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1 **“Green pointillism”: detecting the within-population variability of**
2 **budburst in temperate deciduous trees with phenological cameras**

3

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13

14 **Running headline:** phenological variability in tree populations

15

16 **Abstract**

17

- 18 • Phenological cameras have been used over a decade for identifying plant phenological
19 markers (budburst, leaf senescence) and more generally the greenness dynamics of
20 forest canopies. The analysis is usually carried out over the full camera field of view,
21 with no particular analysis of the variability of phenological markers among trees.
- 22 • Here we show that images produced by phenological cameras can be used to quantify
23 the within-population variability of budburst (WPVbb) in temperate deciduous forests.
24 Using 7 site-years of image analyses, we report a strong correlation ($r^2=0.97$) between
25 the WPVbb determined with a phenological camera and its quantification through
26 ground observation.
- 27 • We show that WPVbb varies strongly (by a factor of 4) from year to year in a given
28 population, and that those variations are linked with temperature conditions during the
29 budburst period, with colder springs associated to a higher differentiation of budburst
30 (higher WPVbb) among trees.
- 31 • Deploying our approach at the continental scale, i.e. throughout phenological cameras
32 networks, would improve the understanding of the spatial (across populations) and
33 temporal (across years) variations of WPVbb, which have strong implications on
34 forest functioning, tree fitness and phenological modelling.

35

36 **Keywords:** image analysis, phenology, temperate forests, leaf-out, within-population
37 variability

38

39 **Introduction**

40

41 In the temperate and boreal climate zones, the flushing-out of leaves from dormant buds in
42 spring (*alias* ‘budburst’) is a key step in the seasonal cycle of trees’ activity. It marks the start
43 of the carbon acquisition and water loss (photosynthetic) period and is in close relation with
44 the tree’s other organs or tissues seasonal growth and resource acquisition (reviewed in
45 Delpierre *et al.*, 2016b). To this respect, budburst is hypothesized to influence tree growth (to
46 what extent is not clear, see e.g. Čufar *et al.*, 2015; Bontemps *et al.*, 2017; Delpierre *et al.*,
47 2017). In some temperate angiosperms (e.g. deciduous oaks), the timing of flowering, which
48 is closely related to the flushing-out of leaf buds (Franjic *et al.*, 2011), influences the
49 production of fruits (Lebourgeois *et al.*, 2018; Schermer *et al.*, 2019). This makes budburst an
50 essential trait for the tree functioning, a trait subject to natural selection (Ducouso *et al.*,
51 1996; Savolainen *et al.*, 2007). Yet, budburst is a very variable trait in forest tree populations.
52 The duration of the budburst period (from the first to the last tree leafing-out in a given year)
53 in temperate forest tree populations is about three weeks (19 days, averaged over 67
54 populations of *Quercus petraea* (Matt.) Liebl., *Quercus robur* L. and *Fagus sylvatica* L. in
55 Europe; Delpierre *et al.*, 2017). This is about 30% of the amplitude of the continental gradient
56 of budburst observed for those species (Delpierre *et al.*, 2017). The high within-population
57 variability of budburst (WPVbb) in natural tree populations is probably related to biotic
58 (herbivores and pathogens) and abiotic (frost) fluctuating selection pressures that contribute to
59 maintaining high genetic variation on this trait (Crawley & Akhteruzzaman, 1988; Alberto *et*
60 *al.*, 2011; Dantec *et al.*, 2015).

61 Interestingly, WPVbb varies across tree populations (Salmela *et al.*, 2013), and across years
62 for a given population (Denéchère *et al.*, 2019). The within-population standard deviation of
63 budburst averaged 4.0 days, but ranged from 1.7 to 9.7 days in 14 populations of nine
64 temperate deciduous tree species (Denéchère *et al.*, 2019). This variability was related to
65 temperature conditions during the budburst period, with colder conditions associated to an
66 increased WPVbb (Denéchère *et al.*, 2019). Whatever their causes, the year-to-year variations
67 of WPVbb have potentially strong ecological implications, influencing the competition of
68 trees for resource (light, water and nutrient) acquisition and transfer throughout the food web
69 (van Dongen *et al.*, 1997; Thackeray *et al.*, 2016). Unfortunately, WPVbb has seldom been
70 documented to date in natural tree populations (but see Denéchère *et al.*, 2019), probably
71 because its quantification remains laborious based on ground phenological observations,
72 which are still needed for observing individual trees (Chesnoiu *et al.*, 2009; Cole & Sheldon,

73 2017; Delpierre *et al.*, 2017). Indeed, quantifying WPVbb requires observing bud
74 development on a relatively high number of trees per population (*ca.* 30, see Denéchére *et al.*,
75 2019), which is rarely attained in most phenological studies. Beside this sampling
76 requirement, it is also more demanding in terms of the number of observations campaigns
77 during spring, since one has to “wait” for all trees to burst buds, whereas classical
78 phenological studies typically record the date at which 50% trees of the surveyed population
79 have reached budburst.

80 Phenological cameras (hereafter phenocams) have been used for over a decade to monitor the
81 phenology of forest canopies (Richardson *et al.*, 2007; Ahrends *et al.*, 2008; Richardson,
82 2019). They are a very appealing, automated alternative to ground phenological observations.
83 Basically, phenocams periodically (e.g. every hour) take a RGB picture of the canopy. The
84 pictures are post-processed (Filippa *et al.*, 2016) to extract colour indices quantifying
85 continuously the “colour-state” of the canopy, from which particular phenological metrics
86 (e.g. budburst or leaf senescence) can be inferred. The comparison of budburst dates obtained
87 from ground observations and from phenocams are usually good (e.g. Keenan *et al.*, 2014;
88 Xie *et al.*, 2018). To date, the potential of phenocams has mostly been assessed at the canopy
89 scale, corresponding to the camera field of view (Keenan *et al.*, 2014; Klosterman *et al.*,
90 2014). Some studies have also considered the scale of individual trees (Ahrends *et al.*, 2008;
91 Berra *et al.*, 2016; Kosmala *et al.*, 2016; Xie *et al.*, 2018), but those studies pointed to tree
92 inter-specific differences, not pointing particularly to the within-population (i.e. intra-specific)
93 variability of phenology and the characterization of its inter-annual variability. Here, we
94 explore the potential of phenocams to investigate WPVbb, targeting two research questions:
95 (1) can phenological cameras be used to quantify the year-to-year variations of WPVbb in
96 deciduous forest tree populations?, (2) do WPVbb determined from phenocams show a
97 similar temperature response to the one established previously from ground observations?

98

99 **Material and methods**

100

101 *Study sites and phenological ground observations*

102

103 We monitored the development of buds in two sessile oak (*Quercus petraea* (Matt.) Liebl.)
104 populations located in the state-owned forests of Barbeau and Orsay, 50 km from each other
105 in the South of the Paris area, France (Table 1). In both populations, we monitored budburst
106 for more than 15 years following an ‘extensive’ sampling. According to this sampling, we

107 monitored bud development over a large number (>100) of individual dominant oaks, from
 108 early signs of budburst (typically in mid-March) until 50% of them have reached budburst
 109 (yielding the median date of budburst at the population scale). We considered that a tree had
 110 reached budburst when 50% of its crown showed open buds. A bud was considered open
 111 when the limb of one out of the *ca.* 12 leaves preformed in the bud (Fontaine *et al.*, 1999) was
 112 unfolding as visible from the ground (all observations were made with high-magnification
 113 binoculars, minimum x8). In this ‘extensive’ sampling, we did not follow the spread of
 114 budburst in crowns of particular trees. Instead, we picked randomly >100 dominant oaks in
 115 the forest for each observation campaign. Besides the ‘extensive sampling’, we applied for
 116 some years an ‘intensive’ sampling over our two populations, focusing on 27 to 66 tagged,
 117 dominant oaks (depending on the site and observation year, Table 1) for which we followed
 118 the spread of budburst (from all dormant buds to 100% open buds) in each tree crown,
 119 typically from mid-to early-May. The ‘extensive’ sampling yielded the population median
 120 date of budburst for each oak population over the whole study period (2012-2018). For the
 121 years when we applied the ‘intensive’ sampling, we could compute both the median budburst
 122 date and the among-trees standard deviation of the budburst date (SD_{ground} , expressed in days).
 123 The standard deviation is a measure of the average duration between each tree individual
 124 budburst date and the average date established over all individuals. In the following, we
 125 consider SD as our metric for quantifying WPVbb. For both the ‘extensive’ and ‘intensive’
 126 samplings, we conducted our observations from once a week during the dormant phase to
 127 three times a week during the actual budburst period (average time resolution was 3.8 days in
 128 Barbeau and 2.5 days in Orsay).
 129

130 **Table 1. Characteristics of the study sites.** $N_{\text{trees}_{\text{int}}}$ and $Years_{\text{int}}$ report the number of
 131 individual trees and the years for which we applied the ‘intensive’ phenological sampling at a
 132 particular site (see text for details). The ‘extensive’ phenological sampling was applied at both
 133 sites over the whole study period (2012-2018). At Barbeau, the phenological camera was run
 134 over 2012-2018. March temperatures are averages \pm SD for 2012-2018.

Site	Site locations	$N_{\text{trees}_{\text{int}}}$	$Years_{\text{int}}$	Temperature data acquisition	March temperature (°C)	Observation method	Reference
Barbeau*	48.48°N, 2.78°E	28 to 66 (average = 38)	2013, 2015- 2017	Top of flux tower, above the tree canopy	7.91±1.96	Phenological camera, Ground observation	(Delpierre <i>et al.</i> , 2016a)
Orsay	48.70°N	27 to 58	2012-	Meteorological	7.49±1.97	Ground	(Delpierre <i>et al.</i> , 2017)

2.17°E	(average	2015,	station (4 km	observation
	= 49)	2018	from site),	
			measured at 2-m	
			height over	
			grassland	

135 * The Barbeau site is part of the ICOS flux network (under the name FR-Fon, Fontainebleau-
136 Barbeau; see www.barbeau.u-psud.fr).

137

138 *Phenological camera and RGB data processing*

139

140 In the Barbeau forest, we installed a phenological camera (model P1347, Axis
141 Communications, Lund, Sweden) on April 4 (DoY 95), 2012 which has been running
142 continuously since then, covering the whole study period (2012-2018). The camera is
143 mounted at the top of the Fontainebleau-Barbeau flux tower (see Delpierre *et al.*, 2016a for
144 site details), five meters above the tallest trees. RGB pictures of the forest canopy (resolution
145 of 2590 x 1920 Px), were acquired continuously every hour from 8 am to 5 pm (UT), yielding
146 10 images per day from year 2013. In year 2012, only 1 image per day (at 10 am) was
147 recorded. In order to access to the within-population variability of budburst, thirty regions of
148 interest (ROIs; 43 kPx on average, range 16-102 kPx) were delineated among 16 visible tree
149 crowns from the top of the canopy on a spring image (Fig. 1). In order to minimize effects of
150 changing illumination conditions, two small ROIs were delineated on a white PVC sheet
151 installed in the camera field of view and used as a white reference standard (3 kPx and 1.4
152 kPx, respectively; Fig. 1). To convert radiance to pseudo-reflectance, the Red, Green and Blue
153 radiance averages of each ROI were respectively divided by the R, G and B radiance averages
154 of the two white standards. These pseudo-reflectances (ρ) were averaged on a daily basis (10
155 values per day, corresponding to the hourly sampling) and used to determine a daily greenness
156 index for each ROI, as: $G_i = \rho G / (\rho R + \rho G + \rho B)$.

157 *Extraction of RGB-based phenological metrics*

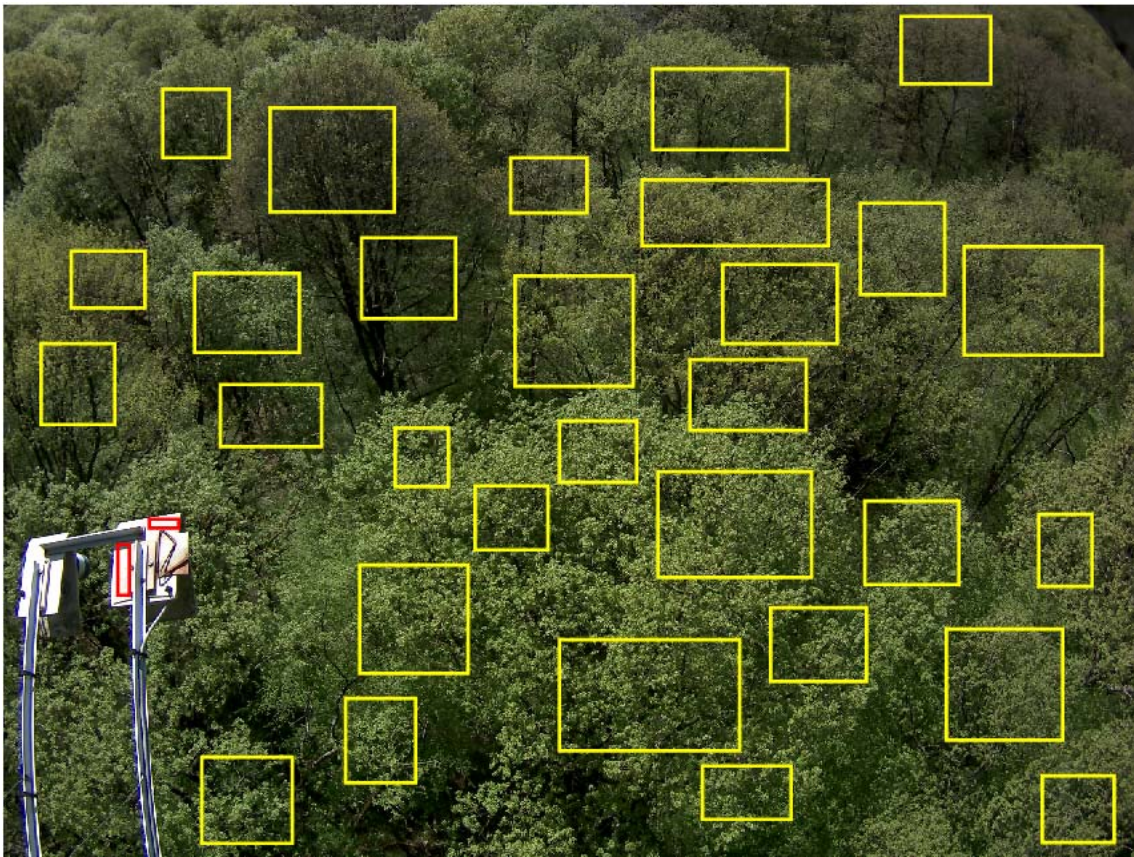
158 For each ROI and each year, we extracted the date of spring transition from a sigmoid curve
159 fit to G_i time-series (Soudani *et al.*, 2008). The sigmoid curve equation is:

160

161
$$G_{i_{pred}}(t) = w1 + w2 + \frac{1}{2}(w1 - w2) \tanh(w3(t - u))$$
 [eq. 1]

162

163 where $G_{i_{pred}}(t)$ is the predicted greenness index at day of year t ; \tanh is the hyperbolic tangent
164 and $w1$, $w2$, $w3$, and u are the fitting parameters. $(w1+w2)$ is the minimum $G_{i_{pred}}$, reached in
165 the non-leafy season. $(w1-w2)$ is the total amplitude of $G_{i_{pred}}$ temporal variations. Parameter u
166 is the date (DoY) corresponding to the highest rates of change of $G_{i_{pred}}(t)$ (maximum peak of
167 the first derivative of $G_{i_{pred}}(t)$, i.e. the inflexion point, corresponding to 50% of the spring
168 greenness amplitude). There is no consensus in the literature as regards the most appropriate
169 way to quantify budburst from Gi time series. Here, we considered u as our proxy for the
170 budburst inferred from phenocam images. Since we were interested in the spring phase, we
171 considered Gi series acquired from DoY 1 to DoY 240. We fitted eq. 1 by minimizing the
172 sum of squares of differences between $G_{i_{pred}}$ and the measured Gi values using MATLAB
173 v8.5. Fitting eq. 1 to each ROI for each year, we ended up with 30 (ROIs) times 7 (from 2012
174 to 2018) estimates of budburst dates inferred from the phenocam.



175
176 **Figure 1. View from the Barbeau phenological camera, on April 19th 2018 (4 pm).** The
177 camera is mounted on the platform of the FR-Fon flux tower, 5 meters above the tallest oaks.
178 Yellow rectangles mark the position of 30 regions of interest (ROIs). Red rectangles identify
179 the white reference standards used to calculate RGB pseudo-reflectances. See text for details.
180
181

182 **Results**

183

184 The population median budburst dates determined according to the ‘extensive’ sampling
185 averaged DoY 104.3 in Barbeau and DoY 104.7 in Orsay over 2012-2018 (Table 2). The
186 dates observed at both populations varied from DoY 97 to 114 and differed at maximum by
187 two days for a particular year. The distributions of the Barbeau and Orsay median budburst
188 dates determined according to the extensive sampling were virtually equal (Student $t=-0.13$,
189 $p<0.89$). The ‘intensive’ sampling yielded median budburst dates within one-day of those
190 determined by the ‘extensive’ sampling, at both populations (Table 2). Overall, these results
191 show that both the Barbeau and Orsay populations show virtually identical budburst dates,
192 whatever the sampling scheme considered. At Barbeau, we could determine WPVbb from
193 ground phenological observations for 4 out of 7 years from 2012 to 2018 (Table 1), hence
194 missing 3 years. Considering the high similarity of budburst dates observed for the Orsay and
195 Barbeau site, we proposed to use data from the Orsay ‘intensive’ sampling campaigns as a
196 proxy for those missing at Barbeau (Table 2) for comparison with the phenocam dates.

197

198 **Table 2. Budburst dates of sessile Oak over the study sites.** These are the median dates (in day of
199 year, DoY) of budburst determined over the Barbeau and Orsay populations, located 50 km apart. The
200 median date has been determined with two sampling schemes (see text for details). Dash denotes
201 missing data.

Year	Barbeau _{extensive}	Barbeau _{intensive}	Orsay _{extensive}	Orsay _{intensive}
2012	101	-	103	103
2013	114	114	114	113
2014	98	-	97	98
2015	105	105	105	104.5
2016	109	108	110	-
2017	98	98	97	-
2018	105	-	107	108

202

203 The dynamics of the greenness index in ROIs (Fig. 2a, b) and the percentage of open buds in
204 individual oak crowns (Fig. 2c, d) were similar, both for year of low (2015) or high (2017)
205 WPVbb. At Barbeau, the median budburst date observed from the ground was close to the
206 estimate from the phenocam data processing (RMSD= 4.8 days, $n=7$; reduced to 1.2 days
207 when excluding year 2012, $n=6$; Fig. 3a), the latter averaging DoY 105.7 over 2012-2018.

208

209 The standard deviation of budburst calculated from the Barbeau phenocam (SD_{cam}) ranged
210 from 2.5 days in 2015 to 9.4 days in 2012, and averaged 4.5 days over 2012-2018 (Fig. 3b).
211 The SD_{cam} values were close to the estimates established from Barbeau ground observations
212 (RMSD= 0.56 days, $n=4$, Fig. 3b). The standard deviations of budburst observed from the
213 ground in Barbeau and Orsay compared well (RMSD= 0.21 days, $n=2$) (Fig. 3b). SD_{cam} was

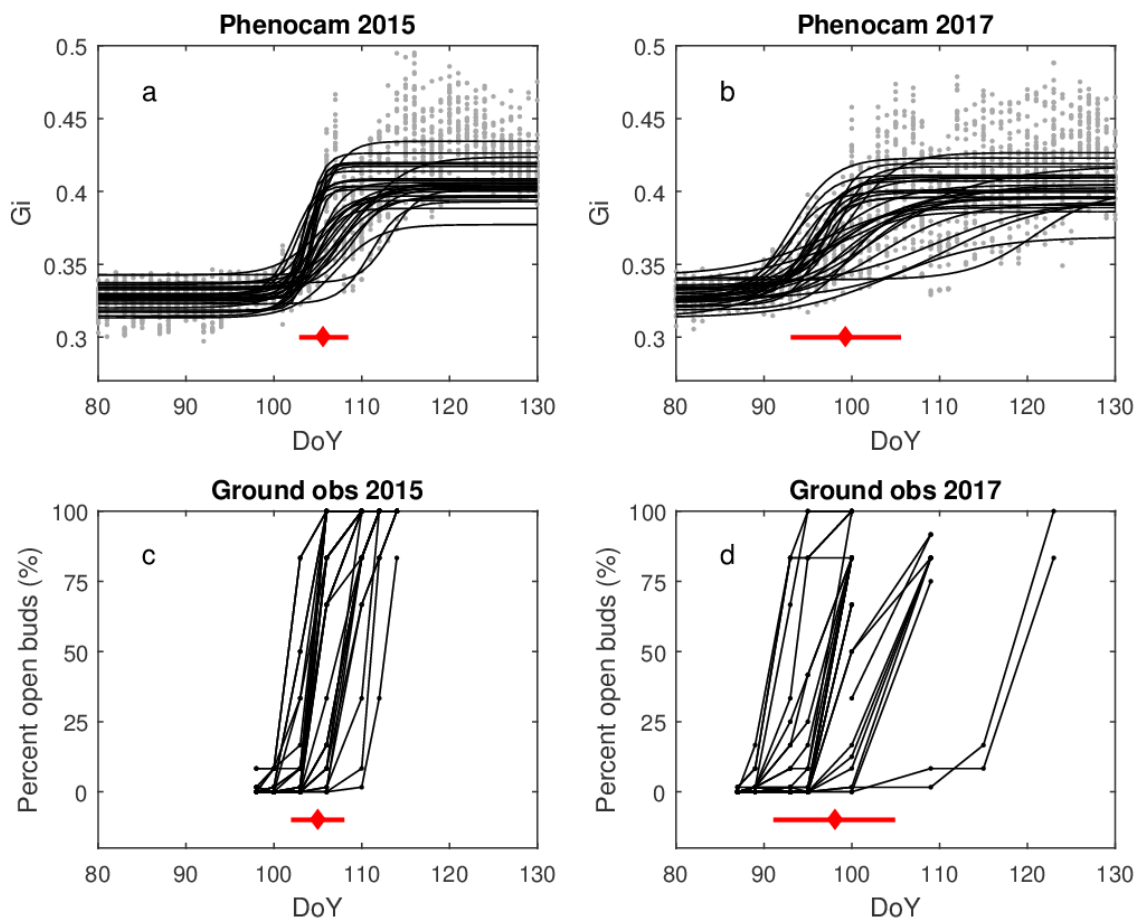
214 strongly correlated, and mostly unbiased, with the SD series obtained from the ground in
215 Orsay and Barbeau (Fig. 3b and Fig. 4).

216

217 Either determined from ground observations (in Orsay and Barbeau) or from processing
218 phenocam images (in Barbeau), the standard deviation of budburst was negatively related
219 with the minimum temperature occurring during the budburst period (defined as the time from
220 the first to the last tree bursting its buds in the population sample) (Fig. 5; Spearman's rank
221 correlation coefficient $\rho=-0.66$; $p<0.006$).

222

223



224

225

226 **Figure 2. Comparing the dynamics of Greenness index (a, b) and percent open buds**
227 **observed from ground (c, d) of oaks at the Barbeau forest.** Data are from years 2015 (a, c)

228 and 2017 (b, d) which are representative of a year with a low (2015) and a high (2017)

229 WPVbb. On plots (a) and (b), grey dots are the actual data (30 ROIs) and black lines are fits

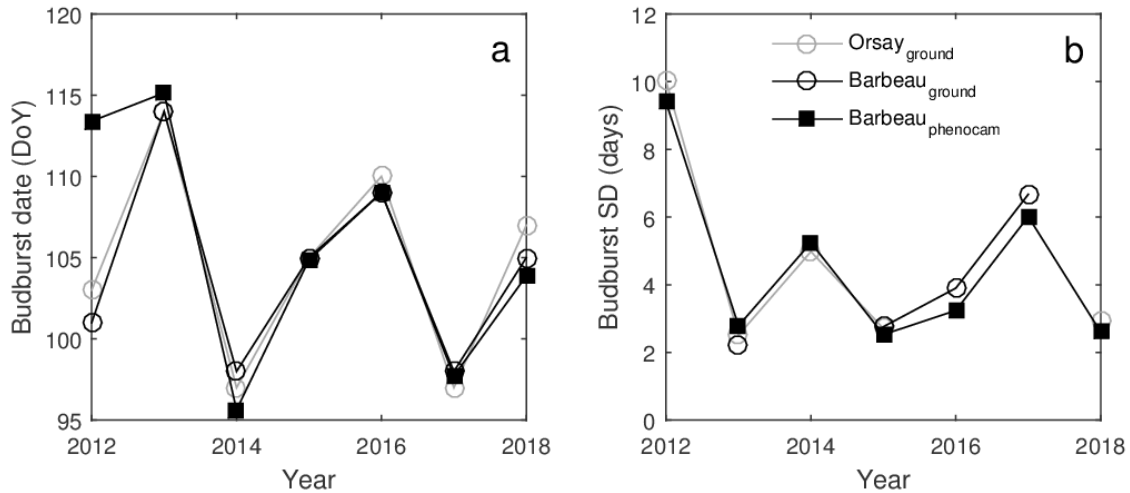
230 from eq. 1 (one curve per ROI). On plots (c) and (d), black dots are individual observations of

231 percent open buds in tree crowns, with data from one tree joined by a continuous line (n=31

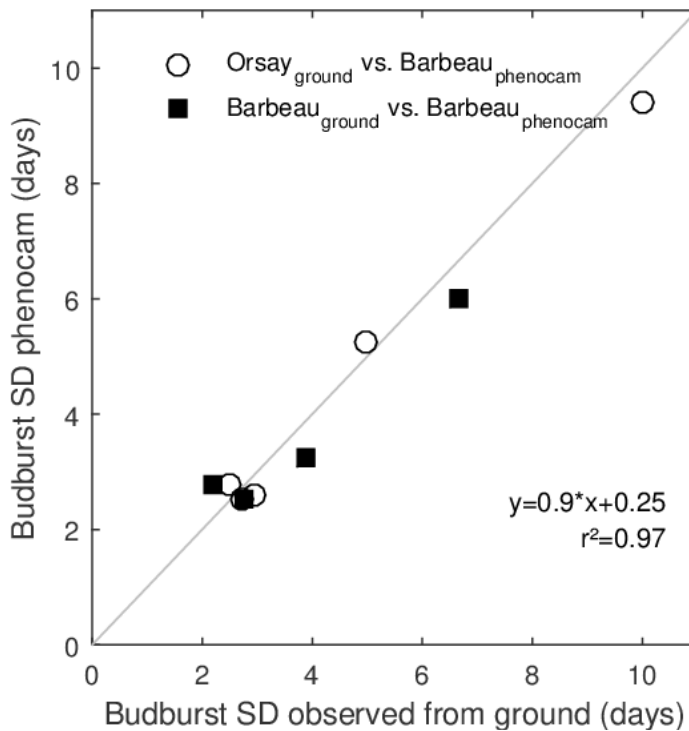
232 individual trees in 2015, n=30 in 2017). On each subplot, the red diamond marks the median

date of budburst determined across ROIs (a, b) or individual tree crowns from the ground (c,

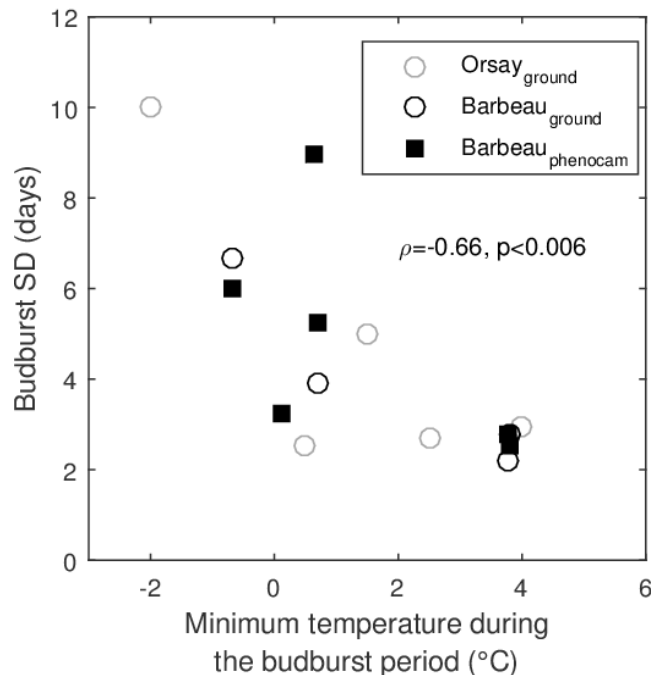
233 d). The horizontal red lines crossing the diamond represent plus/minus one standard deviation.
 234 The position of red symbols on the ordinate axis is arbitrary.
 235



236
 237 **Figure 3. Comparing the population median budburst date (a) and standard deviation**
 238 **(b) for the Orsay and Barbeau populations.** The ground observation data shown in (a) were
 239 acquired according to the ‘extensive’ sampling scheme.
 240



241
 242 **Figure 4. The standard deviation of budburst estimated from the phenocam data**
 243 **processing align with those observed from the ground.** Individual points represent one site-
 244 year. The linear equation displayed on the graph is established over all data points. The
 245 identity line appears in grey.
 246



247
248 **Figure 5.** The standard deviation of budburst is related to minimum temperatures during the
249 budburst period. Individual points represent one site-year.
250

251 Discussion

252

253 Phenological cameras have been used multiple times to detect phenological transitions from
254 tree individuals to the landscape scale, with errors in the identification of budburst ranging
255 from 1.7 to 9 days (Table 3). Those differences between ground observations and phenocam-
256 derived estimates average 4.5 days (Table 3), and are comparable to the time resolution of
257 ground phenological observations (usually once to three times a week in spring). Here we
258 observed a 4.8 days root mean squared difference between the date of budburst determined
259 with phenocam and the one observed from the ground over of the 7-year time series at the
260 Barbeau forest (Fig. 3a). We notice a lesser comparability of the ground observations and
261 phenocam-derived budburst date for year 2012 at Barbeau (phenocam lags 12 days behind
262 ground observations; Fig. 3a). This was the year when we started phenocam data acquisition,
263 and we installed the camera relatively late (on DoY 95, see Material and Methods), after the
264 first trees has leafed-out in our population. In fact, data from our ‘extensive’ sampling at
265 Barbeau indicate that on this very date, 38% of 210 trees had already burst their buds (data
266 not shown).

267 There is no consensus in the literature as regards the way to process phenocam images to
268 detect the date of budburst (Table 3). In this study, we used the inflection point of a sigmoid

269 model fitted to the spring Gi time series as our phenocam-derived metric of budburst. Our
 270 results show that this method compares well to the median date of budburst observed from the
 271 ground over the Barbeau oak population (Fig. 3a). More generally, we notice that there is no
 272 universal protocol for the ground observation of phenological transitions at the scale of tree
 273 crowns. The BBCH scale (Finn *et al.*, 2007), often considered as a reference for phenological
 274 observations is defined at the scale of organs (buds, leaves), and there is no common protocol
 275 at higher (i.e. the tree crown) scale. Phenological cameras are appealing as they offer a way to
 276 process imagery signals in a uniform way (Richardson *et al.*, 2018), going over uncertainties
 277 associated with the acquisition of data by multiple human observers (Cole & Sheldon, 2017);
 278 Liu *et al.* in prep). On the other hand, phenological metrics derived from phenocams need
 279 comparisons with ground-truth phenological data, at least for making them comparable with
 280 the multi-decade phenological time series acquired in the field (Templ *et al.*, 2018).

281

282 **Table 3. Survey of published literature reporting comparisons between ground**
 283 **phenological observations and spring phenological transition determined with**

284 **phenocams.** Gcc= green chromatic coordinate; FOV= field of view.

Reference	RMSD (days)	N	Phenocam method	Independent observation method
(Ahrends <i>et al.</i> , 2009)	3-4	7 ROIs in the same FOV, 2 years	Gcc spring, 50% greenness amplitude	Visual assessment of phenocam images (looking for “visible leaf-out”)
(Keenan <i>et al.</i> , 2014)	1.7	5 years	Gcc thresholding (=0.38)	Ground observation of budburst (95% open buds) averaged over 4 individuals
(Klosterman <i>et al.</i> , 2014)	7-9	73 site-years	Various sigmoid models fitted to Gcc, 10% greenness amplitude	Visual assessment of phenocam images (majority of trees start to leaf-out)
(Klosterman & Richardson, 2017)	4.7	30 tree individuals (1 year)	Sigmoid model fitted to Gcc, 10% greenness amplitude	Ground observations of 10% budburst for 30 trees
This study	4.1 (1.1)	7 years	Sigmoid model fitted to Gi, 50% greenness amplitude	Ground observations of 50% budburst for >100 trees

285

286 Our main objective here was to assess whether the within-population variability of budburst
287 (WPVbb) could be detected with phenocam data. For this purpose, we needed a ground-truth
288 quantification of WPVbb. Quantifying WPVbb with ground phenological observations is
289 time-consuming. Indeed, in order to derive a robust estimate of WPVbb, one needs to observe
290 at least 30 trees (Denéchére *et al.*, 2019), with a typical amplitude of around 20 days from the
291 first to the latest tree to burst buds (Delpierre *et al.*, 2017); note that we attained a 35 days
292 amplitude in Orsay 2012, corresponding to our maximum standard deviation of budburst, Fig.
293 3b). This is why we did not monitor ground phenology over the whole period of phenocam
294 data acquisition at Barbeau (2012-2018, i.e. 7 years), located 70-km away from our lab. We
295 completed this time series with data acquired at Orsay, which allowed us to cover the 7-year
296 period of phenocam observation. The population median dates of budburst compare very well
297 (they are within two days, Table 2) in Barbeau and Orsay over the study period, which is not
298 surprising since both populations are separated by 50 km in plain and essentially experiment
299 the same climate conditions (Table 1). What is more interesting is that the WPVbb determined
300 from ground observations was very similar for both sites and compared well with WPVbb
301 derived from phenocam (Fig. 3b). Beyond the validation of the use of phenocam to detect
302 WPVbb, this result implies that our two oak populations show very similar budburst but also
303 WPVbb. This result is very interesting and mirrors the comparability of oak populations at
304 regional scales (see Suppl. Mat. 1 for a comparison of budburst dates at the continental scale),
305 notably driven by pollen dispersal (Kremer *et al.*, 2002).

306

307 The standard deviation of budburst we report here averaged 4.5 days (as derived from the
308 Barbeau phenocam). This is comparable to the average of 4.0 days (range 1.7 to 9.7 days)
309 observed in 14 tree populations of nine temperate deciduous tree species (Denéchére *et al.*,
310 2019). It is also comparable to the value of 3.5 days detected by the analysis of RGB-derived
311 greenness index time series acquired with an unmanned aerial vehicle (UAV, i.e. a drone) for
312 one year over 60 grid cells (100 m² each) containing deciduous trees in the Harvard forest
313 (Klosterman *et al.*, 2018). Coniferous tree species may display larger standard deviation of
314 budburst: Salmela *et al.* (2013) report an average value of 7.4 days (ranging from 4.3 to 11.1
315 days) in 21 populations of Scots pine grown in a common garden. Though being an adaptive
316 trait in Scots pine (Salmela *et al.*, 2013), budburst may undergo less selection pressure for
317 evergreens (that by definition remain at least potentially photosynthetically active throughout
318 winter and spring; Mäkelä *et al.*, 2004) than for deciduous trees.

319

320 Our analysis of the Barbeau phenocam data evidenced a high interannual variability of
321 WPVbb for a given tree population (Figure 3b). We observed that lower minimum
322 temperatures during the budburst phase are associated with higher WPVbb (Fig. 5). This
323 result is similar to the one observed across 14 European tree populations (Denéchère *et al.*,
324 2019). Our hypothesis is that as the accumulation of degree-days occurs faster during a warm
325 spring, the time interval from the first to the last tree bursting buds in the population is
326 reduced as compared to a colder spring (see Denéchère *et al.*, 2019, their suppl. Mat).

327

328 **Conclusion and perspectives**

329

330 Phenological cameras have been used for over a decade to detect spring transition from the
331 dormant to the active phase in temperate deciduous canopies. Here, we demonstrated through
332 comparison with ground observations acquired over 7 years on sessile oak populations that
333 phenological cameras can further be used to quantify and monitor the year-to-year variations
334 of the within-population variability of budburst (WPVbb) in temperate deciduous forests.
335 Generalizing our approach over continental scale phenocam networks (Wingate *et al.*, 2015;
336 Richardson *et al.*, 2018) would increase our understanding of the spatial (i.e. across
337 population) and temporal variability of WPVbb. The implications of considering WPVbb in
338 phenological modelling are two-folds: (1) phenological models are classically built to
339 represent the year-to-year variations of the average date of budburst of a tree population, and
340 we hypothesize that the accuracy of phenological models is lower for years of higher WPVbb;
341 (2) the emerging class of physio-demo-genetic models (Kramer *et al.*, 2008, 2015; Oddou-
342 Muratorio & Davi, 2014), aiming at simulating the micro-evolution of tree populations, needs
343 accurate parameterizations of the within-population variability of leaf phenological traits.
344 Quantifying WPVbb with phenological cameras will help documenting those aspects.

345

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353

354 **Authors' contribution**

355 ND designed the research and wrote the manuscript. KS processed the phenological camera
356 images. DB and GH operated the phenological camera. ND, ED, GV and DB made ground
357 phenological observations. All the authors commented and approved the paper.

358

359 **References**

360

361 **Ahrends HE, Bräugger R, Stöckli R, Schenk J, Michna P, Jeanneret F, Wanner H, Eugster W. 2008.**
362 Quantitative phenological observations of a mixed beech forest in northern Switzerland with digital
363 photography. *Journal of Geophysical Research: Biogeosciences*.

364

365 **Ahrends HE, Etzold S, Kutsch WL, Stoeckli R, Bruegger R, Jeanneret F, Wanner H, Buchmann N,**
366 **Eugster W. 2009.** Tree phenology and carbon dioxide fluxes: Use of digital photography for process-based
367 interpretation at the ecosystem scale. *Climate Research* **39**: 261–274.

368

369 **Alberto F, Bouffier L, Louvet JM, Lamy JB, Delzon S, Kremer A. 2011.** Adaptive responses for seed and
370 leaf phenology in natural populations of sessile oak along an altitudinal gradient. *Journal of Evolutionary*
371 *Biology* **24**: 1442–1454.

372

373 **Berra EF, Gaulton R, Barr S. 2016.** Use of a digital camera onboard a UAV to monitor spring phenology at
374 individual tree level. In: International Geoscience and Remote Sensing Symposium (IGARSS).

375

376 **Bontemps A, Davi H, Lefèvre F, Rozenberg P, Oddou-Muratorio S. 2017.** How do functional traits
377 syndromes covary with growth and reproductive performance in a water-stressed population of *Fagus sylvatica*?
378 *Oikos*.

379

380 **Chesnoiu EN, Sofletea N, Curtu AL, Toader A, Radu R, Enescu M. 2009.** Bud burst and flowering
381 phenology in a mixed oak forest from Eastern Romania. *Annals of Forest Research* **52**: 199–206.

382

383 **Cole EF, Sheldon BC. 2017.** The shifting phenological landscape: Within- and between-species variation in leaf
384 emergence in a mixed-deciduous woodland. *Ecology and Evolution* **7**: 1135–1147.

385

386 **Crawley MJ, Akhteruzzaman M. 1988.** Individual variation in the phenology of oak trees and its consequences
387 for herbivorous insects. *Functional Ecology* **2**: 409–415.

388

389 **Čufar K, De Luis M, Prislán P, Gričar J, Črepinšek Z, Merela M, Kajfež-Bogataj L. 2015.** Do variations in
390 leaf phenology affect radial growth variations in *Fagus sylvatica*? *International Journal of Biometeorology*.

391

392 **Dantec CF, Ducasse H, Capdevielle X, Fabreguettes O, Delzon S, Desprez-Loustau ML. 2015.** Escape of

- 393 spring frost and disease through phenological variations in oak populations along elevation gradients. *Journal of*
394 *Ecology* **103**: 1044–1056.
- 395
- 396 **Delpierre N, Berveiller D, Granda E, Dufrêne E. 2016a.** Wood phenology, not carbon input, controls the
397 interannual variability of wood growth in a temperate oak forest. *New Phytologist* **210**: 459–470.
- 398
- 399 **Delpierre N, Guillemot J, Dufrêne E, Cecchini S, Nicolas M. 2017.** Tree phenological ranks repeat from year
400 to year and correlate with growth in temperate deciduous forests. *Agricultural and Forest Meteorology* **234–235**:
401 1–10.
- 402
- 403 **Delpierre N, Vitasse Y, Chuine I, Guillemot J, Bazot S, Rutishauser T, Rathgeber CBK. 2016b.** Temperate
404 and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. *Annals of Forest*
405 *Science* **73**: 5–25.
- 406
- 407 **Denéchère R, Delpierre N, Apostol E, Berveiller D, Bonne F, Cole E, Delzon S, Dufrêne É, Gressler E,**
408 **Jean F, et al. 2019.** The within-population variability of leaf spring and autumn phenology is influenced by
409 temperature
410 in temperate deciduous trees. *in press in International Journal of Biometeorology*.
- 411
- 412 **van Dongen S, Backeljau T, Matthysen E, Dhondt AA. 1997.** Synchronization of hatching date with budburst
413 of individual host trees (*Quercus robur*) in the winter moth (*Operophtera brumata*) and its fitness consequences.
414 *Journal of Animal Ecology* **66**: 113–121.
- 415
- 416 **Ducousso A, Guyon JP, Kremer A. 1996.** Latitudinal and altitudinal variation of bud burst in western
417 populations of sessile oak (*Quercus petraea* (Matt) Liebl). *Annales des Sciences Forestieres* **53**: 775–782.
- 418
- 419 **Filippa G, Cremonese E, Migliavacca M, Galvagno M, Forkel M, Wingate L, Tomelleri E, Morra di Cella**
420 **U, Richardson AD. 2016.** Phenopix: A R package for image-based vegetation phenology. *Agricultural and*
421 *Forest Meteorology*.
- 422
- 423 **Finn GA, Straszewski AE, Peterson V. 2007.** A general growth stage key for describing trees and woody
424 plants. *Annals of Applied Biology* **151**: 127–131.
- 425
- 426 **Fontaine F, Chaar H, Colin F, Clément C, Burrus M, Druelle J-L. 1999.** Preformation and neoformation of
427 growth units on 3-year-old seedlings of *Quercus petraea*. *Canadian Journal of Botany*.
- 428
- 429 **Franjic J, Sever K, Bogdan S, Skvorc Z, Krstonosic D, Aleskovic I. 2011.** Phenological Asynchronization as
430 a Restrictive Factor of Efficient Pollination in Clonal Seed Orchards of Pedunculate Oak (*Quercus robur* L.).
431 *CROATIAN JOURNAL OF FOREST ENGINEERING*.
- 432

- 433 **Keenan TF, Darby B, Felts E, Sonnentag O, Friedl MA, Hufkens K, O’Keefe J, Klosterman S, Munger**
434 **JW, Toomey M, et al. 2014.** Tracking forest phenology and seasonal physiology using digital repeat
435 photography: A critical assessment. *Ecological Applications* **24**: 1478–1489.
- 436
437 **Klosterman ST, Hufkens K, Gray JM, Melaas E, Sonnentag O, Lavine I, Mitchell L, Norman R, Friedl**
438 **MA, Richardson AD. 2014.** Evaluating remote sensing of deciduous forest phenology at multiple spatial scales
439 using PhenoCam imagery. *Biogeosciences* **11**: 4305–4320.
- 440
441 **Klosterman S, Melaas E, Wang J, Martinez A, Frederick S, O’Keefe J, Orwig DA, Wang Z, Sun Q, Schaaf**
442 **C, et al. 2018.** Fine-scale perspectives on landscape phenology from unmanned aerial vehicle (UAV)
443 photography. *Agricultural and Forest Meteorology* **248**: 397–407.
- 444
445 **Klosterman S, Richardson AD. 2017.** Observing spring and fall phenology in a deciduous forest with aerial
446 drone imagery. *Sensors (Switzerland)*.
- 447
448 **Kosmala M, Crall A, Cheng R, Hufkens K, Henderson S, Richardson AD. 2016.** Season spotter: Using
449 citizen science to validate and scale plant phenology from near-surface remote sensing. *Remote Sensing*.
- 450
451 **Kramer K, Buiteveld J, Forstreuter M, Geburek T, Leonardi S, Menozzi P, Povillon F, Schelhaas MJ,**
452 **Teissier du Cros E, Vendramin GG, et al. 2008.** Bridging the gap between ecophysiological and genetic
453 knowledge to assess the adaptive potential of European beech. *Ecological Modelling* **216**: 333–353.
- 454
455 **Kramer K, van der Werf B, Schelhaas M-J. 2015.** Bring in the genes: genetic-ecophysiological modeling of
456 the adaptive response of trees to environmental change. With application to the annual cycle. *Frontiers in Plant*
457 *Science* **5**.
- 458
459 **Kremer A, Petit RJ, Ducousso A. 2002.** Biologie évolutive et diversité génétique des chênes sessile et
460 pédonculé. *Rev. For. Fr.* **54**: 111–130.
- 461
462 **Lebourgeois F, Delpierre N, Dufrene E, Cecchini S, Macé S, Croisé L, Nicolas M. 2018.** Assessing the roles
463 of temperature, carbon inputs and airborne pollen as drivers of fructification in European temperate deciduous
464 forests. *European Journal of Forest Research*.
- 465
466 **Mäkelä A, Hari P, Berninger F, Hänninen H, Nikinmaa E. 2004.** Acclimation of photosynthetic capacity in
467 Scots pine to the annual cycle of temperature. *Tree Physiology* **24**: 369–376.
- 468
469 **Oddou-Muratorio S, Davi H. 2014.** Simulating local adaptation to climate of forest trees with a Physio-Demo-
470 Genetics model. *Evolutionary applications* **7**: 453–67.
- 471
472 **Richardson AD. 2019.** Tracking seasonal rhythms of plants in diverse ecosystems with digital camera imagery.

473 *New Phytologist*.

474

475 **Richardson AD, Hufkens K, Milliman T, Aubrecht DM, Chen M, Gray JM, Johnston MR, Keenan TF,**
476 **Klosterman ST, Kosmala M, et al. 2018.** Tracking vegetation phenology across diverse North American
477 biomes using PhenoCam imagery. *Scientific Data* **5**.

478

479 **Richardson AD, Jenkins JP, Braswell BH, Hollinger DY, Ollinger S V., Smith ML. 2007.** Use of digital
480 webcam images to track spring green-up in a deciduous broadleaf forest. *Oecologia*.

481

482 **Salmela MJ, Cavers S, Cottrell JE, Iason GR, Ennos RA. 2013.** Spring phenology shows genetic variation
483 among and within populations in seedlings of Scots pine (*Pinus sylvestris* L.) in the Scottish Highlands. *Plant*
484 *Ecology and Diversity*.

485

486 **Savolainen O, Pyhäjärvi T, Knürr T. 2007.** Gene Flow and Local Adaptation in Trees. *Annual Review of*
487 *Ecology, Evolution, and Systematics* **38**: 595–619.

488

489 **Schermer É, Bel-Venner MC, Fouchet D, Siberchicot A, Boulanger V, Caignard T, Thibaudon M, Oliver**
490 **G, Nicolas M, Gaillard JM, et al. 2019.** Pollen limitation as a main driver of fruiting dynamics in oak
491 populations. *Ecology Letters*.

492

493 **Soudani K, le Maire G, Dufrêne E, François C, Delpierre N, Ulrich E, Cecchini S. 2008.** Evaluation of the
494 onset of green-up in temperate deciduous broadleaf forests derived from Moderate Resolution Imaging
495 Spectroradiometer (MODIS) data. *Remote Sensing of Environment* **112**.

496

497 **Templ B, Koch E, Bolmgren K, Ungersböck M, Paul A, Scheifinger H, Rutishauser T, Busto M,**
498 **Chmielewski FM, Hájková L, et al. 2018.** Pan European Phenological database (PEP725): a single point of
499 access for European data. *International Journal of Biometeorology*.

500

501 **Thackeray SJ, Henrys PA, Hemming D, Bell JR, Botham MS, Burthe S, Helaouet P, Johns DG, Jones ID,**
502 **Leech DI, et al. 2016.** Phenological sensitivity to climate across taxa and trophic levels. *Nature*.

503

504 **Wingate L, Ogeé J, Cremonese E, Filippa G, Mizunuma T, Migliavacca M, Moisy C, Wilkinson M,**
505 **Moureaux C, Wohlfahrt G, et al. 2015.** Interpreting canopy development and physiology using a European
506 phenology camera network at flux sites. *Biogeosciences* **12**: 5995–6015.

507

508 **Xie Y, Civco DL, Silander JA. 2018.** Species-specific spring and autumn leaf phenology captured by time-lapse
509 digital cameras. *Ecosphere* **9**.

510

511

512 **Figure Captions**

513

514 **Figure 1. View from the Barbeau phenological camera, on April 19th 2018 (4 pm).** The
515 camera is mounted on the platform of the FR-Fon flux tower, 5 meters above the tallest oaks.
516 Yellow rectangles mark the position of 30 regions of interest (ROIs). Red rectangles identify
517 the white reference standards used to calculate RGB pseudo-reflectances. See text for details.
518

519 **Figure 2. Comparing the dynamics of Greenness index (a, b) and percent open buds**
520 **observed from ground (c, d) of oaks at the Barbeau forest.** Data are from years 2015 (a, c)
521 and 2017 (b, d) which are representative of a year with a low (2015) and a high (2017)
522 WPVbb. On plots (a) and (b), grey dots are the actual data (30 ROIs) and black lines are fits
523 from eq. 1 (one curve per ROI). On plots (c) and (d), black dots are individual observations of
524 percent open buds in tree crowns, with data from one tree joined by a continuous line (n=31
525 individual trees in 2015, n=30 in 2017). On each subplot, the red diamond marks the median
526 date of budburst determined across ROIs (a, b) or individual tree crowns from the ground (c,
527 d). The horizontal red lines crossing the diamond represent plus/minus one standard deviation.
528 The position of red symbols on the ordinate axis is arbitrary.
529

530 **Figure 3. Comparing the population median budburst date (a) and standard deviation**
531 **(b) for the Orsay and Barbeau populations.** The ground observation data shown in (a) were
532 acquired according to the ‘extensive’ sampling scheme.
533

534 **Figure 4. The standard deviation of budburst estimated from the phenocam data**
535 **processing align with those observed from the ground.** Individual points represent one site-
536 year. The linear equation displayed on the graph is established over all data points. The
537 identity line appears in grey.
538

539 **Figure 5.** The standard deviation of budburst is related to minimum temperatures during the
540 budburst period. Individual points represent one site-year.