Leafy season length is reduced by a prolonged soil water deficit but not by repeated defoliation in beech trees (Fagus sylvatica L.): comparison of response among regional populations grown in a common garden

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To cite this version:

Catherine Massonnet, Pierre-Antoine Chuste, Joseph Levillain, François Gérémia, Daniel E Silva, et al.. Leafy season length is reduced by a prolonged soil water deficit but not by repeated defoliation in beech trees (Fagus sylvatica L.): comparison of response among regional populations grown in a common garden. Agricultural and Forest Meteorology, 2021, 297, pp.1-13. 10.1016/j.agrformet.2020.108228 . hal-03209549

HAL Id: hal-03209549
https://hal.inrae.fr/hal-03209549v1

Submitted on 3 Feb 2023

Research Paper _ revised version

Leafy season length is reduced by a prolonged soil water deficit but not by repeated defoliation in beech trees (*Fagus sylvatica* L.): comparison of response among regional populations grown in a common garden.

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Highlights

- Three years of soil water deficit delayed bud-burst and advanced leaf-yellowing.
- Three years of annual experimental defoliations had no impact on leaf phenology.
- Leafy season length varied among populations along a small latitudinal gradient.
- Populations presented different leaf phenology response to soil water deficit.

Abstract

Bud-burst and leaf-senescence determine the length of the growing season for deciduous trees and therefore the duration of potential carbon assimilation with consequences on biomass production. In *Fagus sylvatica* L., leaf phenology depends on both photoperiod and temperature. The future climate is expected to induce more frequent soil water deficits and biotic attacks (possibly resulting in severe defoliation). The aim of the study is to assess whether these constrains may alter leaf phenology. In a common garden, we sowed seeds collected from six beech forests along a small latitudinal gradient (140 km) in North-Eastern France. In 2014, after seven years growth, a rain exclusion was installed above the trees to test how recurrent soil water deficits impacted bud-burst (BB) and leaf-yellowing (LY) over three years. We also analyzed the response of leaf phenology to annual defoliation, aiming at affecting carbon and nitrogen availability in trees. Delayed BB and early LY were observed, reducing the growing season (GS) until 14 days in response to soil water deficit whereas no influence of defoliation was detected. These time lags were not in relation with leaf nitrogen content. In the control treatment, BB occurred earlier and LY later in the northernmost populations than in the southernmost without clear relationships with local climate. A significant treatment x population interaction was observed revealing a plasticity in the leaf phenology response to soil water deficit among populations. These results suggest that beech trees present a genetic differentiation of leaf phenology even within a small latitudinal gradient but that these differentiations could be disrupted by soil water deficit that is predicted to increase in the future.

Keywords: *Fagus sylvatica* L., bud-burst, leaf-senescence, leaf phenology, drought, intraspecific variability.

1. Introduction

Phenology describes the timing of recurrent biological events in response to seasonal variations in climate. Phenology is one of the plant traits where responses to climate change are the most visible (Menzel *et al.*, 2006). Since 1950, shifts in phenology have been observed and used as evidence of global warming (Menzel and Fabian, 1999; Menzel, 2000; Sparks *et al.*, 2000; Peñuelas *et al.*, 2002, Menzel et al, 2020). For instance, in vineyards, historical recordings of harvest dates helped to detect changing temperatures over several centuries (Chuine *et al.*, 2004).

Leaf phenology events such as bud-burst (BB) and leaf senescence are particularly important in deciduous forest trees because they determine the length of the leafy season and consequently the duration of new carbon production by assimilation that is essential for biomass production (Richardson *et al.*, 2010). The leaf phenology of perennial plants is expected to optimize their carbon gain (Manzoni *et al.*, 2015; Vico *et al.*, 2015) and water uptake (Zapater *et al.,* 2013). Leaf senescence implies nutrient resorption from leaves to perennial organs. It usually happens before autumn frosts and nutrient resorption efficiency affects leaf production during the following year (Estiarte and Peñuelas, 2015).

In the two last decades, numerous experimental and modelling approaches have been developed to understand the drivers of leaf phenology and its variations with climate (Cooke *et al.*, 2012). Leaf phenology is strongly controlled by local temperature (Hunter and Lechowicz, 1992; Peaucelle *et al.*, 2019). To summarize, in temperate tree species, BB results from the succession of two phases: i) breaking endodormancy by the fulfilment of chilling temperature requirements and ii) the accumulation of warm temperatures (forcing temperature) during the ecodormancy phase (Lang *et al.*, 1987). The temperature requirements during the two phases are species-specific (Kramer, 1995; Chuine and Cour, 1999; Morin *et al.*, 2009; Vitasse *et al.*, 2009a; Basler and Körner, 2014; Schuster *et al.*, 2014; Zohner and Renner, 2014; Dantec *et al.*, 2014; Laube *et al.*, 2014; Fu *et al.*, 2015). Moreover, in some tree species like beech, photoperiod may also interact with temperature to determine bud-burst date, though the mechanisms of this interaction remain unclear (Heide, 1993; Partanen *et al.*, 1999; Körner and Basler, 2010; Vitasse and Basler, 2013; Basler and Körner, 2014; Laube *et al.*, 2014; Hamilton *et al.*, 2016; Fu *et al.*, 2019b). Day-length may interact negatively with heat requirements during ecodormancy to avoid that BB occurred too late (if abnormally cold spring) or too early (if warm spring) (Fu *et al.*, 2019b).

The role of climate as a driver of leaf senescence (i.e. yellowing and shedding) is less well understood than that of spring phenology (Richardson *et al.*, 2013). Long-term investigations on the links between leaf-senescence and air temperature have sometimes revealed a delay in leaf senescence in response to global warming, sometimes an advance, and sometimes no effect at all (Peñuelas *et al.*, 2002; Menzel *et al.*, 2006; Morin *et al.*, 2009). A recent meta-analysis showed that leaf senescence seemed to be particularly dependent on October temperatures, a warmer autumn leading to delayed senescence (Gill *et al.*, 2015). Several models have been designed to predict leaf-yellowing or leaf-shedding while considering both temperature and photoperiod (Delpierre *et al.*, 2009), or only temperature (Richardson *et al.*, 2006; Keenan and Richardson, 2015) but more complex interactions among factors, including soil water availability should be integrated for accurate predictions (Xie *et al.*, 2018; Liu et al, 2019). Furthermore, leaf senescence may also affect spring bud-burst timing the following year (Nielsen and Jorgensen, 2003; Heide, 2003), and BB timing could impact the leaf senescence timing of the current year (Fu *et al.*, 2014; Keenan and Richardson, 2015).

Extreme drought events occurred more frequently in Europe in the last decades (e.g.1976, 2003, 2018, and 2019) and their frequency and severity are projected to increase under future climate scenarios (IPCC 2014). Experiments that directly evaluate the effects of soil water deficit on leaf phenology are scarce and present contrasted results. Leaf unfolding responses to rainfall seem to be positive, i.e. a later unfolding date with higher water availability (Peñuelas *et al.* 2004; Adams *et al.* 2015). Ogaya and Penuelas (2004) showed that a 15% reduction in soil water availability induced by a rainfall exclusion system, delayed all the phenophases in Arbutus Toledo but not in *Quercus ilex* or in *Phillyrea latifolia*. Another more drastic rainfall exclusion experiment reducing rainfall by 50% in autumn showed no impact on leaf development the following spring for *Quercus ilex* whereas a 58% reduction in rainfall during spring led to severe aborting of buds (Misson et al, 2011). How soil water deficits interact with warm temperature in leaf senescence is complex; the two parameters have yet to be disentangled (Estiarte and Peñuelas, 2015; Liu et al, 2019). Escudero and Del Arco (1987) showed that soil water deficit induced earlier leaf fall, but Pallardy and Loewenstein (2004) observed that this response was species dependent. Estrella and Menzel (2006) also observed advanced leaf senescence during autumn drought, though leaf yellowing date may be dependent on climatic drivers occurring not only during autumn but also throughout the leafy season (Liu et al, 2019).

During the growing season, a prolonged soil water deficit limits water and carbon uptake by trees (Cowan, 1982; Farquhar and Sharkey, 1982) and slows down nutrients uptake and phloem transports (Sevanto, 2014; Dannoura et al, 2019). The question remains, however, whether these modifications affect leaf phenology. Indeed, in spring, for the establishment of new organs, deciduous trees use carbon reserves (Barbaroux and Bréda 2002; Hoch *et al.*, 2003; Gilson *et al.*, 2014) and nutrient reserves (El Zein et al, 2011a; Bazot et al, 2016) and need water to remobilize these reserves towards the sink organs (i.e, buds and leaves). During leaf senescence, nutrients are resorbed from the leaves towards perennial organs, and this also implies important fluxes (Estiarte and Penuelas, 2015) which may be disrupted by severe soil water deficits.

Finally, phenology is also controlled by complex interactions between genetic and environmental factors. Indeed, studies on beech species have shown differences in leaf phenology among populations from a large climatic gradient within the distribution area of species (Von Wuelish *et al.*, 1995; Zohner and Renner, 2014; Harter *et al.*, 2015; Schueler and Liesebach, 2015; Kramer *et al.*, 2017) or along altitudinal clines (Vitasse *et al.*, 2009a; Vitasse *et al.*, 2009b). These results suggest that leaf phenology in beech trees is adapted to large variations in climatic conditions, and this capacity could help populations to cope with climate change. However, the phenotypic plasticity and adaptive capacity of populations at a regional scale within a small climatic range have rarely been investigated. Moreover, it is important to study to what extent this adaptation could be challenged by recurrent extreme events, like droughts.

In the present study, we used a common garden experiment to investigate the variability of leaf phenology among regional beech (*Fagus sylvatica* L.) populations along a small latitudinal gradient of 140 km in lowlands located in the central area of the European beech distribution range (North-eastern France). We also compared the response of these populations to repeated soil water deficit or defoliation events. Our main aim was to assess whether or not leaf phenology would be modified by disturbances i) in tree water status and/or ii) in tree carbon and nitrogen status. For three years, these statuses were experimentally modified by provoking recurrent prolonged soil water deficits in a rain exclusion system or annually repeated defoliation. In response to these constraints, carbon assimilation was reduced either by stomatal closure under soil water deficit or by reducing leaf area under defoliation. We examined the impact of these constraints on the mean tree BB and LY, on the length of growing season (GS) and on leaf unfolding and leaf yellowing dynamics. We analyzed these traits in the offspring of six regional beech populations. We addressed three questions: (1) Do three years of soil water deficit and defoliation modify budburst and leaf-yellowing days and dynamics in beech trees? (2) How does leaf phenology vary among regional populations? (3) Do prolonged soil water deficits and repeated defoliation modify leaf phenology similarly in all regional populations?

2. Materials and methods

2.1. Study site, plant material and treatments

In October 2006, beechnuts from *Fagus sylvatica* L. trees were collected on the ground in six forests in Lorraine (North-eastern France) along a latitudinal gradient of 140 km (Fig. 1). For each forest, seed collection was conducted in plots of at least 0.5 ha, which included at least 20 mother trees with at least 120 seeds on the ground (E Silva, 2010). All the beechnuts collected in a forest were combined in order to constitute a population. After being rehydrated to a water content of 30-34% and having received an antifungal treatment, the beechnuts were stored in a cold chamber at 3°C in the dark for three months to break their dormancy. In 2007, the seeds were sown in a nursery and 144 randomly selected seedlings per forest were transplanted by groups of 24 into the soil in six different blocks in a common garden (INRAE Grand Est Nancy, Champenoux, France, 48°75’2’’N/6°34’15’’E, elevation: 257 m, Supplemental Information Table S1).

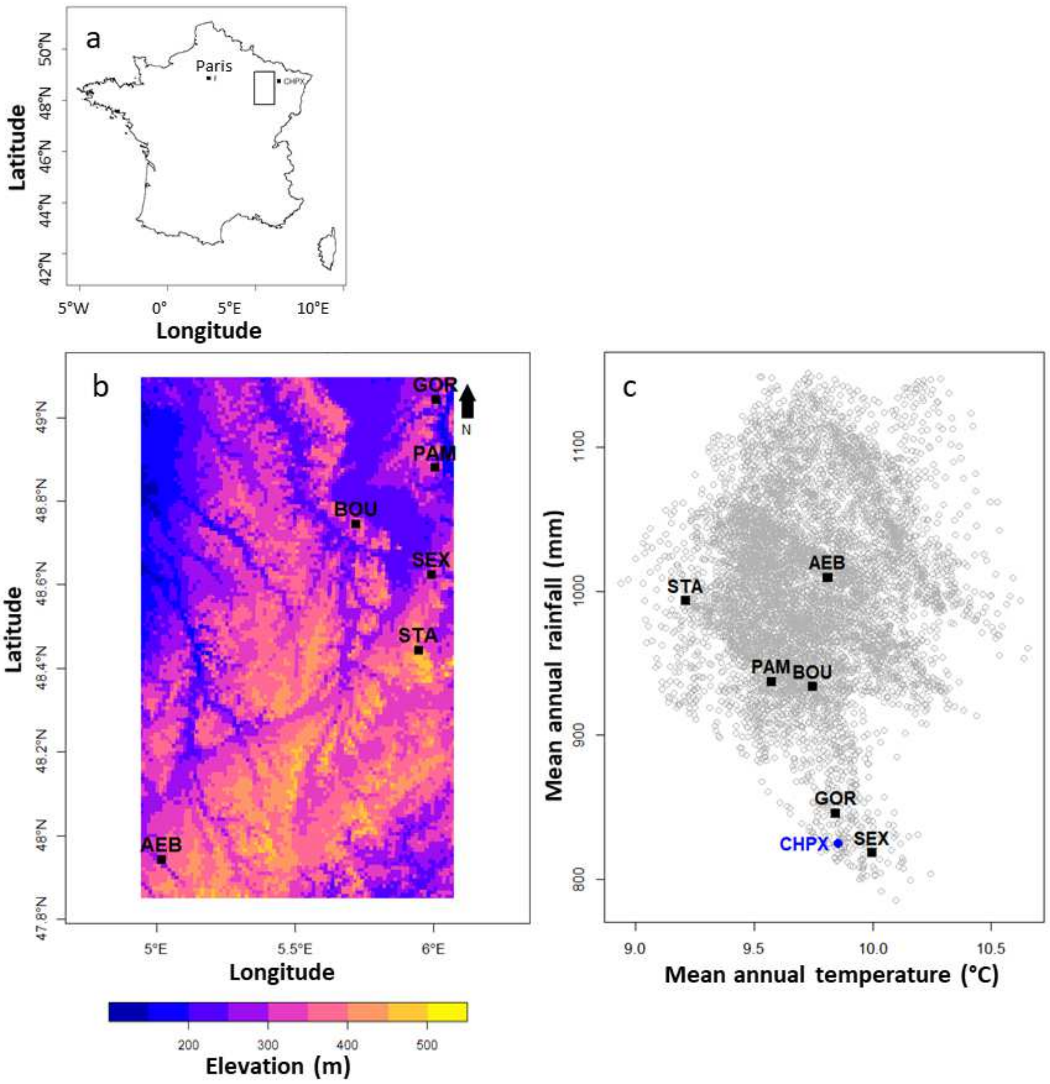

Figure 1. Localization of the study zone represented by the rectangle on the map of France (a), map of the elevation distribution in the study zone represented by the longitude and latitude positions (the elevation range is represented by the color scale presented below the map) (b), variation of the mean annual rainfall and the mean annual temperature in the study zone (grey points (c). In (c), only the points in the range of elevations ± 5% where seeds were collected (i.e., between 297m and 432m) are shown. The mean climatic characteristics were calculated at 1km resolution over the period 1981 - 2010 with the Aurehly model (Météo France, Bénichou and Le Breton, 1987; Canellas *et al.*, 2014). , The six sites where the seeds to be sown in the common garden were collected, are presented by black squares using the following names: Gorze (GOR), Pont-à-Mousson (PAM), Boucq (BOU), Sexey-aux-Forges (SEX), Saint-Amond (STA) and Arc-en-Barrois (AEB) from North to South. In c, the common garden (CHPX) is presented with a blue point. The climatic data of the six forest and the common garden are presented in the Supplemental Information Table S1.

In 2014, a transparent roof built of polycarbonate sheets was installed 5m above all the trees to intercept rainfall. Four treatments were imposed on the seven-year-old trees (average height

1.5 m, average diameter 25 mm, see Fig. S3 for information per population) for three years (2014-2016): i) an irrigated control treatment (n=48 trees per population split into two blocks of 24 individuals each); ii) an irrigated defoliation treatment (n= 48 trees per population split into two blocks of 24 individuals each) where defoliation was done once per year as follows: the first two years (2014 and 2015), 75% of the foliage was manually removed from each tree in June after primary growth was finished (3 short shoots, 3 long shoots and the terminal shoot elongation plus leaves area monitored on 20 trees in each treatment every year), and the third year (2016), 90% of the foliage was removed in May; thanks to the irrigation in both control and defoliation treatments, predawn twig water potential remained above -0.25 MPa during the whole experiment (Chuste et al., 2019); iii) a moderate soil water deficit treatment without defoliation (MWD, n=24 trees per population in one block). The trees in this treatment were near the edge of the roof and were lightly irrigated by lateral rain entry; their predawn twig water potential reached until -1.2 MPa (Chuste et al., 2019); and iv) a severe soil water deficit treatment without defoliation (SWD, n= 24 trees per population in one block) inducing predawn twig water potential down to -2.0 MPa (Chuste et al., 2019). Tree root systems in the MWD and SWD treatments were isolated with a rigid waterproof plastic sheet (DELTA®-MS) buried around the two blocks of the two treatments to a depth of 1.80 m. The control and defoliation treatments were done with an automatic drip watering system, which delivered between two and four liters of water per tree two to three times a week. Irrigation was adjusted to avoid any water shortage in these two treatments, i.e. to maintain Relative Extractable soil Water (REW) above 40%, the threshold below which stomatal closure reduces transpiration (Granier *et al.*, 1999). In the MWD and SWD treatments, rain was excluded all year round, including winter, and the trees were slightly irrigated only once (about 40 mm) in November.

2.2. Meteorological data and soil water content

Air temperature and relative humidity were automatically recorded at 30s intervals with a probe (HMP35A; Vaisala Oy, Helsinki, Finland), 2.50 m above the ground under the rain exclusion roof in the middle of the common garden. The measurements were averaged and stored every 30 min in a datalogger (CR5000, Campbell scientific, Shepshed, UK).

Soil water content was monitored with a neutron probe (TROXLER TX 4301, Research Triangle Park, North Carolina, USA) to a maximum depth of 1.60 m. Neutron probe access tubes (aluminum) were installed in the soil to quantify water content at different depths. The tubes were distributed equally among the control, defoliation and two soil water deficit treatments: for each treatment, there were two tubes ranging from 0 to 100 cm in depth and one ranging from 0 to 160 cm. During the growing season of each year, measurements were carried out every two weeks. Counts were logged every 10 cm for the upper 100 cm, and every 20 cm below that. Relative Extractable Water (REW, in %) was calculated according to Bréda *et al.* (1995).

We used the Aurélhy meteorological model (1km resolution, Météo France, Bénichou and Le Breton, 1987; Canellas *et al.*, 2014) and a Digital Elevation Model with a resolution of 25 m (BD Alti ® 25m, IGN) according to geographical coordinates to obtain the meteorological conditions and altitude for the zone of origin of each population (Fig.1) and for the common garden site. For each of the seven sites (six forests and the common garden), we calculated mean annual temperature, mean number of freezing days and mean annual rainfall over the period 1981-2010 (Supplemental Information Table S1).

2.3. Phenological observations

We monitored bud development on each tree during spring (between April 1st and May 30th) for three consecutive years (2014-2016). Observations were made every three or four days and bud development of each tree was noted from 0 to 39 according to the BBCH code (Biologische **B**undesanstalt **B**undessortenamt und **CH**emische Industrie) (Supplemental Information Fig. S1). For each tree, bud-burst (BB) day was set when the majority of buds on the tree had reached stage 7 (Supplemental Information Fig. S1), as proposed by Chuine and Cour (1999).

Leaf-yellowing (LY) was monitored every one to two weeks depending on the color change dynamics in autumn (September 1st - December 15th) during the same three years. Leaf color changes were assessed according to a specific code that we defined for our young beech trees (Supplemental Information Fig. S1). For each tree, LY day was set when at least 50% of a tree's leaves had no green color left (stage 6, Supplemental Information Fig. S1). As many of these young beech trees were marcescent (i.e. trees keep their leaves during winter until the arrival of the new leaves at the following spring), we did not follow leaf fall.

The BB and LY of the trees in the control treatment were monitored during a fourth year (2017).

2.4. Leaf nitrogen content

Five leaves per tree were collected at 4 dates: July 2015, October 2015, June 2016 and October 2016. According to the dates and treatments, between 3 and 6 trees were sampled. At each date, the leaves of the same tree were pooled, frozen in liquid nitrogen and stored at -80 °C. The samples were then freeze dried [Dura-Top ®, Dura-Dry ®, FTS Systems ®, Stone Ridge, NY, USA], weighed and ground into a fine powder in a ball mill (CEPI SODEMI CB2200, Cergy, France). Leaf N concentration (% of dry matter) was measured with an elemental analyser (NA 1500 NCS, Carlo Erba,Milan, Italy). Analyses were carried out at the

SilvaTec platform (UMR Silva, INRAE Grand Est-Nancy, France). The average and standard deviation were calculated per treatment and date.

2.5. Data analysis

We first transformed the BBCH code into a continuous variable (resulting in a new code from 0 to 17, Supplemental Information Fig. S1) before proceeding with the data analysis described hereafter. BB day was defined for each tree as the date when the tree was noted stage 3 (new code Supplemental Information Fig. S1). Given the rapid development of beech buds and the three-to-four-day time lapse between two observations, the precise stage 3 date (new code) was not always observed for each tree in the field. For those trees, BB day was calculated by linear interpolation between the dates when stages 2 and 4 were observed. Leaf-yellowing day of each tree was defined at stage 6. When the precise stage 6 date was not observed in the field, the LY day was calculated by linear interpolation between the dates when stages 5 and 7 were observed. Growing season duration (GS) was calculated for each tree as the number of days between BB and LY days. The average and standard deviation were calculated for BB, LF and GS for each combination of population and treatment.

BB and LY days and GS length were compared among treatments and among populations within each treatment with a linear model fitted in the R software (R version 3.3.2, 2016-10-31, http://www.r-project.org). For the ANOVA analysis, done with the “car” package, the fixed effects were treatment, population and their interactions. BB and LY days and GS length were also ranked among populations within each treatment thanks to a Spearman correlation analysis between the phenological variables and latitude. Results were considered significant when the test p-values were below 0.05.

The seasonal progress of the mean bud development and leaf yellowing was also calculated for each treatment and was fitted with sigmoidal ($y = A/[1 + e\ (-(X-X_0)/B)]$) or double sigmoidal functions ($y = A_1/[1 + e\ (-(X-X_1)/B_1)]+ A_2/[1 + e\ (-(X-X_2)/B_2)]$).

3. Results

3.1. Bud-burst and leaf-yellowing responses to soil water deficit and defoliation

The trees in the control and defoliation treatments were irrigated and REW was maintained above a 40% threshold (Fig. 2). In the MWD treatment, REW was maintained below 40% from June 2014 until June 2016, with a minimum of 12% at the end of the 2014 and 2015 summers. In 2016, a very rainy spring caused a rise in groundwater and a transitory increase in REW in this treatment, which exceeded 40% between DOY160 and DOY220. In the SWD treatment, REW was maintained below 40% all the three years with a minimum of around 5% at the end of each summer (Fig. 2).

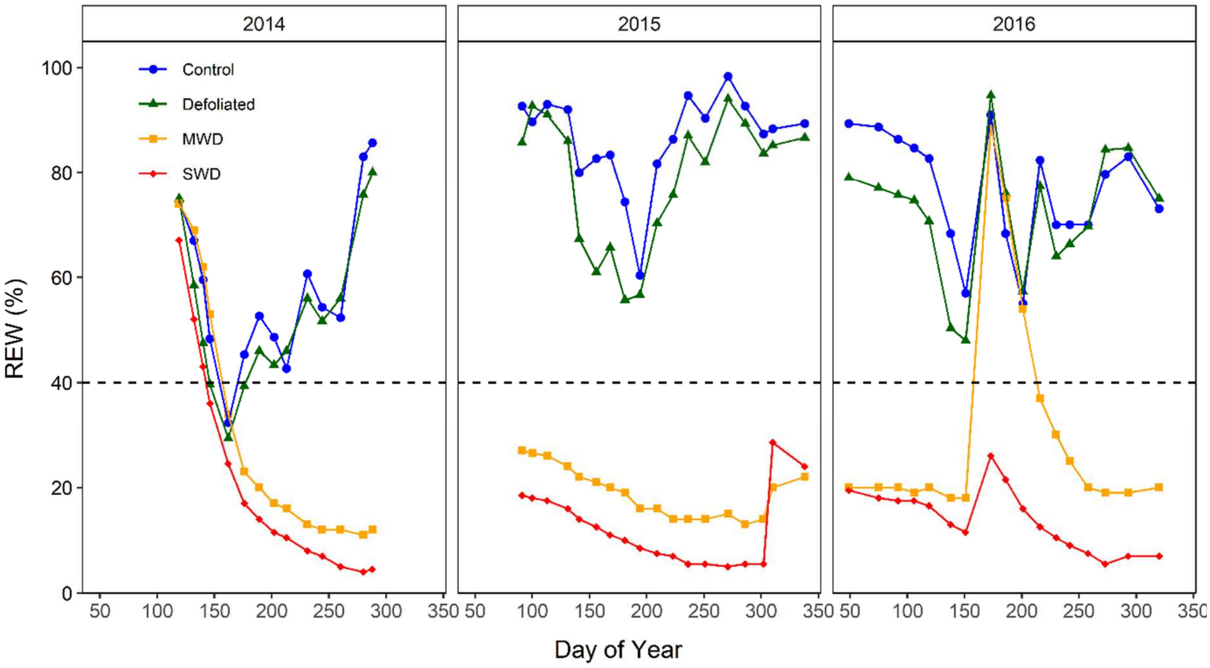

Figure 2. Time course (Day of Year) of Relative Extractable Water (REW, %) over three consecutive years (2014 to 2016) in four treatments: control, defoliation, moderate water

deficit (MWD) and severe water deficit (SWD). The horizontal dashed line indicates the REW threshold value (40%) below which stomatal conductance is affected, according to Granier *et al.* (1999). n=3 for control and defoliation treatments, n=2 for SWD, n=1 for MWD.

During spring 2014, the rain exclusion system had not been yet installed and bud development was similar among treatments, following a sigmoid curve from bud opening until the leaf area was fully deployed (Fig.3).

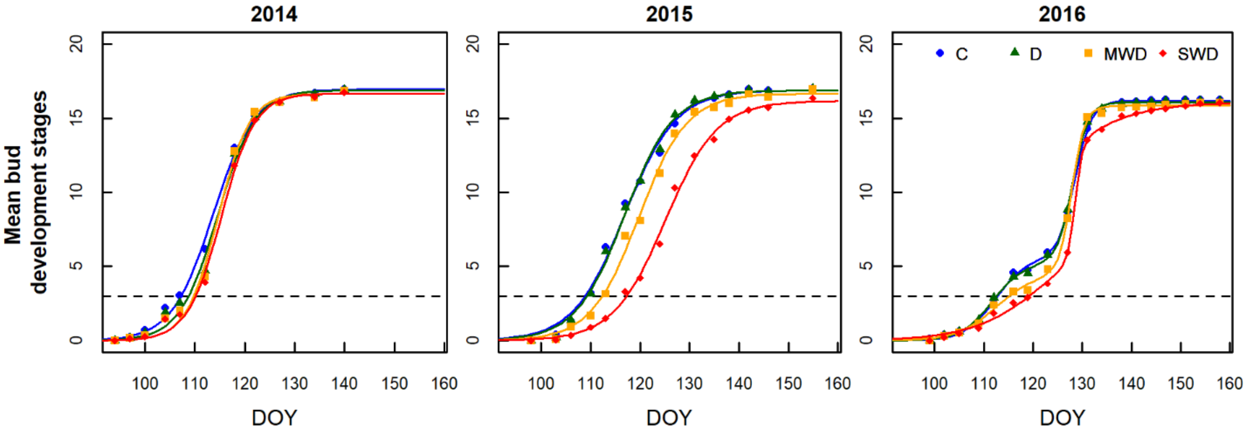

Figure 3. Time course (DOY, day of year) of the mean bud development stages according to the modified BBCH scale for three consecutive years (2014 to 2016) in beech trees under four treatments: control (C), defoliation (D), moderate water deficit (MWD) and severe water deficit (SWD). The horizontal dashed line represents bud-burst stage. Sigmoïdal curves were fitted for 2014 and 2015, and double sigmoïdal curves for 2016.

During 2015, the year following the beginning of soil water restrictions and defoliation, the dynamics of bud development were similar in the control and defoliation treatments (Fig. 3, Table 1) whereas they were delayed in the MWD and SWD treatments (Fig. 3, Table 1). The drought treatments presented a delay in the beginning of bud development compared to the control and defoliation treatments whereas the speed (slope of the sigmoidal curve) and the duration of leaf deployment were similar among all treatments (Fig. 3). In 2016, after two years of defoliation and soil water deficit, control and defoliated trees presented similar bud development dynamics whereas trees in MWD and SWD treatments reached bud burst later (Fig. 3).

Table 1. Mean ± standard deviation bud-burst (BB) day, leaf-yellowing day (LY) and growing season (GS) length for the four treatments (control, defoliation, moderate soil water deficit (MWD) and severe soil water deficit (SWD) for three consecutive years (2014, 2015 and 2016). For each variable and each year, the *P-value*s of the treatment effect analyzed by a one-way ANOVA are noted in italics and the treatments with significantly different values are noted with different superscript letters. n=288 trees for control and defoliation treatments, n=144 for MWD and SWD treatments.

	2014			2015			2016		
Treatment	BB	LY	GS	BB	LY	GS	BB	LY	GS
Control	110 ± 5 ^{a}	307 ± 12 ^{c}	197 ± 12 ^{c}	114 ± 6 ^{a}	302 ± 8 ^{c}	188 ± 9 ^{b}	120 ± 8	314 ± 8 ^{c}	194 ± 10 ^{b}
Defoliation	111 ± 5 ^{ab}	303 ± 11 ^{b}	192 ± 11 ^{b}	113 ± 5 ^{a}	302 ± 6 ^{c}	189 ± 8 ^{b}	120 ± 8	313 ± 8 ^{c}	193 ± 9 ^{b}
MWD	111 ± 4 ^{ab}	293 ± 17 ^{a}	182 ± 17 ^{a}	116 ± 5 ^{b}	292 ± 7 ^{a}	176 ± 9 ^{a}	120 ± 7	300 ± 8 ^{a}	180 ± 10 ^{a}
SWD	112 ± 4 ^{b}	296 ± 12 ^{a}	184 ± 12 ^{a}	120 ± 5 ^{c}	298 ± 7 ^{b}	178 ± 8 ^{a}	120 ± 6	303 ± 9 ^{b}	183 ± 11 ^{a}
P-value	***0.002***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	*0.569*	***<0.001***	***<0.001***

Due to peculiar climatic conditions during the spring 2016 (very cold temperatures with a daily mean of 6°C from day 114 to day 122 followed by warm temperatures with a daily mean of 14.8°C from day 123 to day 132 during the bud-burst period, (Supplemental Information Fig. S4), the dynamics of bud development followed a double sigmoid curve (Fig. 3). These particular dynamics were particularly marked in the treatments with the earliest development (the control and defoliation treatments), which were more strongly slowed down by the late cold. Consequently, whereas the bud development trajectory showed differences among treatments (Fig. 3), there was no difference in mean BB day among treatments for the year 2016; BB day was delayed until day 120 for all treatments (Table 1).

Leaf-yellowing followed a sigmoid curve each year (Fig. 4). In all treatments, majority of tree displayed a leaf coloration corresponding to stage 3 from the spring, stages 1 and 2 were observed for very few trees. Similar LY dynamics were observed in the control and defoliation treatments in 2015 and 2016 whereas LY occurred four days earlier in the defoliation treatment compared to the control in 2014 (Table 1). The MWD and SWD trees displayed earlier LY than the controls during the three years.

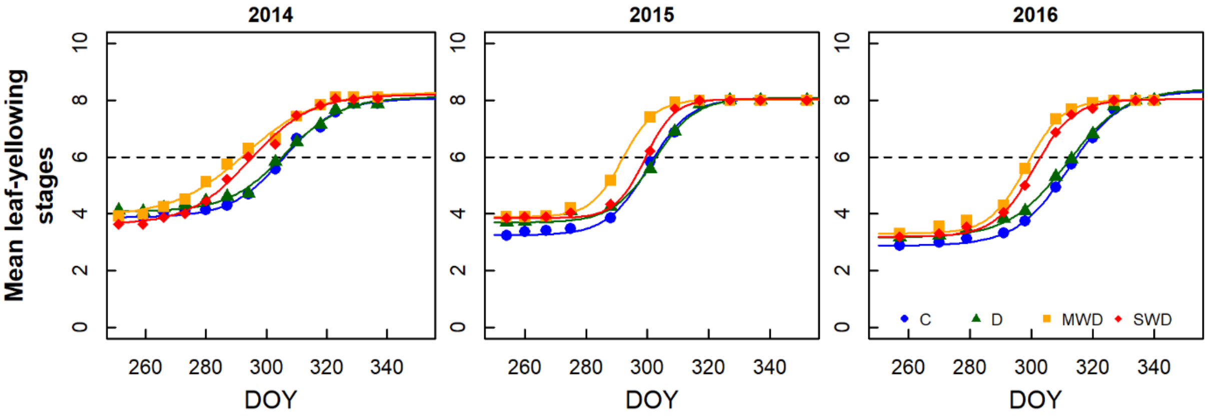

Figure 4. Time course (DOY, day of year) of the mean leaf-yellowing stages according to leaf colour code (see Supplemental Information figure S1) for three consecutive years (2014 to 2016) in beech trees under four treatments: control (C), defoliation (D), moderate water deficit (MWD) and severe water deficit (SWD). The horizontal dashed line represents leaf-yellowing stage. Sigmoïdal curves were fitted for all three years.

LY occurred slightly earlier in the MWD than in the SWD, though the difference was significant in 2015 only. In 2014 and 2015, LY began earlier and finished earlier in the water deficit treatments, with the same rate of yellowing (Fig. 4). In 2016, leaf yellowing started at the same time in all the treatments but proceeded faster in the water deficit treatments than in controls, leading to an earlier end of LY. LY occurred earlier in the drought treatments compared to the controls (for MWD and SWD treatments, respectively, by 14 and 11 days in 2014, 10 and 4 days in 2015 and 14 and 11 days in 2016, Table 1)

As a result, length of the growing season (GS), varied among treatments (Table 1). In 2014, GS was longer in control than defoliated trees, whereas during the following two years, both treatments presented similar GS lengths (Table 1). Over the three years, GS was shorter in SWD and MWD than in control and defoliated trees. The shortest GS was observed in the MWD treatment. When all individual trees were considered over the three years and the four treatments, the variation in GS length depended more on LY day (R^2=0.65, data not shown) than on BB day (R^2=0.15, data not shown), and no correlation was observed between LY and BB (R^2=0.06, data not shown). The correlation coefficient (R^2) between GS and LY varied among treatments between 0.51 and 0.73 whereas the correlation coefficient between GS and BB was between 0.12 and 0.23 (Fig. 5).

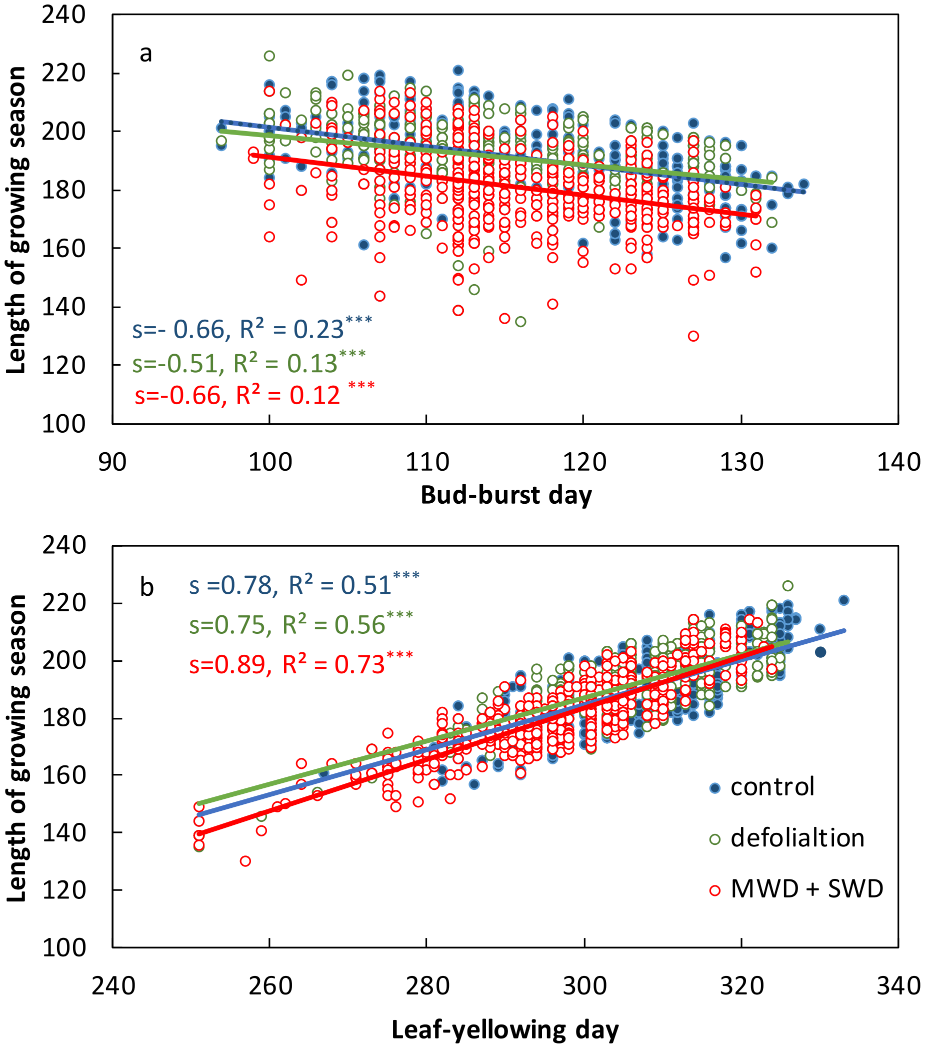

Figure 5. Correlations between the length of the growing season (in days) and (a) bud-burst day and (b) leaf-yellowing day over the three years of the experiment in the combined moderate (MWD) and severe (SWD) soil water deficit, defoliation and control treatments. Each point is a single tree belonging to one of the three treatments during one of the three years of the experiment (2014-2016). The trees in the control treatment monitored during a fourth year were added. The slope (s), the correlation coefficients (R^2) and their significance (*** when $p<0.001$) are indicated in the corresponding color for each treatment.

3.2. Leaf nitrogen response to soil water deficit and defoliation

Leaf nitrogen content was similar between all treatments in October 2015 and October 2016 but presented some differences earlier in the season (Table 2). In July 2015, a higher N content was measured in the leaves of the Defoliation treatment than in that of the Control. In June 2016 the trees in the SWD and MDW treatments presented significant lower N content in their leaves than the trees in the Control and Defoliation treatments.

Table 2. Mean ± standard deviation leaf nitrogen content (g.100g^{-1} Dry Matter) for the four treatments (control, defoliation, moderate soil water deficit (MWD) and severe soil water deficit (SWD) at two dates per year for two years (2015 and 2016). For each date, the *P-values* of the treatment effect analyzed by a one-way ANOVA are noted in italics and the treatments with significantly different values are noted with different superscript letters. n=3 to 6 trees per date and treatment. In October 2016, only trees in SWD treatment were measured.

	Treatment				**Treatment effect**
Date	Control	Defoliation	MWD	SWD	*P-value*
July-15	1.83±0.1 ^{b}	2.28±0.12 ^{a}	1.86±0.1 ^{b}	2.08±0.11 ^{ab}	**<0.001**
Oct-15	1.45±0.07	1.62±0.48	1.50±0.13	1.22±0.7	0.82
June-16	2.24±0.05 ^{a}	2.18±0.05 ^{a}	1.99±0.04 ^{b}	1.99±0.03 ^{b}	**<0.001**
Oct-16	1.63±0.24	1.5±0.08	-	1.56±0.08	0.51

3.3. Variability in bud-burst and leaf-yellowing days among populations under well-watered conditions

The latitudinal gradient presented also an altitudinal variability (between 313m and 411m), a range of mean annual temperature between 9.2°C and 10°C and a range of mean annual rainfall between 818mm and 1009mm among the populations (Fig. 1 and supplemental information Table S1). BB and LY days and the length of the GS displayed a correlation with the population's latitude of origin (Fig. 6). Populations ranking according to latitude was tighter for BB and GS length than for LY (Spearman rank correlation, Table 3). Even if all the correlation coefficients (R^2) varied among years, the slope of the relationship with latitude was well conserved over the four years (slopes between -3.5 and -4.3 days.degré$^{-1}$ for BB, between 6.2 and 7.9 days.degré$^{-1}$ for LY and between 9.8 and 11 days.degré$^{-1}$ for GS). This shows some stability in the ranking of the populations and indicates a similar phenological response of the populations to inter-annual variations in weather conditions. During the four years, BB was negatively correlated with latitude; the northern populations displaying an earlier BB than the southern ones (Fig. 6a, R^2 from 0.51 to 0.91 according to the year). A maximal delay of five days was observed between the two most distant populations (Table 3). On the contrary, a positive correlation was observed between LY and latitude; the northern populations senesced later than did the southern ones (Fig. 6b). A delay of 7 to 12 days according to year was observed between the earliest and the latest populations (Table 3).

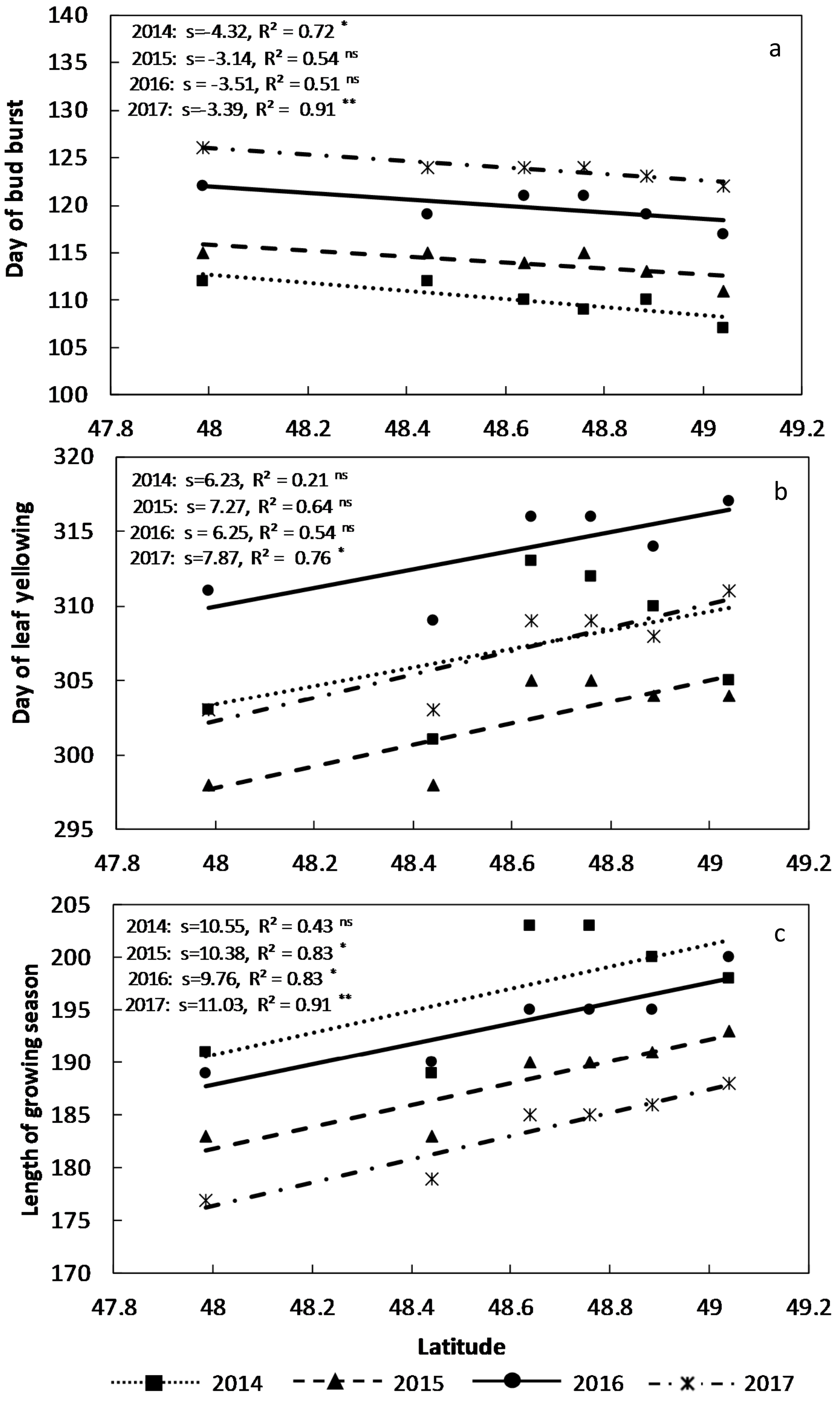

Figure 6. Relationships between the latitude of origin of the trees grown in the common garden experiment under well-watered conditions (controls) and (a) bud-burst day, (b) leaf-

yellowing day and (c) growing season length in 2014 (squares and dotted line), 2015 (triangles and dashed line), 2016 (circles and solid line) and 2017 (crosses and dashed-dotted line). For each year, the slopes (s), the correlation coefficients (R^2) and their significance (ns when $p>0.05$, * when $p<0.05$, ** when $p<0.01$, *** when $p<0.001$) are given.

Table 3. Mean ± standard deviation of bud-burst day, leaf-yellowing day and growing season length for six populations under four treatments (control, defoliation, moderate soil water deficit (MWD) and severe soil water deficit (SWD) for three years (2014, 2015 and 2016). n=48 trees for each population in the control and defoliation treatments and n=24 in the MWD and SWD treatments. The populations are listed following a latitudinal gradient from North to South. For each variable, each year and each treatment, populations ranking was tested with the Spearman correlation coefficient (*ρ*) between the phenological variables and the latitude. Different superscript letters note the statistically significant differences among populations revealed by a one-way ANOVA in each treatment. The comparison of populations (*Pop effect*) ,treatments (*Treat effect*) and their interaction (*Treat x Pop inter*) was analysed with a two-way ANOVA (The *F*-values and their significance *** = P<0.001, ** = P<0.01 and *= P<0.05, ns= non-significant are noted).

		2014				2015				2016			
		Control	Defoliation	MWD	SWD	Control	Defoliation	MWD	SWD	Control	Defoliation	MWD	SWD
BUD-BURST	Gorze	107 ± 5 ^{a}	110 ± 4 ^{ab}	110 ± 3	110 ± 4 ^{ab}	111 ± 5 ^{a}	111 ± 4 ^{a}	113 ± 3 ^{a}	117 ± 3	117 ± 7 ^{a}	115 ± 7 ^{a}	118 ± 7	116 ± 5 ^{a}
	Pont-à-Mousson	110 ± 5 ^{ab}	109 ± 5 ^{a}	110 ± 4	110 ± 4 ^{a}	113 ± 6 ^{ab}	111 ± 4 ^{a}	115 ± 3 ^{ab}	118 + 5	119 ± 8 ^{ab}	116 ± 7 ^{ab}	120 ± 6	118 ± 7 ^{ab}
	Boucq	109 ± 6 ^{ab}	109 ± 5 ^{a}	110 ± 5	110 ± 5 ^{ab}	115 ± 7 ^{b}	112 ± 4 ^{ab}	115 ± 6 ^{ab}	123 + 5	121 ± 8 ^{ab}	118 ± 7 ^{abc}	119 ± 8	120 ± 5 ^{ab}
	Sexey-aux-Forges	110 ± 5 ^{ab}	111 ± 5 ^{abc}	112 ± 3	112 ± 4 ^{abc}	114 ± 7 ^{ab}	113 ± 5 ^{ab}	114 ± 2 ^{ab}	122 + 5	121 ± 8 ^{ab}	120 ± 8 ^{bc}	121 ± 5	121 ± 7 ^{ab}
	Saint-Amond	112 ± 4 ^{b}	113 ± 4 ^{bc}	113 ± 4	114 ± 4 ^{bc}	115 ± 6 ^{b}	115 ± 5 ^{bc}	118 ± 6 ^{bc}	121 + 4	119 ± 8 ^{ab}	122 ± 6 ^{cd}	122 ± 6	122 ± 5 ^{ab}
	Arc-en-Barrois	112 ± 5 ^{b}	113 ± 3 ^{c}	113 ± 3	115 ± 3 ^{c}	115 ± 5 ^{b}	117 ± 4 ^{c}	119 ± 5 ^{c}	120 + 5	122 ± 6 ^{b}	126 ± 3 ^{d}	123 ± 6	125 ± 5 ^{b}
	Spearman ρ	***-0.89*** *	***-0.83*** *	***-0.94*** *	***-0.94*** *	*0.66* ^{ns}	***-1*** **	***-0.83*** *	*-0.43* ^{ns}	*-0.6* ^{ns}	***-1*** **	***-0.94*** *	***-1*** **
	Treat effect	***5.5*** ***				***55.4*** ***				*0.5* ^{ns}			
	Pop effect	***22.7*** ***				***19.7*** ***				*19.0* ***			
	Treat x Pop inter	*1.1* ^{ns}				***2.2*** **				*1.5* ^{ns}			
LEAF-YELLOWING	Gorze	305 ± 14 ^{ab}	305 ± 12	307 ± 13 ^{b}	292 ± 12	304 ± 8 ^{bc}	305 ± 5 ^{b}	299 ± 6 ^{b}	298 ± 7	317 ± 7 ^{c}	314 ± 8	305 ± 9	302 ± 7
	Pont-à-Mousson	310 ± 11 ^{ab}	304 ± 10	290 ± 20 ^{a}	294 ± 12	304 ± 6 ^{abc}	304 ± 5 ^{ab}	292 ± 10 ^{a}	301 ± 5	314 ± 6 ^{abc}	311 ± 8	302 ± 10	305 ± 7
	Boucq	312 ± 10 ^{b}	301 ± 9	282 ± 16 ^{a}	302 ± 10	305 ± 7 ^{c}	302 ± 6 ^{ab}	289 ± 7 ^{a}	301 ± 8	316 ± 7 ^{c}	312 ± 9	300 ± 6	306 ± 7
	Sexey-aux-Forges	313 ± 12 ^{b}	304 ± 10	294 ± 12 ^{ab}	298 ± 11	305 ± 9 ^{bc}	300 ± 6 ^{a}	291 ± 4 ^{a}	299 ± 6	316 ± 8 ^{bc}	312 ± 7	298 ± 5	304 ± 10
	Saint-Amond	301 ± 11 ^{a}	302 ± 11	295 ± 9 ^{ab}	293 ± 15	298 ± 9 ^{ab}	300 ± 7 ^{a}	293 ± 4 ^{ab}	296 ± 9	309 ± 11 ^{a}	313 ± 8	299 ± 7	300 ± 16
	Arc-en-Barrois	303 ± 9 ^{a}	301 ± 12	288 ± 17 ^{a}	298 ± 10	298 ± 7 ^{a}	301 ± 7 ^{ab}	291 ± 6 ^{a}	297 ± 9	311 ± 7 ^{ab}	314 ± 7	298 ± 7	301 ± 7
	Spearman ρ	*0.37* ^{ns}	*0.71* ^{ns}	*0.31* ^{ns}	*-0.31* ^{ns}	*0.54* ^{ns}	***0.83*** *	*0.43* ^{ns}	*0.6* ^{ns}	*0.77* ^{ns}	*-0.14* ^{ns}	***0.94*** *	*0.54* ^{ns}
	Treat effect	***54.9*** ***				***72.0*** ***				***116.0*** ***			
	Pop effect	***4.4*** ***				***9.9*** ***				***5.5*** ***			
	Treat x Pop inter	***6.3*** ***				***3.5*** ***				***2.4*** **			
GROWING SEASON	Gorze	198 ± 13 ^{bc}	195 ± 12 ^{ab}	197 ± 13 ^{b}	182 ± 12 ^{ab}	193 ± 8 ^{c}	194 ± 6 ^{c}	186 ± 7 ^{b}	181 ± 7 ^{ab}	200 ± 8 ^{c}	199 ± 9 ^{c}	187 ± 13 ^{b}	186 ± 9
	Pont-à-Mousson	200 ± 10 ^{c}	195 ± 9 ^{b}	180 ± 20 ^{a}	184 ± 12 ^{ab}	191 ± 7 ^{c}	193 ± 6 ^{c}	177 ± 10 ^{a}	183 ± 6 ^{b}	195 ± 9 ^{bc}	195 ± 8 ^{bc}	182 ± 11 ^{ab}	187 ± 8
	Boucq	203 ± 9 ^{c}	192 ± 11 ^{ab}	172 ± 17 ^{a}	192 ± 10 ^{b}	190 ± 7 ^{bc}	190 ± 7 ^{bc}	174 ± 8 ^{a}	178 ± 9 ^{ab}	195 ± 8 ^{bc}	194 ± 11 ^{abc}	181 ± 9 ^{ab}	186 ± 6
	Sexey-aux-Forges	203 ± 9 ^{c}	193 ± 10 ^{ab}	182 ± 12 ^{a}	186 ± 11 ^{ab}	190 ± 9 ^{bc}	187 ± 8 ^{ab}	177 ± 5 ^{a}	177 ± 6 ^{ab}	195 ± 8 ^{bc}	192 ± 9 ^{ab}	177 ± 6 ^{a}	183 ± 13
	Saint-Amond	189 ± 11 ^{a}	189 ± 11 ^{ab}	182 ± 10 ^{a}	179 ± 15 ^{a}	184 ± 8 ^{ab}	185 ± 6 ^{ab}	180 ± 7 ^{a}	175 ± 8 ^{a}	190 ± 12 ^{ab}	191 ± 8 ^{ab}	177 ± 8 ^{ab}	178 ± 17
	Arc-en-Barrois	191 ± 10 ^{ab}	188 ± 13 ^{a}	175 ± 16 ^{a}	183 ± 11 ^{ab}	183 ± 8 ^{a}	184 ± 8 ^{a}	172 ± 8 ^{a}	177 ± 9 ^{ab}	189 ± 8 ^{a}	188 ± 7 ^{a}	175 ± 8 ^{a}	176 ± 8
	Spearman ρ	*0.37* ^{ns}	***0.89*** *	*0.31* ^{ns}	*0.14* ^{ns}	***0.94*** *	***1*** **	*0.71* ^{ns}	***0.89*** *	***0.94*** *	***1*** **	***0.94*** *	***0.89*** *
	Treat effect	***67.8*** ***				***134.1*** ***				***95.3*** ***			
	Pop effect	***13.2*** ***				***35.7*** ***				***25.4*** ***			
	Treat x Pop inter	***5.8*** ***				***2.3*** **				***0.6*** ^{ns}			

The differences in both BB and LY days among populations acted in the same direction on growing season length, which showed as many as 14 days of difference between the northern and southern populations; the northern populations displayed longer GS than the southern populations (Fig. 6c). GS length presented higher correlation coefficients with latitude than did BB and LY days in 2015 and 2016.

3.4. Bud-burst and leaf-yellowing responses to soil water deficit and defoliation among populations

For BB, in 2014 and 2016, the population ranking was stable whatever the treatment, as shown by the Spearman rank correlation results and the non-significance of the treatment - population interaction (Table 3). But in 2015, the SWD treatment presented a different population ranking, leading to a significant treatment - population interaction. LY often presented a lower Spearman correlation coefficient than did BB, with a less clear ranking of the phenological dates according to population latitude, but the ranking of the extreme populations in the latitudinal gradient was well maintained. The treatments significantly impacted LY and differently according to the populations as revealed by the significant treatment - population interaction for the three years. For GS, in 2015 and 2016, the ranking of populations was stable whatever the treatment (high spearman correlation coefficients). In 2014 and 2015 a significant treatment-population interaction was observed.

4. Discussion

4.1 Annual variability of leaf phenology in beech trees

Over the three years of our experiment, for the beech trees in the control treatment, the maximal inter-annual variability in bud-burst date was 14 days. LY seems to play an important role on the GS length in beech trees since GS was more strongly dependent on LY than on BB. This was also observed by Vitasse *et al.* (2009a) on beech populations along an altitudinal gradient. Consequently, LY date variability could significantly impact the annual carbon balance in beech trees. Dragoni *et al.* (2011) showed that variations in leaf senescence date would have more impact on the C balance than the variations in BB date in a broadleaf forest. However, under our latitude with low sun elevation and short photoperiod in October, cumulated daily irradiance is smaller in autumn than in spring. These properties could limit the impact of the LY variations on the seasonal C balance. Indeed, at the beginning of our experiment, when the trees were seven years old, the phenological differences among populations did not seem to have a significant influence in tree height or diameter growth which were similar among populations (Supplemental Information Fig. S2).

4.2. Responses of beech leaf phenology to soil water deficit and defoliation

In a context of climate change, beech has been described as a species whose leaf phenology (or at least BB) would be little affected by global warming (Fu *et al.*, 2019a) because: i) BB would occur only when a defined photoperiod, which is a fixed parameter, is reached, and ii) the absence of a sufficient chilling temperature would be compensated for an increase in a forcing temperature, as observed during warm years in the past (Cannell, 1997; Dantec *et al.*, 2014). However it is obvious from our study that leaf phenology is also modified by a long soil water deficit. We observed that a soil water deficit caused delayed bud-burst, and overall, early leaf-yellowing, thus significantly reducing the length of the growing season. These results are valid for our young beech trees but could be attenuated in mature trees due to a potential deeper root system. As a reference, under natural condition the duration of one of the most extreme water deficit during the last-10-years in beech stand in 2003 lasted 124 days (Granier *et al.*, 2008), from DOY 178 to DOY 300 with minimum REW close to zero (Peiffer *et al.*, 2014). Similar extreme soil water deficits were computed in European forests in 2003 (Granier *et al.*, 2007) and in 2018 (Schuldt et al, 2020). Depending on the intensity of the water deficit and on year, GS was shortened by up to 15 days, which is within the same range of variation as the inter-annual variability of GS length observed in the control treatment. Surprisingly, MWD treatment presented earlier LY than SWD treatment. This is a possible response to variation of microclimate under the roof, the trees of the MWD being situated at the edge of the roof. Reducing GS in response to soil water deficit may help the tree save water by shortening the transpiration period, thus avoiding extreme dehydration and reducing the risk of hydraulic dysfunction as was suggested in the study on the impact of rainfall exclusion on a Mediterranean forest (Misson et al, 2011). An early leaf fall affecting green leaves in summer, without any yellowing process, has sometimes been reported in case of extreme drought (Bréda *et al.*, 2006; Marchin *et al.*, 2010), probably as a result of petiole embolism. But this was not the case in our study since the duration of the leaf yellowing process was similar for drought-stressed and control trees. Reducing GS may also allow the tree to save carbon and nitrogen. Indeed, prolonged soil water deficit induces a long-term source-sink imbalance because some carbon sinks are maintained active such as maintenance respiration whereas carbohydrates production is reduced due to stomatal closure (Farquhar and Sharkey, 1982; Calister and Adams, 2006; Flexas *et al.*, 2006). Both carbon and nitrogen metabolisms are enhanced in response to soil water deficit to help save internal water and ensure cell survival (Chuste *et al.*, 2019, 2020). Although some carbon sinks, such as primary and secondary growths, are sacrificed under soil water deficit (Chuste et al, 2020), other important *C* sinks remain active (*e.g.* transport, maintenance respiration) or may even be up-regulated (*e.g.* defense, starch interconversion to soluble sugars for osmoregulation and protection against cell dehydration) (Chuste, 2018). Beech trees have to compensate for this carbon imbalance. They may remobilize their carbon reserves to ensure survival (Chuste *et al.*, 2020). In response to soil water deficit, early leaf senescence may save carbon by reducing the carbon used in the maintenance respiration of living organs and to avoid tissue dehydration (Hinckley *et al.*, 1979; Xie *et al.*, 2018). As carbon and nitrogen metabolisms are closely linked, early leaf yellowing may also save nitrogen and would allow an early resorption of leaf nitrogen before leaf death and dehydration in case of extreme soil water deficit (Marchin *et al.*, 2010; Chuste, 2018). These regulations could participate in the survival strategy of the beech trees in response to soil water deficit. However, even if shortening GS is an adaptive response of trees to drought, it is not the best mean for saving water and carbon; other adaptive mechanisms such as stomatal closure or leaf area reduction are much more efficient.

In our study, neither BB nor LY changed in response to defoliation. By defoliating trees, we limited i) the tree's capacity to assimilate carbon by strongly reducing photosynthetic leaf area (75% of defoliation in 2014 and 2015 and 90% in 2016) and ii) the nitrogen available to the trees since 30% of the N total stock is contained in the beech leaves in spring (El Zein *et al.*, 2011b), at the period when defoliation was carried out. This reduction of the nitrogen and carbon availability did not affect the leaf phenology of our beech trees. However, another consequence of defoliation is to limit the tree consumption of carbon (by reducing maintenance respiration), in the absence of re-foliation (as was our case in 2014 and 2015, but not in 2016). In addition, higher leaf N concentrations was measured in the foliage remaining on our defoliated trees in 2015 as also observed by Pinkard *et al.* (2011) in *Eucalyptus globulus*. This leaf nitrogen increase did not significantly affect leaf phenology contrarily to the results suggested by the study of Fu *et al.* (2019c). As a large fraction of leaf N is invested in Rubisco (Evans, 1989), this leaf N increase could increase the C assimilation in the remaining leaves of the defoliated trees, a response to defoliation often reported in the literature (Hart *et al.*. 2000; Handa *et al*, 2005). Moreover defoliating part of crown undoubtedly allowed remaining, previously shaded leaves to receive more light which may have stimulated carbon assimilation in these leaves. Consequently, the defoliation treatment may have only slightly affected carbon assimilation at the tree scale. Therefore, the absence of a phenological response to defoliation could also be because defoliation affected the carbon and nitrogen balances of the trees less than expected.

4.3. Plasticity of leaf phenology among regional beech forests

We examined the question of the phenological differentiation among six populations issued from a small latitudinal gradient presenting a small climatic range in the central distribution area of *Fagus sylvatica* L. From one year to the next, we often observed a similar population ranking for both BB and LY in the control treatment: Delpierre *et al.* (2017) observed that leaf phenology ranking was stable from year to year among trees of temperate forest, including *Fagus sylvatica,* over a large distribution area. The relationship between BB and LY and the latitudinal origin of the populations that we observed, suggests a genetic differentiation at the regional scale that could be adaptive or not. We checked the literature for the factors controlling the expansion of beech in Europe during the post-glaciation period. We found three main drivers: i) climatic conditions, ii) human activities and iii) the natural, slow migration of beech forests due to dispersal limitation (Willner *et al.*, 2009; Magri, 2008). In our study, we observed few significant correlations between the latitudinal gradient and the mean climatic trends along our gradient suggesting that the genetic differentiation could result from factors other than climate (Supplementary Information Fig S3). However, this absence of climatic links could also be due to the limited number of populations within a small climatic gradient. Moreover, the meteorological model we used to estimate the climatic variables at each site, may not have been enough precise at the regional scale. Finally, we used mean climatic values over 30 years (1981 – 2010) to investigate the climatic gradients and it is possible that a population's adaptation to a local climate is driven more by its ability to survive extreme climatic events than by a mean climatic trend. For instance, one of our populations has been particularly sensitive in term of tree mortality in response to SWD treatment in the common garden experiment (data not shown).

We revealed that in our regional gradient, the northern populations presented a longer GS than the southern ones. This result at the local level contrasts with previous observations done over a large European geographical range: several studies observed that the northern populations would be genetically adapted to a cold climate with later BB and earlier LY than the southern populations (Robson *et al.*, 2013; Delpierre *et al.*, 2017),. Such a response had been observed in Germany and Poland where northern populations flushed later (Von Wuehlisch *et al.*, 1995; Chmura and Rozkowski, 2002). In the Northern hemisphere, Gill *et al.* (2015) observed a negative correlation between leaf-yellowing date and latitude. One possible explanation of our conflicting results is the inversed frost gradient that we identified between the populations situated at the most extreme zones of the latitudinal range (Supplementary Information Fig S3, Table S1): the mean number of frost days per year was lower (69.7 days) in the most northerly site than in the most southerly (81.7 days). At regional scale, small topographic and/or altitudinal variations among forests may have counterbalanced the temperature gradient that we expected along this latitudinal gradient (i.e., southern populations warmer than northern ones). The difference in GS length observed between our northern and southern populations remains in agreement with the trade-off between growth performance and frost resistance suggested by Loehle (1998): the southern populations may have presented the shortest growing season to avoid frost.

We compared the capacity of regional beech populations in the central area of distribution to face future soil water deficits. Globally, the response to soil water deficit was characterized by a late BB and an early LY, thus strongly reducing GS length. However, we also found population-specific responses to soil water deficit with significant treatment-population interactions suggesting that some populations were more impacted by soil water deficit than others. Our results suggest that climate change may challenge the current adaptation of trees to their local growth conditions, and this could be particularly important in the central zone of the species distribution area. Indeed, for a long time studies focused on the fitness of the populations growing in the extreme zones of the distribution area (Jump *et al.*, 2006; Piovesan *et al.*, 2008), but more recent studies suggest a stronger sensitivity to recent drought episodes for trees growing in the wetter mid-latitudes (Friedrichs *et al.*, 2009; Scharnweber *et al.*, 2011). In fact, populations in the central area of distribution, where extreme events are rare, could be more sensitive to soil water deficit than those growing at the south edge of the range, which frequently experience extreme climatic events. Populations in the edge area would retain only the most resistant and best adapted individuals in their populations (Cavin and Jump, 2017).

5. Conclusion

Our study suggests that beech trees present a local variation of leaf phenology, even within a small latitudinal gradient, and that different populations have different phenological response to soil water deficit. The impact of drought on both bud-burst and leaf yellowing dates leads to a shorter growing season and suggests that soil water content should be taken into account more often in studies of inter-annual phenological variability, particularly in the context of future climate change where spring and summer drought events are likely to become more frequent. Accounting for soil water content could help researchers to better estimate the length of the growing season in carbon balance models for sensitive deciduous species like *Fagus sylvatica* under future climatic conditions.

Data accessibility

The data are available from the authors upon request.

Declaration of Competing Interest

None.

Acknowledgements

The authors thank Thierry Paul for the overseeing of the tree planting and roof construction. The authors thank Fabrice Bonne and the Master's students (Mylène Hardy, Hakima Ammour, Marie Doron and Sirine Rommani) who helped to the phenology measurements. The authors also warmly thank i) the middle-school students and their teachers (Collège Duvivier in Einville-au-Jard) invested in the Survivors mediation project supported by Labex ARBRE, and the CPIE (Centre Permanent d'Initiatives pour l'Environnement, Nancy Champenoux) and ii) all the INRAE colleagues ("Hêtre en fête", a project supported by the Labex ARBRE) for their help with defoliation.

Funding

The experiment and operating costs were funded by the French National Research Agency (ANR), ("Investissements d'Avenir" program [ANR-11-LABX-0002-01, Laboratory of Excellence ARBRE] within the framework of the Mepib-Death multidisciplinary project) and the Lorraine Region Project [Survival, contract n°12000453]. PA Chuste received a PhD grant from the Laboratory of Excellence ARBRE.

Appendix A. Supplementary information

Figure S1. Codes used to determine the bud burst day (stage 7 in the BBCH code) and leaf yellowing day (stage 6).

Figure S2. Variability in tree size within and among beech populations at the beginning of the experiment.

Figure S3 – Correlation matrix between the geographic, climatic and phenological variables for the six beech populations.

Figure S4 - Changes in thermal time (°C day) during (a) bud-burst and (b) leaf-yellowing periods in relation to the day of year (DOY).

Table S1. Mean climatic characteristics 1981-2010 from the Aurehly model (Météo France) for the sites of origin for the six populations along a 140-km latitudinal gradient in the Lorraine region (North-eastern France), and for the common garden site.

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