HAL
open science

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

Catherine Massonnet, Pierre-Antoine Chuste, Joseph Levillain, François Gérémia, Daniel E Silva, Pascale Maillard, Erwin Dreyer, Jean-Luc Dupouey, Nathalie Bréda

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

Submitted on 3 Feb 2023

1   Research Paper _ revised version

2

3

4

5 **Leafy season length is reduced by a prolonged soil water deficit but not by**

6 **repeated defoliation in beech trees (*Fagus sylvatica* L.): comparison of**

7 **response among regional populations grown in a common garden.**

8 Massonnet Catherine[1,*], Chuste Pierre-Antoine[1], Levillain Joseph[1], Gérémia

9 François[1], E Silva Daniel[1], Maillard Pascale[1], Dreyer Erwin[1], Dupouey Jean-Luc[1] and

10 Bréda Nathalie[1].

11

12 [1].Université de Lorraine, AgroParisTech, INRAE, UMR 1434 SILVA, F-54000 Nancy,
13 France

14

15 *Corresponding author

16 Catherine MASSONNET

17 Mail:catherine.massonnet@inrae.fr

18 INRAE-UMR 1434 SILVA

19 Route d'Amance

20 F-54280 CHAMPENOUX

21 FRANCE

22

23 E mail addresses:

24 catherine.massonnet@inrae.fr (C. Massonnet), pac.chuste@gmail.com (P.A. Chuste),
25 joseph.levillain@inrae.fr (J. Levillain), francois.geremia@ovh.fr (F. Gérémia),
26 daniel.coelhosilva@gmail.com (D. E Silva), pascale.maillard@inrae.fr (P. Maillard),
27 erwin.dreyer@inrae.fr (E. Dreyer), jean-luc.dupouey@inrae.fr (J.L. Dupouey),
28 nathalie.breda@inrae.fr (N. Bréda)

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.

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.*,

84 2014; Zohner and Renner, 2014; Dantec *et al.*, 2014; Laube *et al.*, 2014; Fu *et al.*, 2015).

85 Moreover, in some tree species like beech, photoperiod may also interact with temperature to

86 determine bud-burst date, though the mechanisms of this interaction remain unclear (Heide,

87 1993; Partanen *et al.*, 1999; Körner and Basler, 2010; Vitasse and Basler, 2013; Basler and

88 Körner, 2014; Laube *et al.*, 2014; Hamilton *et al.*, 2016; Fu *et al.*, 2019b). Day-length may

89 interact negatively with heat requirements during ecodormancy to avoid that BB occurred too

90 late (if abnormally cold spring) or too early (if warm spring) (Fu *et al.*, 2019b).

91 The role of climate as a driver of leaf senescence (i.e. yellowing and shedding) is less well

92 understood than that of spring phenology (Richardson *et al.*, 2013). Long-term investigations

93 on the links between leaf-senescence and air temperature have sometimes revealed a delay in

94 leaf senescence in response to global warming, sometimes an advance, and sometimes no

95 effect at all (Peñuelas *et al.*, 2002; Menzel *et al.*, 2006; Morin *et al.*, 2009). A recent meta-

96 analysis showed that leaf senescence seemed to be particularly dependent on October

97 temperatures, a warmer autumn leading to delayed senescence (Gill *et al.*, 2015). Several

98 models have been designed to predict leaf-yellowing or leaf-shedding while considering both

99 temperature and photoperiod (Delpierre *et al.*, 2009), or only temperature (Richardson *et al.*,

100 2006; Keenan and Richardson, 2015) but more complex interactions among factors, including

101 soil water availability should be integrated for accurate predictions (Xie *et al.*, 2018; Liu et al,

102 2019). Furthermore, leaf senescence may also affect spring bud-burst timing the following

103 year (Nielsen and Jorgensen, 2003; Heide, 2003), and BB timing could impact the leaf

104 senescence timing of the current year (Fu *et al.*, 2014; Keenan and Richardson, 2015).

105   Extreme drought events occurred more frequently in Europe in the last decades

106 (e.g.1976, 2003, 2018, and 2019) and their frequency and severity are projected to increase

107 under future climate scenarios (IPCC 2014). Experiments that directly evaluate the effects of

108 soil water deficit on leaf phenology are scarce and present contrasted results. Leaf unfolding

109 responses to rainfall seem to be positive, i.e. a later unfolding date with higher water

110 availability (Peñuelas *et al.* 2004; Adams *et al.* 2015). Ogaya and Penuelas (2004) showed

111 that a 15% reduction in soil water availability induced by a rainfall exclusion system, delayed

112 all the phenophases in Arbutus Toledo but not in *Quercus ilex* or in *Phillyrea latifolia*.

113 Another more drastic rainfall exclusion experiment reducing rainfall by 50% in autumn

114 showed no impact on leaf development the following spring for *Quercus ilex* whereas a 58%

115 reduction in rainfall during spring led to severe aborting of buds (Misson et al, 2011). How

116 soil water deficits interact with warm temperature in leaf senescence is complex; the two

117 parameters have yet to be disentangled (Estiarte and Peñuelas, 2015; Liu et al, 2019).

118 Escudero and Del Arco (1987) showed that soil water deficit induced earlier leaf fall, but

119 Pallardy and Loewenstein (2004) observed that this response was species dependent. Estrella

120 and Menzel (2006) also observed advanced leaf senescence during autumn drought, though

121 leaf yellowing date may be dependent on climatic drivers occurring not only during autumn

122 but also throughout the leafy season (Liu et al, 2019).

123 During the growing season, a prolonged soil water deficit limits water and carbon uptake by

124 trees (Cowan, 1982; Farquhar and Sharkey, 1982) and slows down nutrients uptake and

125 phloem transports (Sevanto, 2014; Dannoura et al, 2019). The question remains, however,

126 whether these modifications affect leaf phenology. Indeed, in spring, for the establishment of

127 new organs, deciduous trees use carbon reserves (Barbaroux and Bréda 2002; Hoch *et al.*,

128 2003; Gilson *et al.*, 2014) and nutrient reserves (El Zein et al, 2011a; Bazot et al, 2016) and

129 need water to remobilize these reserves towards the sink organs (i.e, buds and leaves). During

130 leaf senescence, nutrients are resorbed from the leaves towards perennial organs, and this also

131 implies important fluxes (Estiarte and Penuelas, 2015) which may be disrupted by severe soil

132 water deficits.

133   Finally, phenology is also controlled by complex interactions between genetic and

134   environmental factors. Indeed, studies on beech species have shown differences in leaf

135   phenology among populations from a large climatic gradient within the distribution area of

136   species (Von Wuelish *et al.*, 1995; Zohner and Renner, 2014; Harter *et al.*, 2015; Schueler

137   and Liesebach, 2015; Kramer *et al.*, 2017) or along altitudinal clines (Vitasse *et al.*, 2009a;

138   Vitasse *et al.*, 2009b). These results suggest that leaf phenology in beech trees is adapted to

139   large variations in climatic conditions, and this capacity could help populations to cope with

140   climate change. However, the phenotypic plasticity and adaptive capacity of populations at a

141   regional scale within a small climatic range have rarely been investigated. Moreover, it is

142   important to study to what extent this adaptation could be challenged by recurrent extreme

143   events, like droughts.

144   In the present study, we used a common garden experiment to investigate the

145   variability of leaf phenology among regional beech (*Fagus sylvatica* L.) populations along a

146   small latitudinal gradient of 140 km in lowlands located in the central area of the European

147   beech distribution range (North-eastern France). We also compared the response of these

148   populations to repeated soil water deficit or defoliation events. Our main aim was to assess

149   whether or not leaf phenology would be modified by disturbances i) in tree water status

150   and/or ii) in tree carbon and nitrogen status. For three years, these statuses were

151   experimentally modified by provoking recurrent prolonged soil water deficits in a rain

152   exclusion system or annually repeated defoliation. In response to these constraints, carbon

153   assimilation was reduced either by stomatal closure under soil water deficit or by reducing

154   leaf area under defoliation. We examined the impact of these constraints on the mean tree BB

155   and LY, on the length of growing season (GS) and on leaf unfolding and leaf yellowing

156   dynamics. We analyzed these traits in the offspring of six regional beech populations. We

157   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).
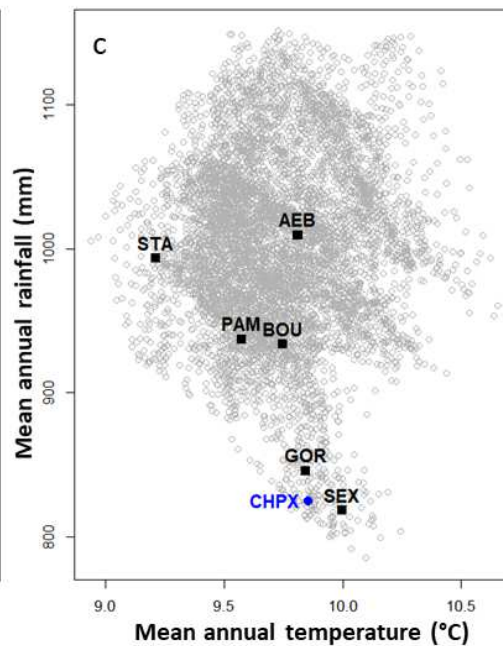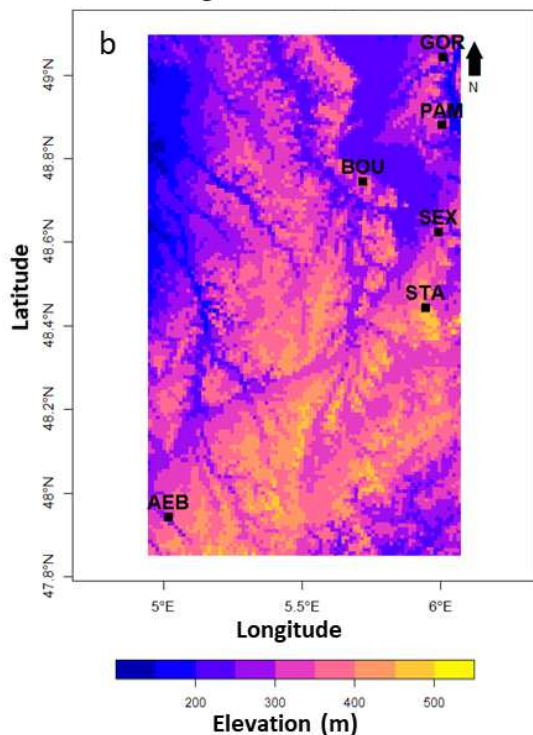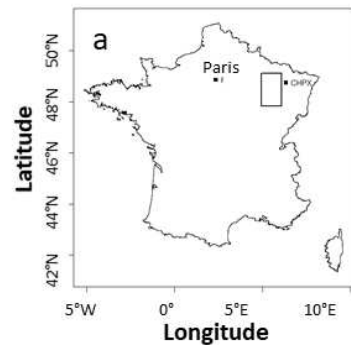
Figure 1. Localization of the study zone represented by the rectangle on the map of France (a), map of the elevation distribution in the study zone represented by the longitude and latitude positions (the elevation range is represented by the color scale presented below the map) (b), variation of the 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 $\pm$ 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

223   1.5 m, average diameter 25 mm, see Fig. S3 for information per population) for three years

224   (2014-2016): i) an irrigated control treatment (n=48 trees per population split into two blocks

225   of 24 individuals each); ii) an irrigated defoliation treatment (n= 48 trees per population split

226   into two blocks of 24 individuals each) where defoliation was done once per year as follows:

227   the first two years (2014 and 2015), 75% of the foliage was manually removed from each tree

228   in June after primary growth was finished (3 short shoots, 3 long shoots and the terminal

229   shoot elongation plus leaves area monitored on 20 trees in each treatment every year), and the

230   third year (2016), 90% of the foliage was removed in May; thanks to the irrigation in both

231   control and defoliation treatments, predawn twig water potential remained above -0.25 MPa

232   during the whole experiment (Chuste et al., 2019); iii) a moderate soil water deficit treatment

233   without defoliation (MWD, n=24 trees per population in one block). The trees in this

234   treatment were near the edge of the roof and were lightly irrigated by lateral rain entry; their

235   predawn twig water potential reached until -1.2 MPa (Chuste et al., 2019); and iv) a severe

236   soil water deficit treatment without defoliation (SWD, n= 24 trees per population in one

237   block) inducing predawn twig water potential down to -2.0 MPa (Chuste et al., 2019). Tree

238   root systems in the MWD and SWD treatments were isolated with a rigid waterproof plastic

239   sheet (DELTA®-MS) buried around the two blocks of the two treatments to a depth of 1.80

240   m. The control and defoliation treatments were done with an automatic drip watering system,

241   which delivered between two and four liters of water per tree two to three times a week.

242   Irrigation was adjusted to avoid any water shortage in these two treatments, i.e. to maintain

243   Relative Extractable soil Water (REW) above 40%, the threshold below which stomatal

244   closure reduces transpiration (Granier *et al.*, 1999). In the MWD and SWD treatments, rain

245   was excluded all year round, including winter, and the trees were slightly irrigated only once

246   (about 40 mm) in November.

247

248

249   *2.2. Meteorological data and soil water content*

250   Air temperature and relative humidity were automatically recorded at 30s intervals with a

251   probe (HMP35A; Vaisala Oy, Helsinki, Finland), 2.50 m above the ground under the rain

252   exclusion roof in the middle of the common garden. The measurements were averaged and

253   stored every 30 min in a datalogger (CR5000, Campbell scientific, Shepshed, UK).

254   Soil water content was monitored with a neutron probe (TROXLER TX 4301, Research

255   Triangle Park, North Carolina, USA) to a maximum depth of 1.60 m. Neutron probe access

256   tubes (aluminum) were installed in the soil to quantify water content at different depths. The

257   tubes were distributed equally among the control, defoliation and two soil water deficit

258   treatments: for each treatment, there were two tubes ranging from 0 to 100 cm in depth and

259   one ranging from 0 to 160 cm. During the growing season of each year, measurements were

260   carried out every two weeks. Counts were logged every 10 cm for the upper 100 cm, and

261   every 20 cm below that. Relative Extractable Water (REW, in %) was calculated according to

262   Bréda *et al.* (1995).

263   We used the Aurélhy meteorological model (1km resolution, Météo France, Bénichou and Le

264   Breton, 1987; Canellas *et al.*, 2014) and a Digital Elevation Model with a resolution of 25 m

265   (BD Alti ® 25m, IGN) according to geographical coordinates to obtain the meteorological

266   conditions and altitude for the zone of origin of each population (Fig.1) and for the common

267   garden site. For each of the seven sites (six forests and the common garden), we calculated

268   mean annual temperature, mean number of freezing days and mean annual rainfall over the

269   period 1981-2010 (Supplemental Information Table S1).

270   *2.3. Phenological observations*

271   We monitored bud development on each tree during spring (between April 1st and May 30th)

272   for three consecutive years (2014-2016). Observations were made every three or four days

273   and bud development of each tree was noted from 0 to 39 according to the BBCH code

274   (Biologische **B**undesanstalt **B**undessortenamt und **CH**emische Industrie) (Supplemental

275   Information Fig. S1). For each tree, bud-burst (BB) day was set when the majority of buds on

276   the tree had reached stage 7 (Supplemental Information Fig. S1), as proposed by Chuine and

277   Cour (1999).

278   Leaf-yellowing (LY) was monitored every one to two weeks depending on the color change

279   dynamics in autumn (September 1st - December 15th) during the same three years. Leaf color

280   changes were assessed according to a specific code that we defined for our young beech trees

281   (Supplemental Information Fig. S1). For each tree, LY day was set when at least 50% of a

282   tree's leaves had no green color left (stage 6, Supplemental Information Fig. S1). As many of

283   these young beech trees were marcescent (i.e. trees keep their leaves during winter until the

284   arrival of the new leaves at the following spring), we did not follow leaf fall.

285   The BB and LY of the trees in the control treatment were monitored during a fourth year

286   (2017).

287   2.4. Leaf nitrogen content

288   Five leaves per tree were collected at 4 dates: July 2015, October 2015, June 2016 and

289   October 2016. According to the dates and treatments, between 3 and 6 trees were sampled. At

290   each date, the leaves of the same tree were pooled, frozen in liquid nitrogen and stored at -80

291   °C. The samples were then freeze dried [Dura-Top ®, Dura-Dry ®, FTS Systems ®, Stone

292   Ridge, NY, USA], weighed and ground into a fine powder in a ball mill (CEPI SODEMI

293   CB2200, Cergy, France). Leaf N concentration (% of dry matter) was measured with an

294   elemental analyser (NA 1500 NCS, Carlo Erba,Milan, Italy). Analyses were carried out at the

295 SilvaTec platform (UMR Silva, INRAE Grand Est-Nancy, France). The average and standard

296 deviation were calculated per treatment and date.

297

298

299 *2.5. Data analysis*

300 We first transformed the BBCH code into a continuous variable (resulting in a new code from

301 0 to 17, Supplemental Information Fig. S1) before proceeding with the data analysis described

302 hereafter. BB day was defined for each tree as the date when the tree was noted stage 3 (new

303 code Supplemental Information Fig. S1). Given the rapid development of beech buds and the

304 three-to-four-day time lapse between two observations, the precise stage 3 date (new code)

305 was not always observed for each tree in the field. For those trees, BB day was calculated by

306 linear interpolation between the dates when stages 2 and 4 were observed. Leaf-yellowing day

307 of each tree was defined at stage 6. When the precise stage 6 date was not observed in the

308 field, the LY day was calculated by linear interpolation between the dates when stages 5 and 7

309 were observed. Growing season duration (GS) was calculated for each tree as the number of

310 days between BB and LY days. The average and standard deviation were calculated for BB,

311 LF and GS for each combination of population and treatment.

312 BB and LY days and GS length were compared among treatments and among populations

313 within each treatment with a linear model fitted in the R software (R version 3.3.2, 2016-10-

314 31, http://www.r-project.org). For the ANOVA analysis, done with the "car" package, the

315 fixed effects were treatment, population and their interactions. BB and LY days and GS

316 length were also ranked among populations within each treatment thanks to a Spearman

317 correlation analysis between the phenological variables and latitude. Results were considered

318 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%
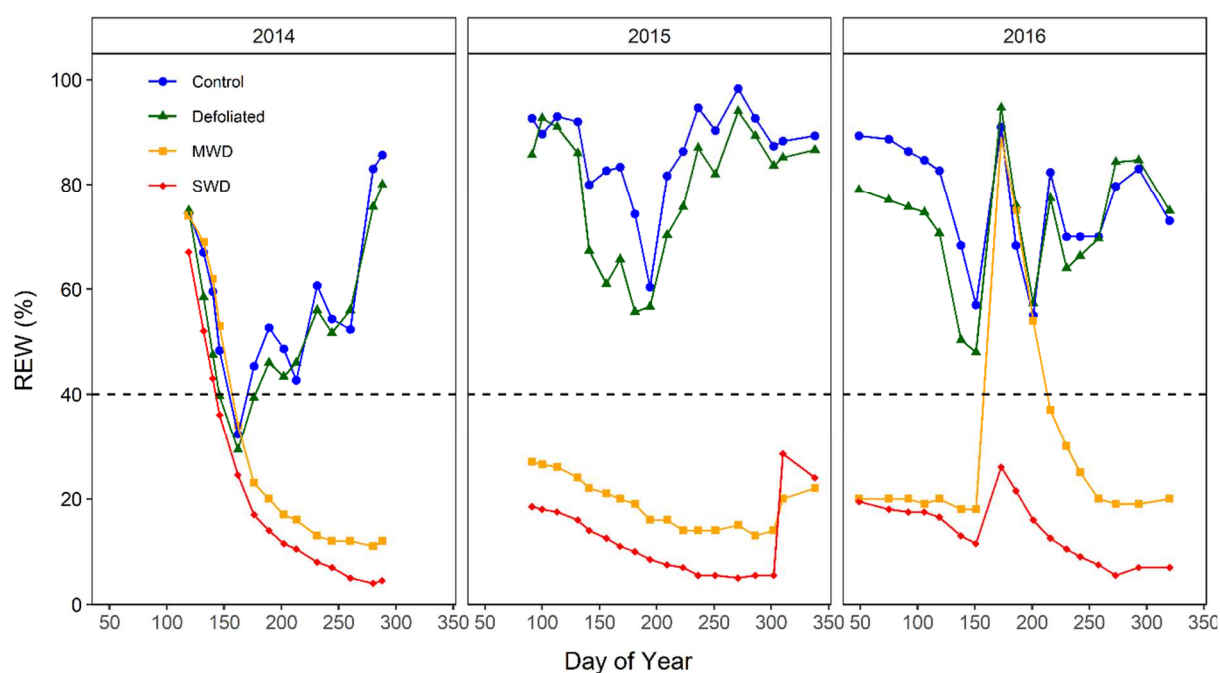at the end of each summer (Fig. 2).

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

14

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).
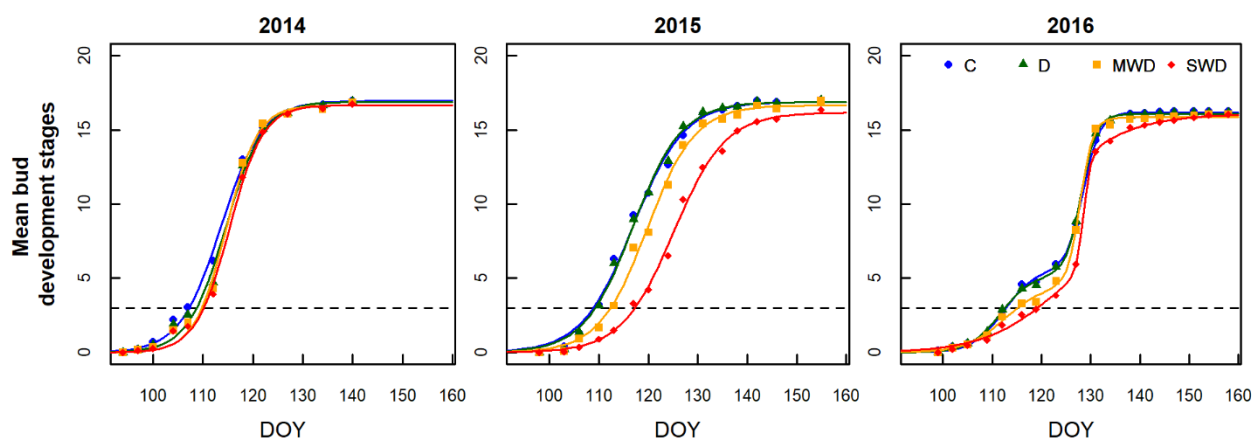

Figure 3. Time course (DOY, day of year) of the mean bud development stages according to the modified BBCH scale for three consecutive years (2014 to 2016) in beech trees under four treatments: control (C), defoliation (D), moderate water deficit (MWD) and severe water deficit (SWD). The horizontal dashed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

373   development dynamics whereas trees in MWD and SWD treatments reached bud burst later

374   (Fig. 3).

375

376

Table 1. Mean $\pm$ 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.

Treatment	2014			2015			2016		
	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*

389 Due to peculiar climatic conditions during the spring 2016 (very cold temperatures with a

390 daily mean of 6°C from day 114 to day 122 followed by warm temperatures with a daily

391 mean of 14.8°C from day 123 to day 132 during the bud-burst period, (Supplemental

392 Information Fig. S4), the dynamics of bud development followed a double sigmoid curve

393 (Fig. 3). These particular dynamics were particularly marked in the treatments with the

394 earliest development (the control and defoliation treatments), which were more strongly

395 slowed down by the late cold. Consequently, whereas the bud development trajectory showed

396 differences among treatments (Fig. 3), there was no difference in mean BB day among

397 treatments for the year 2016; BB day was delayed until day 120 for all treatments (Table 1).

398 Leaf-yellowing followed a sigmoid curve each year (Fig. 4). In all treatments, majority of tree

399 displayed a leaf coloration corresponding to stage 3 from the spring, stages 1 and 2 were

400 observed for very few trees. Similar LY dynamics were observed in the control and

401 defoliation treatments in 2015 and 2016 whereas LY occurred four days earlier in the

402 defoliation treatment compared to the control in 2014 (Table 1). The MWD and SWD trees

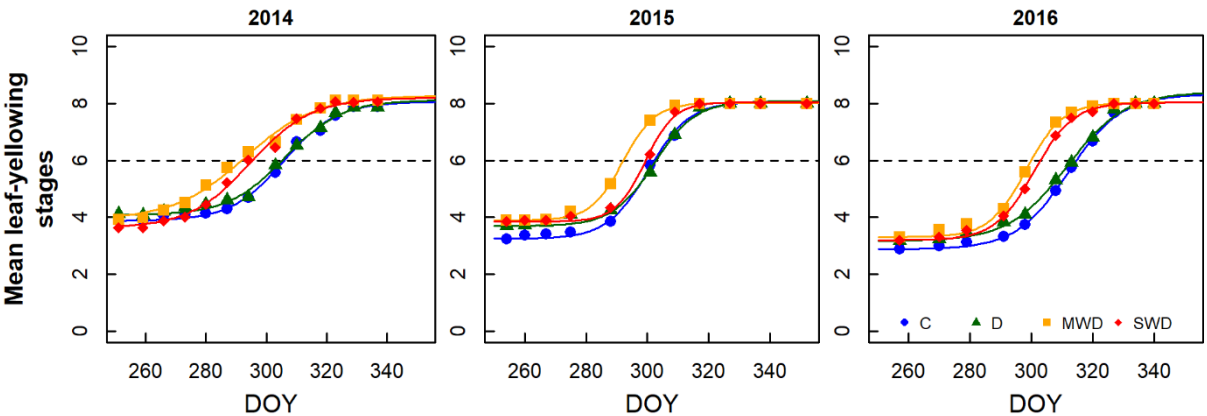403 displayed earlier LY than the controls during the three years.

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).
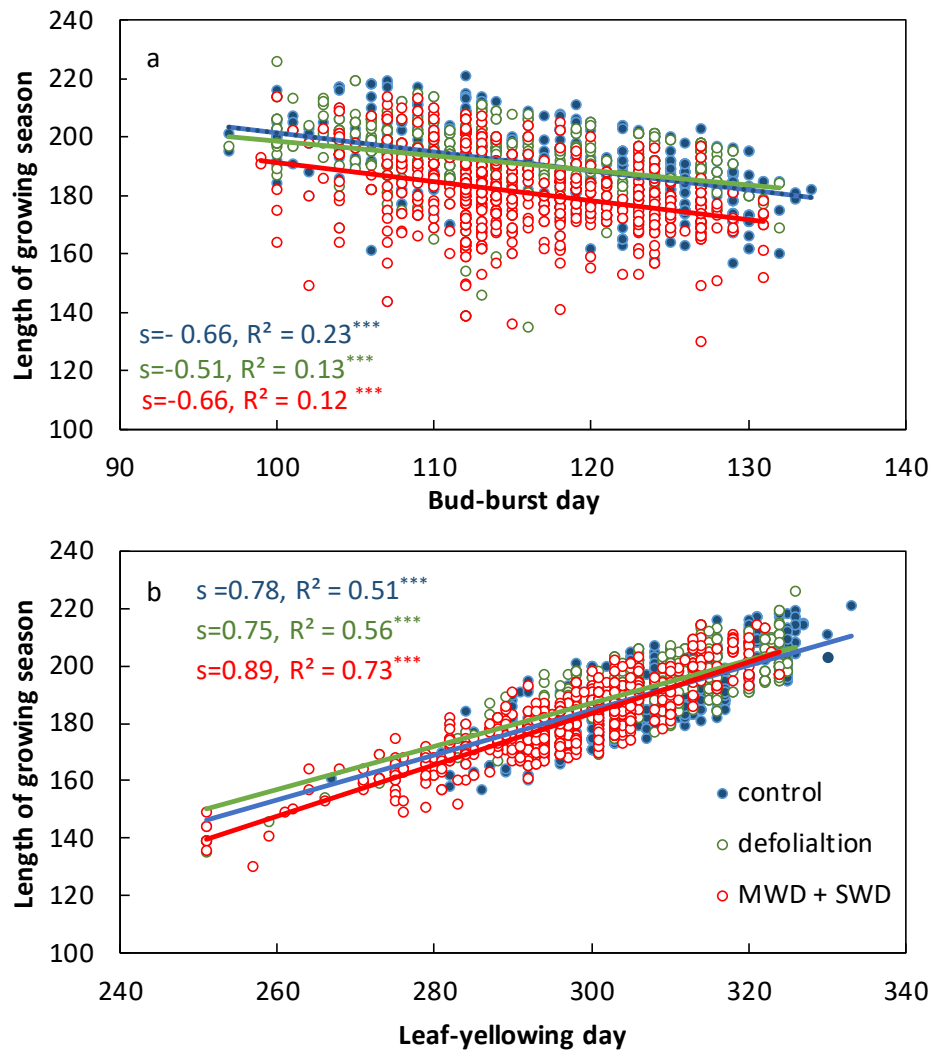
Figure 5. Correlations between the length of the growing season (in days) and (a) bud-burst day and (b) leaf-yellowing day over the three years of the experiment in the combined moderate (MWD) and severe (SWD) soil water deficit, defoliation and control treatments. Each point is a single tree belonging 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 $\pm$ 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-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=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$\pm$0.1 ^{b}	2.28$\pm$0.12 ^{a}	1.86$\pm$0.1 ^{b}	2.08$\pm$0.11 ^{ab}	**<0.001**
Oct-15	1.45$\pm$0.07	1.62$\pm$0.48	1.50$\pm$0.13	1.22$\pm$0.7	0.82
June-16	2.24$\pm$0.05 ^{a}	2.18$\pm$0.05 ^{a}	1.99$\pm$0.04 ^{b}	1.99$\pm$0.03 ^{b}	**<0.001**
Oct-16	1.63$\pm$0.24	1.5$\pm$0.08	-	1.56$\pm$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 (R²) 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, R² 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

494   populations senesced later than did the southern ones (Fig. 6b). A delay of 7 to 12 days

495   according to year was observed between the earliest and the latest populations (Table 3).
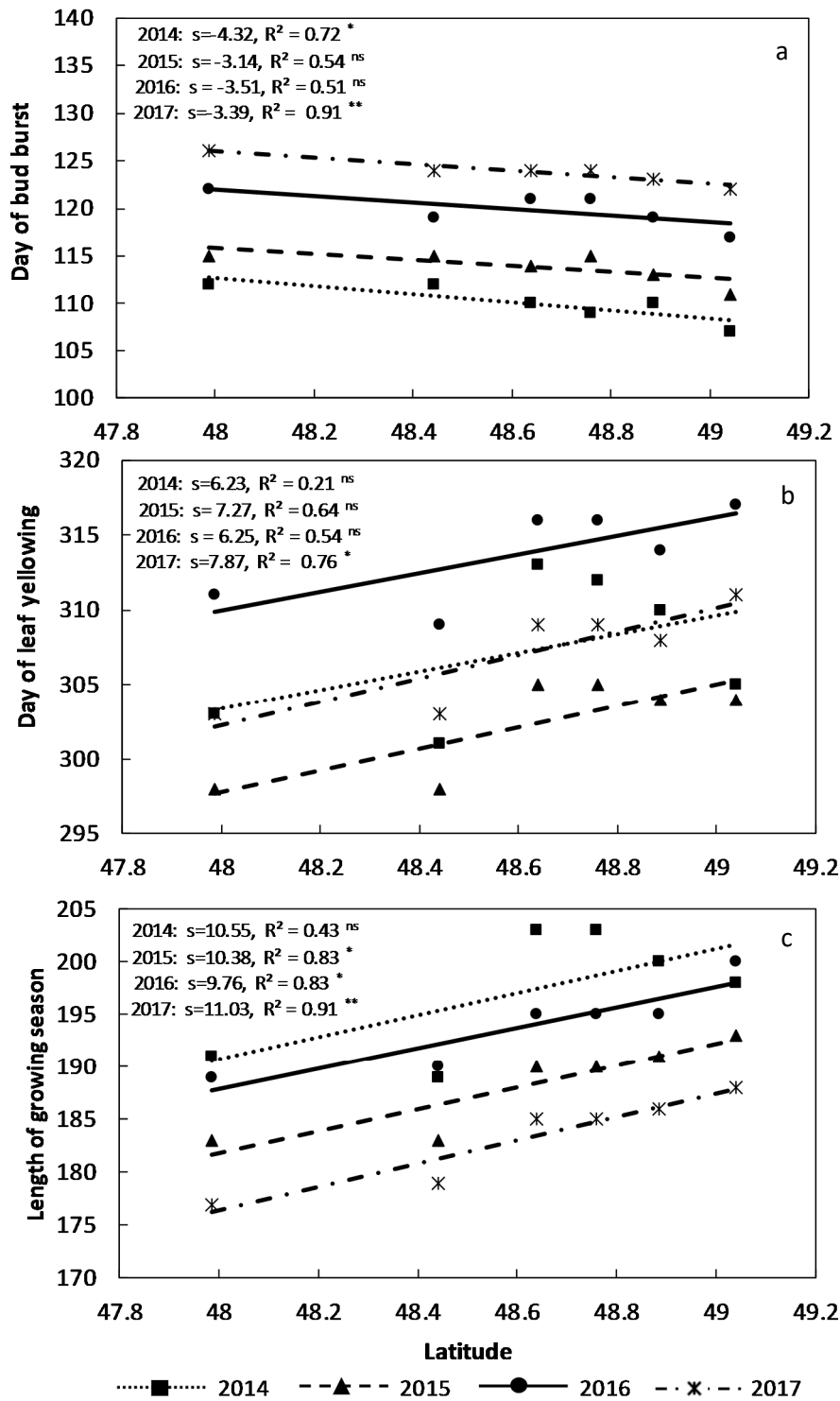

Figure 6. Relationships between the latitude of origin of the trees grown in the common garden experiment under well-watered conditions (controls) and (a) bud-burst day, (b) leaf-

22

513   yellowing day and (c) growing season length in 2014 (squares and dotted line), 2015
514   (triangles and dashed line), 2016 (circles and solid line) and 2017 (crosses and dashed-dotted
515   line). For each year, the slopes (s), the correlation coefficients (R^2) and their significance (ns
516   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 a	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*			

523   The differences in both BB and LY days among populations acted in the same direction on

524   growing season length, which showed as many as 14 days of difference between the northern

525   and southern populations; the northern populations displayed longer GS than the southern

526   populations (Fig. 6c). GS length presented higher correlation coefficients with latitude than did

527   BB and LY days in 2015 and 2016.

528   *3.4. Bud-burst and leaf-yellowing responses to soil water deficit and defoliation among*
529   *populations*

530   For BB, in 2014 and 2016, the population ranking was stable whatever the treatment, as shown

531   by the Spearman rank correlation results and the non-significance of the treatment - population

532   interaction (Table 3). But in 2015, the SWD treatment presented a different population ranking,

533   leading to a significant treatment - population interaction. LY often presented a lower Spearman

534   correlation coefficient than did BB, with a less clear ranking of the phenological dates according

535   to population latitude, but the ranking of the extreme populations in the latitudinal gradient was

536   well maintained. The treatments significantly impacted LY and differently according to the

537   populations as revealed by the significant treatment - population interaction for the three years.

538   For GS, in 2015 and 2016, the ranking of populations was stable whatever the treatment (high

539   spearman correlation coefficients). In 2014 and 2015 a significant treatment-population

540   interaction was observed.

541   **4. Discussion**

542   4.1 Annual variability of leaf phenology in beech trees

543   Over the three years of our experiment, for the beech trees in the control treatment, the maximal

544   inter-annual variability in bud-burst date was 14 days. LY seems to play an important role on the

545   GS length in beech trees since GS was more strongly dependent on LY than on BB. This was

546   also observed by Vitasse *et al.* (2009a) on beech populations along an altitudinal gradient.

547   Consequently, LY date variability could significantly impact the annual carbon balance in beech

548 trees. Dragoni *et al.* (2011) showed that variations in leaf senescence date would have more

549 impact on the C balance than the variations in BB date in a broadleaf forest. However, under our

550 latitude with low sun elevation and short photoperiod in October, cumulated daily irradiance is

551 smaller in autumn than in spring. These properties could limit the impact of the LY variations on

552 the seasonal C balance. Indeed, at the beginning of our experiment, when the trees were seven

553 years old, the phenological differences among populations did not seem to have a significant

554 influence in tree height or diameter growth which were similar among populations

555 (Supplemental Information Fig. S2).

556

557   *4.2. Responses of beech leaf phenology to soil water deficit and defoliation*

558 In a context of climate change, beech has been described as a species whose leaf phenology (or

559 at least BB) would be little affected by global warming (Fu *et al.*, 2019a) because: i) BB would

560 occur only when a defined photoperiod, which is a fixed parameter, is reached, and ii) the

561 absence of a sufficient chilling temperature would be compensated for an increase in a forcing

562 temperature, as observed during warm years in the past (Cannell, 1997; Dantec *et al.*, 2014).

563 However it is obvious from our study that leaf phenology is also modified by a long soil water

564 deficit. We observed that a soil water deficit caused delayed bud-burst, and overall, early leaf-

565 yellowing, thus significantly reducing the length of the growing season. These results are valid

566 for our young beech trees but could be attenuated in mature trees due to a potential deeper root

567 system. As a reference, under natural condition the duration of one of the most extreme water

568 deficit during the last-10-years in beech stand in 2003 lasted 124 days (Granier *et al.*, 2008),

569 from DOY 178 to DOY 300 with minimum REW close to zero (Peiffer *et al.*, 2014). Similar

570 extreme soil water deficits were computed in European forests in 2003 (Granier *et al.*, 2007) and

571 in 2018 (Schuldt et al, 2020). Depending on the intensity of the water deficit and on year, GS

572 was shortened by up to 15 days, which is within the same range of variation as the inter-annual

26

573 variability of GS length observed in the control treatment. Surprisingly, MWD treatment

574 presented earlier LY than SWD treatment. This is a possible response to variation of

575 microclimate under the roof, the trees of the MWD being situated at the edge of the roof.

576 Reducing GS in response to soil water deficit may help the tree save water by shortening the

577 transpiration period, thus avoiding extreme dehydration and reducing the risk of hydraulic

578 dysfunction as was suggested in the study on the impact of rainfall exclusion on a Mediterranean

579 forest (Misson et al, 2011). An early leaf fall affecting green leaves in summer, without any

580 yellowing process, has sometimes been reported in case of extreme drought (Bréda *et al.*, 2006;

581 Marchin *et al.*, 2010), probably as a result of petiole embolism. But this was not the case in our

582 study since the duration of the leaf yellowing process was similar for drought-stressed and

583 control trees. Reducing GS may also allow the tree to save carbon and nitrogen. Indeed,

584 prolonged soil water deficit induces a long-term source-sink imbalance because some carbon

585 sinks are maintained active such as maintenance respiration whereas carbohydrates production is

586 reduced due to stomatal closure (Farquhar and Sharkey, 1982; Calister and Adams, 2006; Flexas

587 *et al.*, 2006). Both carbon and nitrogen metabolisms are enhanced in response to soil water

588 deficit to help save internal water and ensure cell survival (Chuste *et al.*, 2019, 2020). Although

589 some carbon sinks, such as primary and secondary growths, are sacrificed under soil water

590 deficit (Chuste et al, 2020), other important *C* sinks remain active (*e.g.* transport, maintenance

591 respiration) or may even be up-regulated (*e.g.* defense, starch interconversion to soluble sugars

592 for osmoregulation and protection against cell dehydration) (Chuste, 2018). Beech trees have to

593 compensate for this carbon imbalance. They may remobilize their carbon reserves to ensure

594 survival (Chuste *et al.*, 2020). In response to soil water deficit, early leaf senescence may save

595 carbon by reducing the carbon used in the maintenance respiration of living organs and to avoid

596 tissue dehydration (Hinckley *et al.*, 1979; Xie *et al.*, 2018). As carbon and nitrogen metabolisms

597 are closely linked, early leaf yellowing may also save nitrogen and would allow an early

598   resorption of leaf nitrogen before leaf death and dehydration in case of extreme soil water deficit

599   (Marchin *et al.*, 2010; Chuste, 2018). These regulations could participate in the survival strategy

600   of the beech trees in response to soil water deficit. However, even if shortening GS is an adaptive

601   response of trees to drought, it is not the best mean for saving water and carbon; other adaptive

602   mechanisms such as stomatal closure or leaf area reduction are much more efficient.

603   In our study, neither BB nor LY changed in response to defoliation. By defoliating trees, we

604   limited i) the tree's capacity to assimilate carbon by strongly reducing photosynthetic leaf area

605   (75% of defoliation in 2014 and 2015 and 90% in 2016) and ii) the nitrogen available to the trees

606   since 30% of the N total stock is contained in the beech leaves in spring (El Zein *et al.*, 2011b),

607   at the period when defoliation was carried out. This reduction of the nitrogen and carbon

608   availability did not affect the leaf phenology of our beech trees. However, another consequence

609   of defoliation is to limit the tree consumption of carbon (by reducing maintenance respiration), in

610   the absence of re-foliation (as was our case in 2014 and 2015, but not in 2016). In addition,

611   higher leaf N concentrations was measured in the foliage remaining on our defoliated trees in

612   2015 as also observed by Pinkard *et al.* (2011) in *Eucalyptus globulus*. This leaf nitrogen

613   increase did not significantly affect leaf phenology contrarily to the results suggested by the

614   study of Fu *et al.* (2019c). As a large fraction of leaf N is invested in Rubisco (Evans, 1989), this

615   leaf N increase could increase the C assimilation in the remaining leaves of the defoliated trees, a

616   response to defoliation often reported in the literature (Hart *et al.*. 2000; Handa *et al*, 2005).

617   Moreover defoliating part of crown undoubtedly allowed remaining, previously shaded leaves to

618   receive more light which may have stimulated carbon assimilation in these leaves. Consequently,

619   the defoliation treatment may have only slightly affected carbon assimilation at the tree scale.

620   Therefore, the absence of a phenological response to defoliation could also be because

621   defoliation affected the carbon and nitrogen balances of the trees less than expected.

622

623

4.3. Plasticity of leaf phenology among regional beech forests

624

625 We examined the question of the phenological differentiation among six populations issued from

626 a small latitudinal gradient presenting a small climatic range in the central distribution area of

627 *Fagus sylvatica* L. From one year to the next, we often observed a similar population ranking for

628 both BB and LY in the control treatment: Delpierre *et al.* (2017) observed that leaf phenology

629 ranking was stable from year to year among trees of temperate forest, including *Fagus sylvatica,*

630 over a large distribution area. The relationship between BB and LY and the latitudinal origin of

631 the populations that we observed, suggests a genetic differentiation at the regional scale that

632 could be adaptive or not. We checked the literature for the factors controlling the expansion of

633 beech in Europe during the post-glaciation period. We found three main drivers: i) climatic

634 conditions, ii) human activities and iii) the natural, slow migration of beech forests due to

635 dispersal limitation (Willner *et al.*, 2009; Magri, 2008). In our study, we observed few significant

636 correlations between the latitudinal gradient and the mean climatic trends along our gradient

637 suggesting that the genetic differentiation could result from factors other than climate

638 (Supplementary Information Fig S3). However, this absence of climatic links could also be due

639 to the limited number of populations within a small climatic gradient. Moreover, the

640 meteorological model we used to estimate the climatic variables at each site, may not have been

641 enough precise at the regional scale. Finally, we used mean climatic values over 30 years (1981

642 – 2010) to investigate the climatic gradients and it is possible that a population's adaptation to a

643 local climate is driven more by its ability to survive extreme climatic events than by a mean

644 climatic trend. For instance, one of our populations has been particularly sensitive in term of tree

645 mortality in response to SWD treatment in the common garden experiment (data not shown).

646 We revealed that in our regional gradient, the northern populations presented a longer GS than

647 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),

673 but more recent studies suggest a stronger sensitivity to recent drought episodes for trees

674 growing in the wetter mid-latitudes (Friedrichs *et al.*, 2009; Scharnweber *et al.*, 2011). In fact,

675 populations in the central area of distribution, where extreme events are rare, could be more

676 sensitive to soil water deficit than those growing at the south edge of the range, which frequently

677 experience extreme climatic events. Populations in the edge area would retain only the most

678 resistant and best adapted individuals in their populations (Cavin and Jump, 2017).

679 **5. Conclusion**

680 Our study suggests that beech trees present a local variation of leaf phenology, even within a

681 small latitudinal gradient, and that different populations have different phenological response to

682 soil water deficit. The impact of drought on both bud-burst and leaf yellowing dates leads to a

683 shorter growing season and suggests that soil water content should be taken into account more

684 often in studies of inter-annual phenological variability, particularly in the context of future

685 climate change where spring and summer drought events are likely to become more frequent.

686 Accounting for soil water content could help researchers to better estimate the length of the

687 growing season in carbon balance models for sensitive deciduous species like *Fagus sylvatica*

688 under future climatic conditions.

689

690 **Data accessibility**

691 The data are available from the authors upon request.

692

693 **Declaration of Competing Interest**

694 None.

695

696 **Acknowledgements**

710 **Appendix A. Supplementary information**

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

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

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

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

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

722

723 **References**

724 Adams, H.D., Collins, A.D., Briggs, S.P., Vennetier, M., Dickman, L.T., Sevanto, S.A., Garcia-Forner,
725 N., Powers, H.H., McDowell, N., 2015. Experimental drought and heat can delay phenological
726 development and reduce foliar and shoot growth in semiarid trees. Glob. Chang. Biol. 21, 4210–4220.
727 doi: 10.1111/gcb.13030
728

729 Barbaroux, C., Bréda, N., 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves
730 in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. Tree Physiol. 22, 1201-
731 1210.

733 Basler, D., Körner, C., 2014. Photoperiod and temperature responses of bud swelling and bud burst in
734 four temperate forest tree species. Tree Physiol. 34, 377–388. doi:10.1093/treephys/tpu021

736 Bazot, S., Fresneau, C., Damesin, C., Barthes, L., 2016. Contribution of previous year's leaf N and soil N
737 uptake to current year's leaf growth in sessile oak. Biogeosciences 13, 3475–3484.

739 Bénichou, P., Le Breton, O., 1987. AURELHY : une méthode d'analyse utilisant le relief pour les besoins
740 de l'hydrométéorologie. In : Deuxièmes journées hydrologiques de l'ORSTOM à Montpellier. Paris :
741 ORSTOM, 299-304. (Colloques et Séminaires). Journées Hydrologiques de l'ORSTOM à Montpellier, 2.,
742 Montpellier (FRA), 1986/09/16-17. ISBN 2-7099-0865-4

744 Bréda, N., Granier, A., Barataud, F., Moyne, C., 1995. Soil water dynamics in an oak stand. Plant Soil.
745 172, 17-27.

747 Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought:
748 a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci.
749 63, 625-644.

751 Canellas, C., Gibelin, A.L., Lassegues, P., Kerdoncuff, M., Dandin, P., Simon, P., 2014. Les normales
752 climatiques spatialisées Aurelhy1981-2010: température et précipitation. La Météorologie. 85, p47-55.

754 Cannell, M.G.R., 1997. Spring phenology of trees and frost avoidance. Weather. 52, 46-52.

756 Cavin, L., Jump, A., 2017. Highest drought sensitivity and lowest resistance to growth suppression are
757 found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. Glob. Chang. Biol.
758 23, 362-379.

760 Chmura, D.J., Rozkowski, R., 2002. Variability of beech provenances in spring and autumn phenology.
761 Silvae Genet. 51, 2-3.

763 Chuine, I., Cour, P., 1999. Climatic determinants of budburst seasonality in four temperate-zone tree
764 species. New Phytol. 143, 339-349.

766 Chuine, I., Yiou, P., Viovy, N., Seguin, B., Daux, V., Le Roy Ladurie, E., 2004. Grape ripening as a past
767 climate indicator. Nature. 432, 289-290.

769 Chuste, P.A., 2018. Etude de la sensibilité du hêtre lorrain à un événement climatique extrême. Quels sont
770 les rôles des métabolismes carboné et azoté dans la mort des arbres ? These– Université de Lorraine,
771 Nancy, France. 238pp.

773 Chuste, P.A., Massonnet, C., Gérant, D., Zeller, B., Levillain, J., Hossann, C., Angeli, N., Wortemann, R.,
774 Bréda, N., Maillard, P., 2019. Short-term nitrogen dynamics are impacted by defoliation and drought in
775 *Fagus sylvatica* L. branches. Tree Physiol. 39, 792-804.

777 Chuste, P.A., Maillard, P., Bréda, N., Levillain, J., Thirion, E., Wortemann, R., Massonnet, C., 2020.
778 Sacrificing growth and maintaining a dynamic carbohydrate storage are key processes for promoting
779 beech survival under prolonged drought conditions. Trees. 34, 381–394.

781 Cooke, M., Erikson, E., Juntitila, O., 2012. The dynamic nature of bud dormancy in trees: environmental
782 control and molecular mechanisms. Plant Cell Environ. 35, 1707–1728. doi: 10.1111/j.1365-
783 3040.2012.02552.x

784
785 Cowan, I., 1982. Regulation of water use in relation to carbon gain in higher plants. In: Lange OE, Nobel
786 PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology. Springer, Berlin, pp 489–613
787
788 Dannoura, M., Epron, D., Desalme, D., Massonnet, C., Tsuji, S., Plain, C., Priault, P., Gérant, D., 2019.
789 The impact of prolonged drought on phloem anatomy and phloem transport in young beech trees. Tree
790 Pysiol. 39, 201-210.

791
792 Dantec, C.F., Vitasse, Y., Bonhomme, M, Louvet, J.M., Kremer, A., Delzon, S., 2014. Chilling and heat
793 requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of
794 their distribution range. Int. J. Biometeorol. 58(9), 1853-1864. DOI :10.1007/s00484-014-0787-7
795
796 Delpierre, N., Dufrêne, E., Soudani, K., Ulrich, E., Cecchini, S., Boé, J., François, C., 2009. Modelling
797 interannual and spatial variability of leaf senescence for three deciduous tree species in France. Agric.
798 For. Meteorol. 149, 938-948.
799
800 Delpierre, N., Guillemot, J., Dufrêne, E., Cecchini, S., Nicolas, M., 2017. Tree phenological ranks repeat
801 from year to year and correlate with growth in temperate deciduous forests. Agric. For. Meteorol. 234, 1-
802 10.
803
804 Dragoni, D., Schmid, H.P., Wayson, C.A., Potter, H., Grimmond, C.S.B., Randolph, J.C., 2011. Evidence
805 of increased net ecosystem productivity associated with a longer vegetated season in a deciduous forest in
806 south-central Indiana, USA. Glob. Chang. Biol. 17, 886–897
807
El Zein, R., Bréda, N., Gérant, D., Zeller, B., Maillard, P., 2011a. Nitrogen sources for current-year shoot
growth in 50-year-old sessile oak trees: An in situ 15N labeling approach. Tree Physiol. 31, 1390–1400.

El Zein, R., Maillard, P., Bréda, N., Marchand, J., Montpied, P., Gérant, D., 2011b. Seasonal changes of
C and N non-structural compounds in the stem sapwood of adult sessile oak and beech trees. Tree
Physiol. 31, 843-854.

808 Escudero, A. Del Arco, J.M., 1987 Ecological Significance of the Phenology of Leaf Abscission. Oikos.
809 49, 11-14.

E Silva, D., 2010. Ecologie du hêtre (*Fagus sylvatica L.*) en marge sud-ouest de son aire de distribution.
Thèse, Université de Lorraine, Nancy, France.

810 Estiarte, M., Peñuelas, J., 2015. Alteration of the phenology of leaf senescence and fall in winter
811 deciduous species by climate change: effects on nutrient proficiency. Glob. Chang. Biol. 21, 1005–1017.
812 doi: 10.1111/gcb.12804
813
814 Estrella, N., Menzel, A., 2006. Responses of leaf colouring in four deciduous tree species to climate and
815 weather in Germany. Clim. Res. 32, 253-267.
816
817 Evans JR 1989: Photosynthesis and nitrogen relationships in leaves of C3 plants. Oecologia, 78, 9-19 .
818
819 Farquhar, G.D., Sharkey, T.D., 1982. Stomatal conductance and photosynthesis. Annu. Rev.Plant Physiol.
820 33, 317–345.
821
822 Flexas, J., Bota, J., Galmes, J., Medrano, H., Ribas-Carbo, M., 2006. Keeping a positive carbon balance
823 under adverse conditions: responses of photosynthesis and respiration to water stress. Physiol Plant. 127,
824 343–352.
825
826 Friedrichs D.A., Trouet, V., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009. Species-
827 specific climate sensitivity of tree growth in Central-West Germany. Trees. 23, 729-739.

828
829 Fu, Y.S.H., Piao, S., Zhao, H., Jeong, S.J., Wang, X, Vitasse, Y., Ciais, P. and Janssens, I.A., 2014.
830 Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at
831 northern middle and high latitudes. Glob. Chang. Biol. 20, 3743-3755.
832
833 Fu, Y.S.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A.,
834 Penuelas, J., Song, Y., Vitasse, Y., Zeng, Z. and Janssens, I.A. 2015. Declining global warming effects on
835 the phenology of spring leaf unfolding. Nature. 526, 104-107.
836
837 Fu, Y.H., Piao, S., Zhou, X., Geng, X., Hao, F., Vitasse, Y., Janssens, I.A., 2019a. Short photoperiod
838 reduces the temperature sensitivity of leaf-out in saplings of *Fagus sylvatica* but not in horse chestnut.
839 Glob. Chang. Biol. 25, 1696–1703. doi:10.1111/gcb.14599.
840
841 Fu, Y.H., Zhang, X, Piao, X, Hao, X., Geng, X., Vitasse, Y., Zohner, C., Peñuelas, J., Janssens, I.A.
842 2019b. Daylength helps temperate deciduous trees to leaf-out at the optimal time. Glob. Chang. Biol. 25,
843 2410-2418. doi: 10.1111/gcb.14633
844
845 Fu, Y.H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Geng, X., Peñuelas, J., Zhang, X., Janssens, I.A.,
846 Campioli, M., 2019c Nutrient availability alters the correlation between spring leaf-out and autumn leaf
847 senescence dates. Tree Physiol. 39, 1277-1284.
848
849 Gill, A.L., Gallinat, A.S., Sanders-DeMott, R., Rigden, A.J., Short Gianotti, D.J., Mantooth, J.A.,
850 Templer, P.H., 2015. Changes in autumn senescence in northern hemisphere deciduous trees: a meta-
851 analysis of autumn phenology studies. Ann. Bot. 116, 875–888. doi:10.1093/aob/mcv055
852
853 Gilson, A, Barthes, L, Delpierre, N, Dufrêne E., Fresneau, C., Bazot S., 2014. Seasonal changes in
854 carbon and nitrogen compound concentrations in a *Quercus petraea* chronosequence. Tree Physiol. 34,
855 716–729.
856
857 Granier, A., Bréda, N., Biron, P., Villette, S., 1999. A lumped water balance model to evaluate duration
858 and intensity of drought constraints in forest stands. Ecol. Model. 116, 269–283.
859
860 Granier, A., Reichstein, M., Bréda, N., Janssens, I.A., Falge, E., et al., 2007. Evidence for soil water
861 control on carbon and water dynamics in European forests during the extremely dry year: 2003.Agric.
862 For.Meteorl. 143, 123-145.
863
864 Granier, A., Bréda, N., Longdoz, B., Gross, P., Ngao, J., 2008. Ten years of fluxes and stand growth in a
865 young beech forest at Hesse, North-eastern France. Annals of Forest Science 65:704.
866 doi:10.1051/forest:2008052
867
868 Hamilton, J.A., El Kayal, W., Hart , A.T., Runcie, D.E., Arango-Velez, A., Cooke, J.E.K., 2016. The
869 joint influence of photoperiod and temperature during growth cessation and development of dormancy in
870 white spruce (*Picea glauca*). Tree Physiol. 36, 1432–1448. doi:10.1093/treephys/tpw061
871
872 Handa, I.T., Korner, C. Hattenschwiler, S., 2005. A test of the treeline carbon limitation hypothesis by in
873 situ CO2 enrichment and defoliation. Ecology, 86, 1288–1300.
874
875 Hart, M., Hogg, E.H., Lieffers, V.J., 2000. Enhanced water relations of residual foliage following
876 defoliation in *Populus tremuloides*. Can. J. Bot. 78:583–590.
877
878 Harter, D.E.V., Nagy, L., Backhaus, S., Beierkuhnlein, C., Fussi, B., Huber , G., Jentsch, A., Konnert, M.,
879 Thiel, D., Kreyling, J., 2015. A comparison of genetic diversity and phenotypic plasticity among
880 European beech (*Fagus sylvatica* L) populations from Bulgaria and Germany under drought and
881 temperature manipulation. Int. J. Plant Sci. 176(3), 232–244. doi:10.1086/679349
882

883 Heide, O.M., 1993. Dormancy release in beech buds *(Fagus sylvatica)* requires both chilling and long
884 days. Physiol. Plant. 89, 187-191.
885
886 Heide, O.M., 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing
887 the effect of climatic warming. Tree Physiol. 23, 931–936.
888
889 Hinckley, T.M., Dougherty, P.M., Lassoie, J.P., Roberts, J.E., Teskey, R.O., 1979. A severe drought:
890 impact on tree growth, phenology, net photosynthetic rate and water relations. Am. Midl. Nat. 102, 307–
891 316.
892
893 Hoch, G., Richter, A., Körner, C., 2003. Non-structural carbon compounds in temperate forest trees. Plant
894 Cell Envion., 26, 1067-1081.
895
896 Hunter, A. F., Lechowicz, M.J., 1992. Predicting the timing of bud-burst in temperate trees. J. Appl. Ecol.
897 29, 597-604.
898
899 IPCC, 2014. AR5 Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and
900 Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the
901 Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D.
902 Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N.
903 Levy, S. MacCracken, P.R. Mastrandrea, and L.L.White (eds.)]. Cambridge University Press, Cambridge,
904 United Kingdom and New York, NY, USA, 1132 pp.

905 Jump, A., Hunt, J., Peñuelas, J. *et al.*, 2006. Rapid climate change-related growth decline at the southern
906 range edge of *Fagus sylvatica*. Glob. Chang. Biol. 12, 2163–2174.
907
908 Keenan, T.F., Richardson, A.D., 2015. The timing of autumn senescence is affected by the timing of
909 spring phenology: implications for predictive models. Glob. Chang. Biol. 21, 2634-2641.
910
911 Körner, C., Basler, D., 2010. Phenology under global warming. Science. 327, 1461-1462. doi:
912 10.1126/science.1186473

913 Kramer, K., 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to
914 climatic warming. Plant Cell Environ. 18, 93-104. doi:10.1111/j.1365-3040.1995.tb00356.x
915
916 Kramer, K., Ducousso, A., Gömöry, D., Hansen, J.K., Ionita, L., Liesebach, M., Lorent¸ A., Schüler, S.,
917 Sulkowska, M., de Vries, S., von Wühlisch, G., 2017. Chilling and forcing requirements for foliage bud
918 burst of European beech (*Fagus sylvatica* L.) differ between provenances and are phenotypically plastic.
919 Agric. For. Meteorol. 234-235, 172- 181.
920
921 Laube, J., Sparks, T.H., Estrella, N., Ofler, J.H., Ankerst, D.P., Menzel, A., 2014. Chilling outweighs
922 photoperiod in preventing precocious spring development. Glob. Chang. Biol.. 20, 170–182. doi:
923 10.1111/gcb.12360
924
925 Lang G. A., Early J. D., Martin G. C., Darnell R. L., 1987. Endo-, para-, and ecodormancy : physiological
926 terminology and classification for dormancy research. HortSci. 22, 371-377.
927
928 Liu, G., Chen, X., Fu,Y., Delpierre N., 2019 Modelling leaf coloration dates over temperate China by
929 considering effects of leafy season climate. Ecolog. Model. 394, 34-43.
930
931 Loehle, C., 1998. Height growth rate trade-offs determine northern and southern range limits for trees. J.
932 Biogeogr., 25, 735-742.
933

934   Magri, D., 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech
935   (Fagus sylvatica). J. Biogeogr 35, 450–463.

937   Manzoni, S., Vico, G., Thompson, S., Beyer, F., Weih, M., 2015. Contrasting leaf phenological strategies
938   optimize carbon gain under droughts of different duration. Adv. Water Resour. 84, 37-51.

940   Marchin, R., Zeng, H., Hoffmann, W., 2010. Drought-deciduous behavior reduces nutrient losses from
941   temperate deciduous trees under severe drought. Oecologia 163:845-854. doi:10.1007/s00442-010-1614-4

943   Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature. 397, 659.

944   Menzel A., 2000. Trends in phenological phases in Europe between 1951 and 1996. Int. J. Biometeorol.
945   44(2), 76-81. doi: 10.1007/s004840000054

947   Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissoli, P.,
948   Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly,
949   A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, O., Peñuelas, J., Pirinen, P., Remisova, V.,
950   Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Zust, A. , 2006.
951   European phenological response to climate change matches the warming pattern. Glob. Chang. Biol. 12,
952   1969–1976. doi: 10.1111/j.1365-2486.2006.01193.x

954   Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., Estrella, N., 2020. Climate
955   change fingerprints in recent European plant phenology. Glob. Chang. Biol. 26, 2599–2612.

957   Misson, L., Degueldre, D., Collin, C., Rodriguez, R., Rocheteau, A., Ourcival, J.M., Rambal, S., 2011.
958   Phenological responses to extreme droughts in aMediterranean forest. Glob. Chang. Biol. 17, 1036-1048.

960   Morin, X., Lechowicz, M.J., Augspurger, C., O'Keefe, J.O., Viner, D., Chuine, I., 2009. Leaf phenology
961   in 22 North American tree species during the 21st century. Glob. Chang. Biol. 15, 961–975. doi:
962   10.1111/j.1365-2486.2008.01735.x

964   Nielsen, C.N., Jorgensen, F.V., 2003. Phenology and diameter increment in seedlings of European beech
965   (*Fagus sylvatica* L.) as effected by different soil water contents: variation between and within
966   provenances. For. Ecol. Manage. 174, 233-249.

968   Ogaya, R., Peñuelas, J. 2004. Phenological responses to extreme droughts in a Mediterranean forest.
969   Ecosci. 11, 263-270.

971   Pallardy, S.G., *Loewenstein*, N.J. 2004. The role of xylem sap abscisic acid in leaf abscission of
972   droughted seedlings of isohydric and anisohydric temperate deciduous angiosperms. *Proceedings of the*
973   *14th Central Hardwood Forest Conference* 365-372.

975   Partanen, J., Koski, V., Hanninen, H., 1999. Effects of photoperiod and temperature on the timing of bud
976   burst in Norway spruce (*Picea abies*). Tree Physiol. 18, 811-816.

978   Peaucelle, M., Janssens, I.A., Stocker, B.D., Descals Ferrando, A., Fu, Y.H., Molowny-Horas, R., Ciais,
979   P., Peñuelas, J., 2019 Spatial variance of spring phenology in temperate deciduous forests is constrained
980   by background climatic conditions. Nature Comm. 10, 5388.

982   Peiffer, M., Bréda, N., Badeau, V., Granier, A., 2014. Disturbances in European beech water relation
983   during an extreme drought. Annals of Forest Science 71:821-829. doi:10.1007/s13595-014-0383-3

985   Peñuelas J., Filella, Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the
986   Mediterranean region. Glob. Chang. Biol. 8, 531-544.

Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradaset, J., 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. New Phytol. 161, 837–846. doi: 10.1111/j.1469-8137.2003.01003.x

Pinkard, E.A., A. Eyles, A., O'Grady, A.P., 2011. Are gas exchange responses to resource limitation and defoliation linked to source:sink relationships? Plant. Cell. Environ. 34, 1652–1665

Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. Glob. Chang. Biol. 14, 1-17.

Richardson, A.D., Schenck Bailey, A., Denny, E.G., Wayne Martin, C., O'Keefe, J., 2006. Phenology of a northern hardwood forest canopy. Glob. Chang. Biol. 12, 1174–1188. doi: 10.1111/j.1365-2486.2006.01164.x

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. B. 365, 3227-3246.

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.

Robson T. M., Rasztovits, E., Aphalo P.J., Alia, A., Aranda, I., 2013. Flushing phenology and fitness of European beech (*Fagus sylvatica* L.) provenances from a trial in La Rioja, Spain, segregate according to their climate of origin. Agric. For. Meteorol. 180, 76-85. DOI: 10.1016/j.agrformet.2013.05.008

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., Wilmking, M., 2011. Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. For. Ecol. Manage. 262, 947-961.

Schueler, S., Liesebach, M.,·2015. Latitudinal population transfer reduces temperature sum requirements for bud burst of European beech. Plant Ecol. 216(1), 111–122. DOI: 10.1007/s11258-014-0420-1

Schuldt B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgemuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic Appl. Ecol. 45, 86-103. DOI: 10.1016/j.baae.2020.04.003

Schuster, C., Estrella, N., Menzel, A., 2014. Shifting and extension of phenological periods with increasing temperature along elevational transects in southern Bavaria. Plant Biol. 16, 332–344. doi:10.1111/plb.12071

Sevanto, S., 2014. Phloem transport and drought. J. Exp. Bot. 65, 1751–1759.

Sparks, T.H., Jeffree, E. P., Jeefree, C.E., 2000. An examination of relationships between flowering times and temperature at the national scale using long-term phenological record from the UK. Int. J. Biometeorol. 44, 82-87.

Vico, G., Thompson, S.E., Manzoni, S., Molini, A., Albertson, J.D., Almeida-Cortez, J.S., Fay, P.A., Feng, X., Guswa, A.J., Liu, H., Wilson, T.G., Porporato, A., 2015. Climatic, ecophysiological, and

phenological controls on plant ecohydrological strategies in seasonally dry ecosystems. Ecohydrology. 8, 660–681.

Vitasse, Y., Porte, A., Kremer, A., Michalet, R., Delzon, S., 2009a. Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. Oecologia. 161(1), 187-198. DOI 10.1007/s00442-009-1363-4

Vitasse, Y., Delzon, S., Dufrêne E., Pontailler, J.Y., Louvet, J.M., Kremer, A., Michalet, R., 2009b. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? Agric. For. Meteor. 149, 735-744. doi:10.1016/j.agrformet.2008.10.019

Vitasse, Y., Basler, D., 2013. What role for photoperiod in the bud burst phenology of European beech. Eur. J. For. Res. 132, 1–8. DOI 10.1007/s10342-012-0661-2

Von Wuehlisch, G., Krusche, D., Muhs, H.J., 1995. Variation in temperature sum requirement for flushing of beech provenances. Silvae Genet. 44, 5-6.

Willner, W., Di Pietro, R., Bergmeier, E., 2009. Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. Ecography, 32, 1011-1018.

Xie Y., Wang X., Wilson A.M., Silander J.A . 2018. Predicting autumn phenology: How deciduous tree species respond to weather stressors. Agric. For. Meteorol. 250-251,127-137. doi:10.1016/j.agrformet.2017.12.259

Zapater, M., Bréda, N., Bonal, D., Pardonnet, S., Granier, A., 2013. Differential response to soil drought among co-occurring broad-leaved tree species growing in a 15-to 25-year-old mixed stand. Annals of Forest Science 70:31-39. doi:10.1007/s13595-012-0233-0

Zohner, C.M., Renner, S.S., 2014. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. Ecol. Lett. 17, 1016–1025.