Fon forest[c]) |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

[a] 50% colored or fallen leaves.
[b] data from years 2013 and 2015, with late, cold springs.
[c] the FR-Fon forest is member of the ICOS network (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.