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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 (Ducousso *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 ( $SD_{\text{ground}}$ , 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](http://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 ( $\rho$ ) 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:

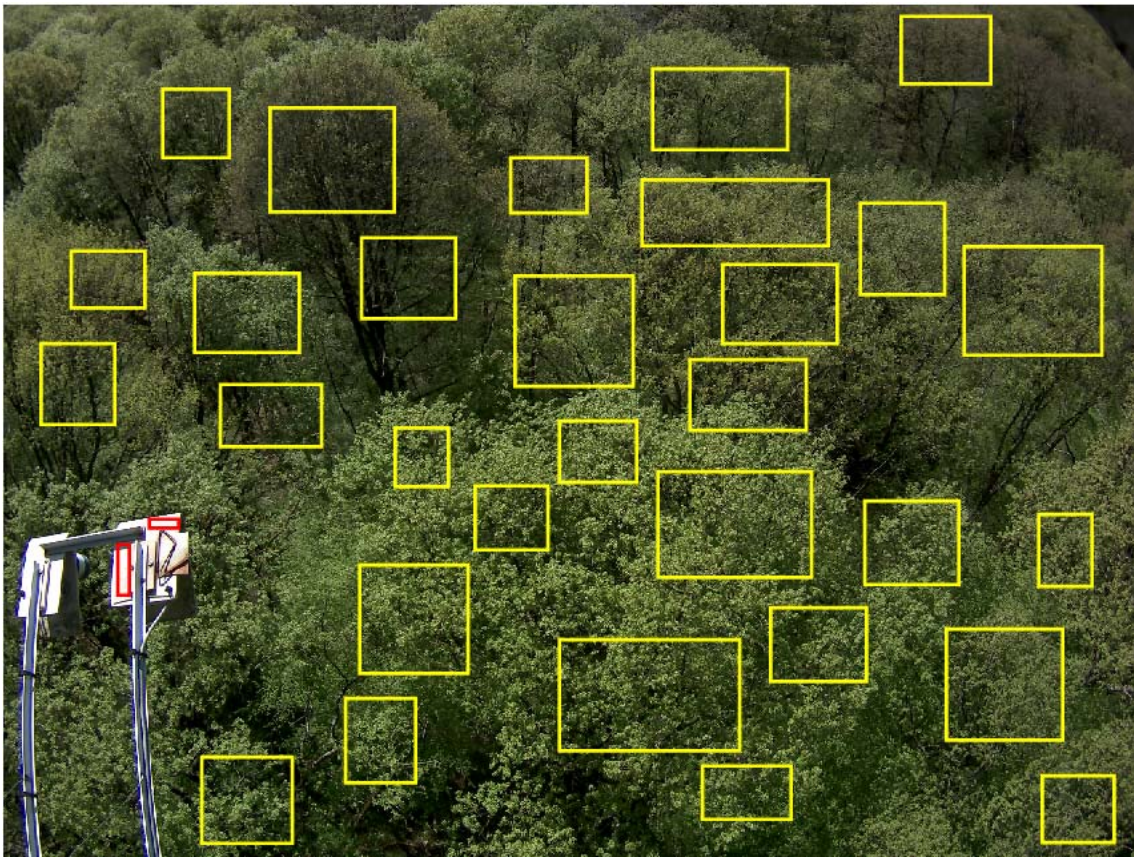
160

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 19<sup>th</sup> 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 <sub>extensive</sub>	Barbeau <sub>intensive</sub>	Orsay <sub>extensive</sub>	Orsay <sub>intensive</sub>
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

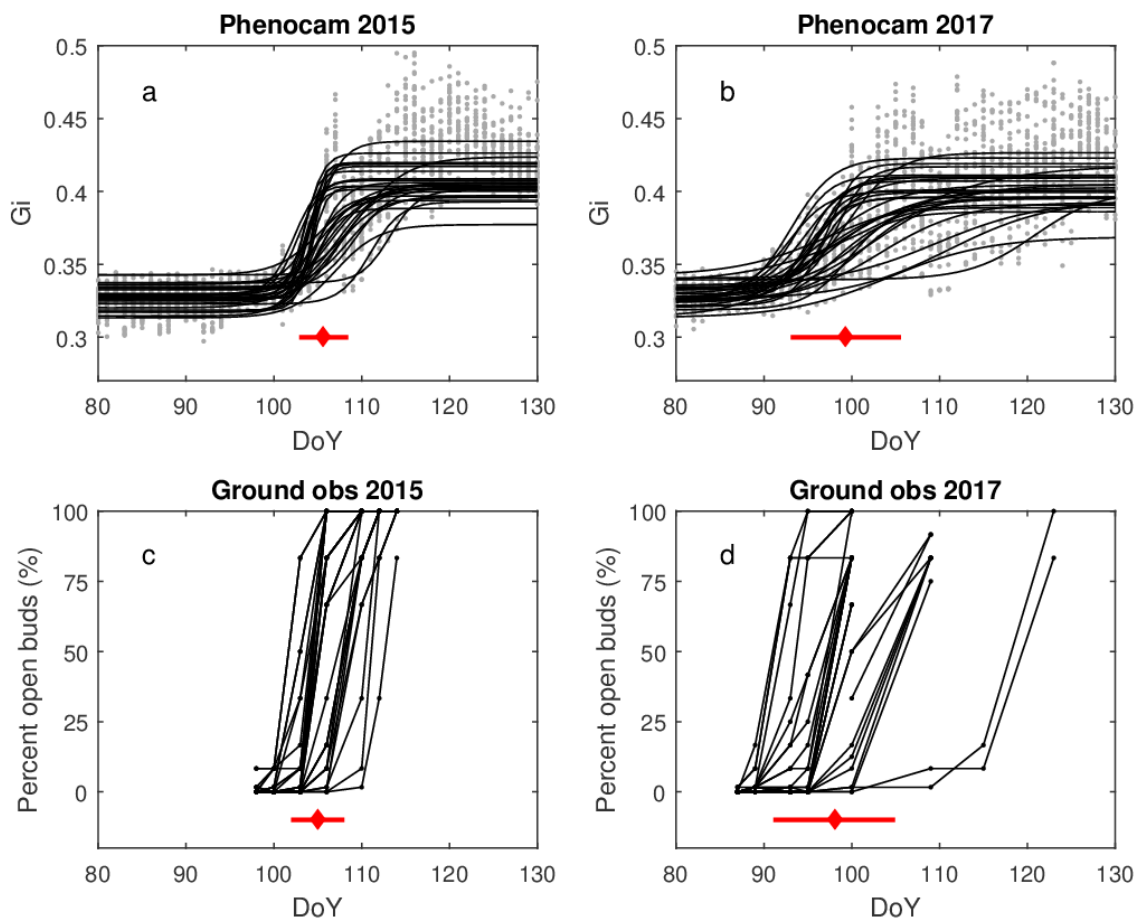
202

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

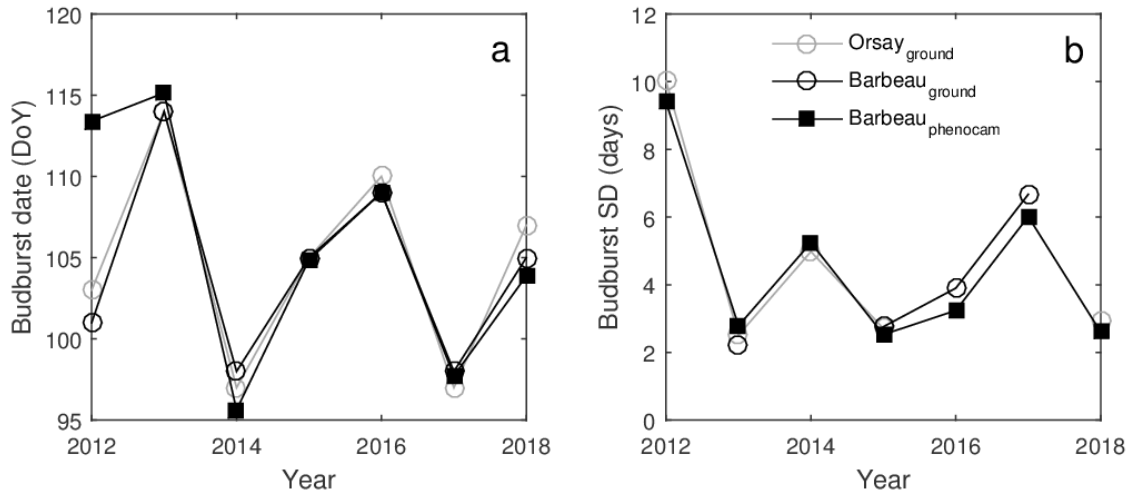
209 The standard deviation of budburst calculated from the Barbeau phenocam ( $SD_{cam}$ ) ranged  
210 from 2.5 days in 2015 to 9.4 days in 2012, and averaged 4.5 days over 2012-2018 (Fig. 3b).  
211 The  $SD_{cam}$  values were close to the estimates established from Barbeau ground observations  
212 (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

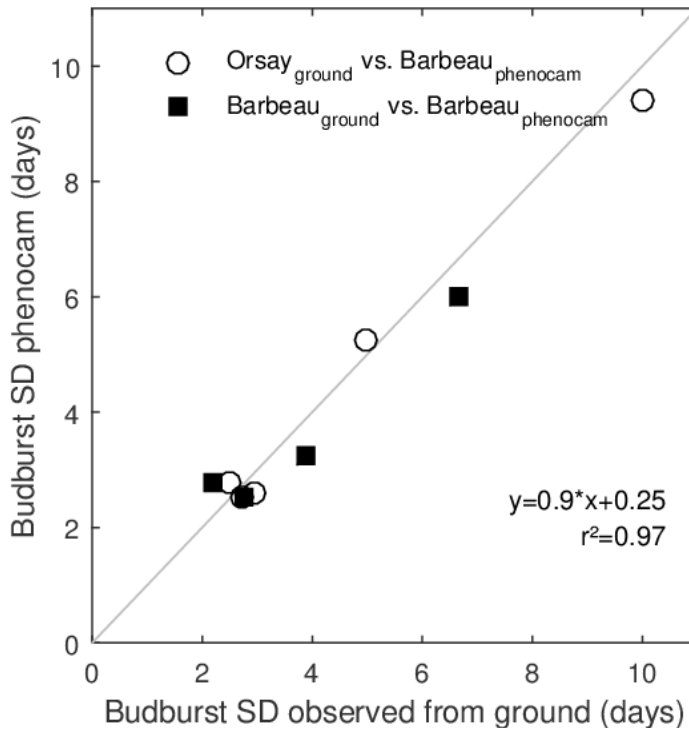


224  
225 **Figure 2. Comparing the dynamics of Greenness index (a, b) and percent open buds**  
226 **observed from ground (c, d) of oaks at the Barbeau forest.** Data are from years 2015 (a, c)  
227 and 2017 (b, d) which are representative of a year with a low (2015) and a high (2017)  
228 WPVbb. On plots (a) and (b), grey dots are the actual data (30 ROIs) and black lines are fits  
229 from eq. 1 (one curve per ROI). On plots (c) and (d), black dots are individual observations of  
230 percent open buds in tree crowns, with data from one tree joined by a continuous line (n=31  
231 individual trees in 2015, n=30 in 2017). On each subplot, the red diamond marks the median  
232 date of budburst determined across ROIs (a, b) or individual tree crowns from the ground (c,

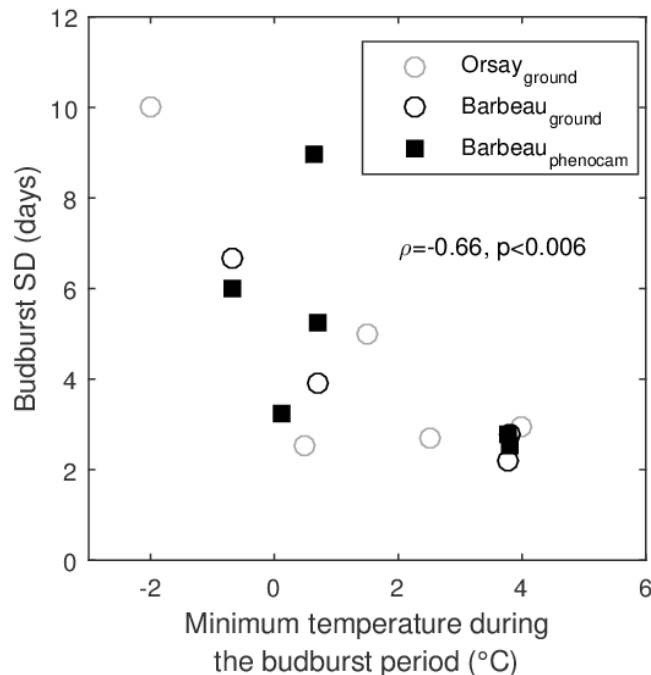
233 d). The horizontal red lines crossing the diamond represent plus/minus one standard deviation.  
 234 The position of red symbols on the ordinate axis is arbitrary.  
 235



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  $G_i$  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 $G_i$ , 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 (Denéchère *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 (Denéchère *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 m<sup>2</sup> 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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351 ground phenological monitoring. The authors have no conflict of interest to declare.

352

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

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511

512 **Figure Captions**

513

514 **Figure 1. View from the Barbeau phenological camera, on April 19<sup>th</sup> 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.