Faculty of Science and Engineering

School of Biological and Marine Sciences

2020-03

# A comparison of ground-based methods for obtaining large-scale, high-resolution data on the spring leaf phenology of temperate tree species

Smith, AM

http://hdl.handle.net/10026.1/15597

10.1007/s00484-019-01839-2 International Journal of Biometeorology Springer Science and Business Media LLC

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

- 1 A comparison of ground-based methods for
- 2 obtaining large-scale, high resolution data on the
- 3 spring leaf phenology of temperate tree species

- 5 Alison M. Smith<sup>1,2</sup> & Paul M. Ramsay<sup>1,\*</sup>
- <sup>1</sup>School of Biological and Marine Sciences, University of Plymouth, Plymouth, PL4 8AA,
- 7 UK
- 8 <sup>2</sup>Plantlife International, Brewery House, 36 Milford Street, Salisbury, Wiltshire SP1 2AP,
- 9 UK
- 10 \*Corresponding author: School of Biological and Marine Sciences, University of
- 11 Plymouth, Plymouth, PL4 8AA, UK; pramsay@plymouth.ac.uk; tel. +44-1752-584600.
- 12 Key words: citizen science, budburst, leaf expansion, canopy greening, climate change.

## A comparison of ground-based methods for obtaining large-scale, high resolution data on the spring leaf phenology of temperate tree species

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

### **Abstract**

Phenological variation in spring leafing between and within species can determine plant responses to warmer winter and spring temperatures in the short term. Methods are needed for monitoring canopy development that can be replicated on a large-scale, while retaining fine-scale resolution at the level of individual trees. Citizen science has potential to provide this, but a range of approaches exist in terms of the phenophase recorded (e.g., budburst or leaf expansion), how the phenophase is characterised (first events or intensity monitoring), and the portion of tree crown assessed and observation frequency. A comparison of spring budburst and leaf expansion of four tree species (Fraxinus excelsior, Fagus sylvatica, Quercus robur and Acer psuedoplatanus) was monitored in one woodland using (1) counts of expanded leaves on three crown sections, (2) percentage estimates of expanded leaves across the whole crown, and (3) a greenness index from photography. Logistic growth models were applied to make comparisons. First-event dates were found to be misleading due to high variation in leaf development rates within and between species. Percentage estimates and counts produced similar estimates of leaf expansion timing and rate. The greenness index produced similar estimates of timing, but not rate, and was compromised by practicalities of photographing individual crowns in closed canopy woodland. Citizen scientists could collect data across the period of spring leafing, with visual counts and/or estimates made every 3-4 days, subject to tests of reliability in pilot citizen science studies.

### 1. Introduction

39

70

40	Changes in leaf phenology of temperate trees are one of the best studied and most
41	recognisable impacts of climate change, with evidence of earlier leafing with warmer
42	spring temperatures over the last 50-60 years (Menzel and Fabian 1999; Menzel et al.
43	2006; Polgar and Primack 2011; Fu et al. 2015; Melaas et al. 2018). Phenological data
44	at the ecosystem level are now often obtained from remote-sensing, capturing
45	phenological trends at regional and global scales, but at coarse temporal and spatial
46	resolutions (Buitenwerf et al. 2015; Crabbe et al. 2016; Hamunyela et al. 2013; Wang et
47	al. 2016; White et al. 2014; Wu and Liu 2013). By contrast, ground-based observations
48	gather species and site-specific information, but tend to lack geographic coverage and
49	vary considerably in their approaches to characterising phenology (Denny et al. 2014).
50	While many studies have focussed on identifying large-scale phenological patterns, few
51	have investigated how changes in phenology affect local-level forest ecosystem
52	dynamics (Cole and Sheldon 2017). Leaf phenology is fundamental to tree growth,
53	fitness and survival (Chuine 2010; Vitasse et al. 2009b), and timing of canopy
54	development has widespread implications for competition dynamics and trophic
55	interactions (Cole and Sheldon 2017; Roberts et al. 2015; Thackeray et al. 2010).
56	Therefore, understanding subtle changes in timing and order of leaf expansion in a
57	forest ecosystem is important.
58	Since forests are highly heterogeneous, there is a need for widespread monitoring of
59	forests at high spatial and temporal resolution. Phenology at the local level varies
60	according to species composition and genetic diversity (Basler 2016; Cleland et al.
61	2007; Polgar and Primack 2011). Environmental factors such as topography (Fisher et
62	al. 2006) and soils (Arend et al. 2016; Lapenis et al. 2017) can vary markedly over smal
63	spatial gradients, and influence phenology at scales missed by remote-sensing.
64	Therefore, harmonised methods that enable large-scale data collection on the
65	phenology of individual trees are needed to understand impacts on ecosystem
66	dynamics and biodiversity.
67	Monitoring methods that detect subtle changes in the sequence of leaf expansion
88	among different tree species will be important for predicting future changes in forest
69	composition. For example, Roberts et al. (2015) predicted a shift away from

phenological complementarity, increasing competition for light and soil moisture, and

```
71
      driving changes in forest composition over time. Monitoring methods also need to detect
72
      within-species variability. Variation within species occurs between populations as a
73
      result of genetic adaptation to environmental conditions, particularly in relation to
 74
      latitude and altitude (Chmura and Rozkowski 2002; Vitasse et al. 2009b). Delpierre et
75
      al. (2017) found that within-population genetic and phenotypic variability in budburst
 76
      dates for oak and beech were more important than local environmental factors though
 77
      this is likely to vary according to the heterogeneity of the forest site. Marked differences
78
      between neighbouring individuals of the same species demonstrate the need for high
 79
      levels of replication of individual trees within and between sites. The extent of genetic
 80
      and/or phenotypic variation within a species population could determine its persistence
 81
      in a forest ecosystem. It could also determine the survival of insect species with
 82
      synchronised life-cycles, and in turn the species that depend on them for food (Cole and
 83
      Sheldon 2017).
 84
      At present the approaches used in observational studies to characterise leaf phenology
 85
      vary considerably. Key historic phenological records are based on first event dates
      (Primack and Miller-Rushing 2012; Sparks and Carey 1995) and many subsequent
 86
87
      studies have characterised tree leaf phenology based on first budburst or first leaf
 88
      expansion (Collinson and Sparks 2008; Menzel and Fabian 1999; Polgar et al. 2014;
 89
      Roberts et al. 2015; Schaber and Badeck 2005; Fu et al. 2015). A number of
 90
      international and national phenology monitoring programmes use first event metrics
91
      (Chmielewski No date; Project Budburst 2017; Nature's Calendar 2017; NatureWatch
92
      Canada 2017) as they need less survey effort (Miller-Rushing et al. 2008). Although
93
      some studies have shown correlations between different phenophases in tree leafing
94
      (e.g., Vander Mijnsbrugge and Janssens 2019), there is some evidence that relying on
 95
      budburst dates alone to represent leafing phenology could lead to the misrepresentation
96
      of leaf development as a whole (Richardson and O'Keefe 2009).
97
      As an alternative to recording first budburst or first leaf expansion dates, some studies
98
      have recorded multiple dates to identify transitions between phenophase growth stages,
99
      using standardised scales such as the BBCH system (Finn et al. 2007) or bespoke
100
      indices (Capdevielle-Vargas et al. 2015; Cole and Sheldon 2017; Richardson et al.
101
      2006; Vitasse et al. 2009a). Recently the USA National Phenology Network (USA-NPN)
102
      introduced status and intensity monitoring into their citizen science programme (Denny
103
      et al. 2014; Elmendorf et al. 2016). Observers are encouraged to record both the
```

104 phenophase growth stage and the intensity, for example by estimating the percentage 105 budburst or leaf expansion, in order to track the entire progress of canopy development 106 for individual trees. The advantage of collecting time-series for individual trees is it 107 enables the rate of canopy development to be established, and peak leaf development 108 timing to be identified. However, as observations increase in complexity, data quality 109 challenges arise. Lower levels of accuracy have been reported when citizen scientists 110 have to identify emerging leaves, as opposed to expanding leaves, as the former is 111 harder to identify, particularly when the canopy is very high (Fuccillo et al. 2015). 112 Subjectivity associated with visual estimates can also be a problem leading to between-113 observer bias (Morrison 2016), particularly where a large and variable canopy is being 114 considered, and can be affected by training and experience (Bison et al. 2019; Feldman 115 et al. 2018). 116 Observations should be made frequently enough to detect subtle variation in leaf 117 expansion timing between and within species. Observational studies have monitored 118 trees every other day (Wesolowski and Rowinski 2006), 2-3 times per week 119 (Capdevielle-Vargas et al. 2015; Cole and Sheldon 2017), once a week (Delpierre et al. 2017; Richardson et al. 2006) and every 10 days (Vitasse et al. 2009a). Remote-120 121 sensing tends to obtain data sets with an 8–16 day resolution due to loss of images 122 from cloud cover and atmospheric interference (Hamunyela et al. 2013; Ahl et al. 2006). 123 It would be useful to determine how estimates of the same phenological process are 124 affected by observations at different temporal grains, i.e., every two days, four days etc. 125 Near-surface remote sensing techniques have emerged that provide high spatial and 126 temporal resolution data on phenology of individual trees (Jeong et al, 2013; Keenan et 127 al. 2014). Digital cameras or Normalised Difference Vegetation Index (NDVI) sensors 128 that track canopy greening can be positioned just above the canopy, and capture data 129 at multiple intervals per day. These methods detect green signals that indicate leaf 130 emergence and development with high accuracy (Inoue et al. 2014; Soudani et al. 131 2012). They are not affected by cloud conditions as is satellite imagery (Polgar and 132 Primack 2011), but may be affected by understorey greening (Inoue et al. 2014). 133 Sideways-facing cameras, as used in the Phenocams network in the USA (Richardson 134 et al. 2007) and the Phenological Eyes Network in Japan (Inoue et al. 2014), are less 135 influenced by the understorey, though image quality can be affected by light conditions 136 (Mizunuma et al. 2012). With both types of imagery it is possible, though sometimes

137 difficult, to isolate trees so that time-series of individual tree canopy development can be 138 derived (Inoue et al. 2014; Polgar and Primack 2011). Despite the lower cost associated 139 with these techniques, in comparison to manually operated techniques such as 140 hemispherical photography (Richardson et al. 2007; Soudani et al. 2012), the cost and 141 logistics of installing equipment still limit this approach to a relatively small number of 142 sites. 143 Given the recent rise in citizen science and phenology monitoring, citizen scientists 144 could repeatedly photograph tree crowns and branches at fine spatial and temporal 145 resolutions, avoiding time-consuming visual estimates with potential for between-146 observer bias. However, the practicalities of photographing individual tree crowns and 147 branches from the ground within a forest requires testing, along with the derivation of 148 phenological metrics from the photographic sequences. 149 In this study, we aim to test three different approaches to monitor the progress of spring 150 canopy leafing in four species of tree in an English woodland: (1) counts of expanded 151 leaves on three crown sections, (2) percentage estimates of expanded leaves across 152 the whole crown, and (3) a greenness index from photography. We used these 153 observations to determine key parameters of the time-series data, including first 154 budburst, 50% completion estimates, and 95% leafing completion. We consider the 155 potential use of these methods by citizen scientists in monitoring programmes 156 associated with climate change.

### 2. Materials and methods

157

188

### 158 2.1. Study site and data collection 159 The study took place in Widey Woods, an 8 ha broadleaved woodland in Plymouth, 160 England (50°24 N, 7°7 W), during spring 2015. The four tree species included were 161 European ash (Fraxinus excelsior), European beech (Fagus sylvatica), pedunculate oak 162 (Quercus robur) and sycamore (Acer pseudoplatanus). These were selected as they 163 were dominant in the canopy of the study site, and are widespread across European 164 temperate forests. Ten mature trees from each species were haphazardly selected for 165 inclusion and GPS-marked for ease of relocation. Trees were selected within the 166 diameter at breast height (DBH) size of 20–60 cm. Average DBH was 35 cm (±10 cm) 167 and average height was 18 m (±4 cm). 168 The same observer visited trees each week from the middle of February 2015 to look for signs of imminent budburst, indicated by swelling. Checks began three weeks prior 169 170 to earliest reported budburst for target species (Elmendorf et al. 2016), based on 171 budburst records from the previous year for south-west England (Nature's Calendar 172 2017). Bud-swelling was evident from the last week in March, so trees were visited 173 every other day from then onwards, until all trees had attained full leaf expansion (2 174 June). 175 First budburst was recorded as the day of year (DOY) when green leaves were first 176 visible emerging between bud scales at any location on the tree. First leaf expansion 177 was recorded as the DOY when the first leaf with characteristic shape for its species 178 was visible on the tree. From the date of first leaf expansion, two different methods of 179 visual estimation were used to monitor canopy development. First, the extent of leaf 180 expansion across the whole crown was estimated as a percentage of buds with 181 expanded leaves. Estimates were made in increments of 5% between 5-100%, but 182 allowed for smaller increments between 1–5% so that early activity could be captured. 183 Secondly, counts were made of expanded leaves in three sections of the crown. These 184 sections were established prior to first budburst, and reference photographs were taken 185 to ensure the same areas were assessed on each visit. In each section, a count was 186 made of the number of buds out of 50 that had at least one fully expanded leaf present. 187 giving a total count out of 150 buds. Binoculars with x10 magnification were used to aid

observations, and a clicker counter used to reduce risk of counting errors.

For each tree, data were converted along a proportional scale from 0 to 1, with 0 representing the crown prior to leaf expansion, and 1 representing the crown with full leaf expansion. For count data, this was achieved using equation (1):

$$a = (x - crown_{MIN}) / (crown_{MAX} - crown_{MIN})$$

193 (1)

Here, a represents the leaf expansion proportion for a given DOY, x is the number of leaves out of 150 buds that were expanded on that DOY,  $crown_{\rm MIN}$  represents the number of leaves expanded at the start of the time series (i.e., 0), and  $crown_{\rm MAX}$  represents the number of buds with at least one fully expanded leaf at the end of the time series. As the canopy estimate data were in percent increments, these were simply divided by 100 to convert them to proportions.

on a subset of eight of the surveyed trees (four ash, two beech, one oak and one sycamore). The same crown sections that were used for counts were photographed, with the photographer standing at a fixed distance from the tree. Photographs were taken using a Panasonic Lumix DMC-TZ35 16.1 MP camera. The camera was handheld, and automatic exposure settings were used. It is important to note that while photos were taken of the same tree sections that counts were conducted on, they captured a larger area of the branch than the 50 buds assessed using the count method. Furthermore, the size of branch area captured in a photo was not standardised across the photographs, as the method was supposed to be rapid and easily used by citizen scientists conducting a walk around a site. Photographing stopped once the count data indicated all buds had expanded leaves.

Images were stored as JPEGs (4608 x 3456) and analysed using the open access software ImageJ (Rueden 2016). The Region of Interest (ROI) manager was used to ensure the area contained in the image for each tree section was consistent for each date, accounting for small discrepancies in the original field of view. To estimate crown greening, red, green and blue colour channels were separated and analysed independently. The analysis was done using the multi-measure tool in the ROI manager to derive mean digital numbers (DN) representing intensity for each colour channel. The Greenness Index for each image was calculated using equation (2), after Richardson et al. (2007).

221 
$$Greenness Index (\%) = \frac{Green DN}{Red DN + Green DN + Blue DN}$$

222 (2)

Greenness Index values were then standardised on a proportional scale using equation (1), to provide a time-series of crown greening from 0 (no leaves) to 1 (maximum green signal). In this case, a in equation (1) is the Greenness Index proportion on a given DOY, x is the absolute Greenness Index value on that DOY,  $crown_{MIN}$  is the minimum Greenness Index value (*i.e.*, from the first photo in the series where the crown section had no budburst), and  $crown_{MAX}$  represents the highest Greenness Index value in the photo series. Proportions were averaged across the three crown sections to obtain a single time series of crown greening for each photographed tree.

### 2.2. Deriving phenological metrics from time-series data

A range of phenological metrics were derived to characterise the phenology of each individual tree. In addition to first budburst DOY and first leaf expansion DOY obtained from visual observation of the whole crown, full leafing was determined as the DOY when it was first observed that expanded leaves exceeded 95% (hereafter referred to as completion DOY). We then fitted each time series, obtained from both observational and photographic methods, using a logistic growth model to identify when expanded leaves/crown greening reached the half maximum (hereafter referred to as 50% DOY) and to characterise the rate of the process. For observational methods, time to 50% expanded leaves was then calculated as the number of days from first budburst to 50% DOY.

Logistic growth models have been widely used to characterise landscape and forest-level phenology from remote sensing data (Calders et al. 2015; Richardson et al. 2007; Zhang et al. 2003). Logistic growth uses non-linear regression to fit a sigmoidal curve, equation (3):

246 
$$y = \frac{\theta_1}{1 + \exp\left[-(\theta_2 + \theta_3 x)\right]}$$
247 (3)

where y is the response variable (proportion of expanded leaves/greening), x is the predictor variable (DOY), and  $\theta_1$ ,  $\theta_2$  and  $\theta_3$  are the model fitting parameters (Fox and Weisberg 2011).  $\theta_1$  is the upper asymptote. As the data were based on proportions,  $\theta_1$ 

251 was fixed at 1, as this was the maximum possible value. Two parameters are derived 252 from the model: the rate parameter  $(\theta_3)$  and the half-maximum  $(\psi)$ . The rate parameter 253 is based on the steepness of the curve at its mid-point and represented the proportional 254 increase per day. The half-maximum is a measure of timing, and represented the DOY 255 when expanded leaves/greening reached 50%, calculated as  $\psi = \theta_2/\theta_3$ , and hereafter 256 referred to as 50% DOY. Standard error and statistical significance of model parameter 257 estimates were assessed to provide a measure of confidence in the model fits for 258 individual trees. All logistic models were fitted using the car package and nls function in 259 R (Fox and Weisberg 2011). 260 Finally, we generated time-series to explore the effect of interval time between sampling 261 days (temporal grain) on 50% DOY and rate values from count and percentage estimate 262 data. The original data was collected every other day (two-day temporal grain), so 263 temporal grains of four-days and six-days were simulated by removing data for different 264 DOYs. Regardless of when leaf expansion began for each tree, the start date for 265 different temporal grains was held constant at DOY 107 for all time-series (which was 266 the DOY when leaf expansion was first observed across the monitored trees), as in 267 practise individual trees at a site would be monitored on the same days. Where the 268 DOY for  $crown_{MAX}$  was removed as a result of altering the temporal grain, we inserted 269 the maximum value on the next DOY when data collection would have been carried out. 270 We then re-ran the logistic growth model for each tree. 271 2.3. Statistical analyses 272 Linear regression was used to explore relatedness between first budburst DOY, first leaf 273 expansion DOY, 50% DOY and completion DOY, based on observational methods 274 (count and percentage estimates). To explore whether these different metrics (and 275 methods) identified different phenological patterns between species, separate one-way 276 analysis of variance (ANOVA) tests were carried out for each metric and method, 277 followed by pairwise comparisons of species using Tukey Honestly Significant 278 Difference (HSD) tests. One-way ANOVA and Tukey HSD tests were also used to 279 identify whether the time to leaf expansion (i.e., from first budburst to 50% DOY) 280 differed between species.

Linear regression was then used to explore relatedness between 50% DOY and rate

metrics from counts, percentage estimates and photographs. Where relationships were

281

identified, paired t-tests were conducted to assess whether the methods produced
different absolute values of 50% DOY and rate for individual trees. Finally, linear
regression and paired t-tests were used to compare 50% DOY and rate metrics derived
from the 2-day temporal grain, with those derived from 4-day and 6-day temporal grains.
All statistical analyses were carried out in R 3.3 (R Core Team, 2016).

288

289

290

291

### 3. Results

# 3.1. Comparison of phenological patterns from first event dates vs. time-series data

292 Species were different in terms of first budburst dates (Supplementary Material Table 1; 293 Fig. 1), with pairwise comparisons showing that ash budburst was significantly later than 294 oak (p = 0.003) and sycamore (p = 0.045), but the other species were not different (p = 0.045) 295 >0.05). There were significant differences between species in terms of first leaf 296 expansion and 50% DOY, and ash did not differ from other species (p > 0.05). 297 According to first leaf expansion dates, beech and oak were significantly different (p =298 0.027) as were sycamore and oak (p = 0.015), with oak leaf expansion beginning later 299 than the other two species. However, using the 50% DOY only oak and sycamore were 300 different, with oak leafing later than sycamore (p = 0.036). Using the completion DOY 301 metric, differences between species were only significant based on visual estimates of 302 percentage expanded leaves across the whole crown, with oak significantly later than 303 sycamore (p = 0.046), but the other species did not differ (p > 0.05). 304 As well as identifying differences between species, it is clear that there is considerable 305 variation within species (Fig. 1 and Fig. 2). Ash is the most variable in terms of first 306 budburst dates, with a 30-day difference in budburst timing from the earliest to the latest 307 individual (Fig. 1). Other species showed lower intra-species variation in budburst timing 308 (16–19 days). Both oak and ash were highly variable in terms of first leaf expansion 309 (varying by 22-28 days respectively). However, oaks were much more consistent in 310 terms of expanded leaves 50% DOY and completion DOY. Ash remained highly 311 variable throughout the whole process of leaf development, with ash trees being both 312 the earliest and latest to achieve full leaf expansion. Beech were fairly consistent in their 313 first budburst and leaf expansion dates, though variability increased as time progressed.

- 314 Sycamore were consistent in first budburst and completion of leaf expansion, but varied
- 315 considerably at the start of leaf expansion and in their 50% DOY.
- 316 There was a significant difference between oak and all three other species, in the time
- taken from first budburst to 50% DOY (Fig. 1), with oak taking significantly longer to
- 318 achieve leaf expansion than the other three species. However, no significant differences
- were found between species in the time taken from first leaf expansion to 50% DOY,
- indicated by the similar rates of leaf expansion. The relationship between all metrics of
- leaf expansion timing, including first leaf expansion dates, were strongly related (all  $R^2$  >
- 322 0.80, p < 0.001). The relationship between first budburst dates and leaf expansion
- 323 appears curved, and was poorly explained by a linear model (Fig. 3;  $R^2 = 0.40$ , p < 0.40
- 324 0.001 based on counts,  $R^2 = 0.42$ , p < 0.001 based on percentage estimates). This
- indicates that trees with later budburst tended to expand leaves more rapidly than trees
- 326 with earlier budburst.

### 3.2. Comparison of methods for obtaining time-series data

- 328 All time series data from count and percentage estimate methods could be fit to the
- 329 logistic model, obtaining model parameters with low standard error and high
- 330 significance, indicating good fits (Supplementary Material Tables 2 and 3). Count and
- percentage estimate methods were highly related in terms of the 50% DOY values
- derived from the logistic model fits ( $R^2 = 0.97$ , p< 0.001) and produced statistically
- 333 similar values for individual trees (Table 1). Both methods identified very similar
- phenological patterns across species based on 50% DOY and completion DOY (Fig. 1).
- 335 They also identified similar rates of leaf expansion between species, though the count
- 336 method showed higher variability of leaf expansion rate for beech and sycamore (Fig.
- 1). However, estimates of leaf expansion rate from the two methods were statistically
- 338 similar (Table 1).
- 339 Logistic models for the remaining eight time-series of Greenness Index values for whole
- crowns produced good fits with significant parameter estimates and low standard error
- 341 (Supplementary Material: Table 4). Statistical comparisons between counts and
- 342 photographs showed that 50% DOY values were related (Fig. 4,  $R^2 = 0.76$ , p < 0.001),
- and pairs of values were not statistically different (paired t-test:  $t_{19} = 0.10$ , p = 0.923).
- However, there was no relationship between the rate parameters from the two methods
- 345  $(R^2 = 0.01, p = 0.696)$ .

After removing every other observation from the time-series to simulate a four-day temporal grain, logistic models could be fitted to all forty time-series based on percentage estimate data, and to thirty-seven time-series based on count data (Supplementary Material: Tables 5 and 6). The three time-series that could not be fitted with the logistic model (one from beech and two from oak) had only three data points remaining after removal of every other observation, since leaf expansion occurred very rapidly in those individuals. Using the 4-day temporal grain, 50% DOY and rate values were highly similar to values obtained from the 2-day temporal grain, for both percentage estimate and count data (Table 1). A six-day temporal grain was tested, but ten logistic models based on count data failed to run due to there being only three data points remaining (Supplementary Material: Table 7). Using estimate data, the six-day temporal grain still produced model fits for all but one time-series, but two further time-series had non-significant parameter estimates (Supplementary Material: Table 8).

### 4. Discussion

The order in which species reached first budburst did not reflect the order in which they reached 50% or full leaf expansion. Oak was a particularly notable case in this study, taking on average twice as long to reach 50% leaf expansion after first budburst, compared to the other species. This appears to be due to a longer delay from first budburst to first leaf expansion, rather than a slower rate of leaf expansion, as there was no difference in leaf expansion rate between species. There was also intra-species variation in the time taken from first budburst to 50% DOY. The curved relationship between first budburst dates and 50% DOY was noticeable for all species, indicating a tendency for individuals with later budburst to leaf more rapidly than conspecific individuals with earlier budburst, as has been observed elsewhere (Cole and Sheldon 2017). Interestingly, the curvature is most pronounced in oak, which is the species that bursts bud earliest. Given that first budburst dates were a poor predictor of leaf expansion timing, we suggest that caution be exercised when interpreting first budburst dates, as they do not fully characterise the trajectory of canopy development, or necessarily signal the order in which tree canopies mature. While first leaf expansion dates show more similar patterns to 50% DOY, they still identify a different ordering of phenology between species, and show different patterns of intra-species variation. In order to predict

impacts of changing phenology on ecosystem processes and function, it is important to

capture the entire process of individual tree canopy development. Later stages of leaf expansion correspond more closely to remote sensing indices, so would better validate satellite data (Elmore et al. 2016; White et al. 2014). In addition, finer-scale detection of variation in leaf development timing between and within species will help to identify environmental cues and improve predictive models for biosphere-climate modelling (Richardson et al. 2012). In this study, there were no significant differences between species in terms of leaf expansion rate, but there was substantial intra-species variation. The majority of phenology studies focus on timing metrics, and the rate of a process is often ignored (Brown et al. 2017), missing important information on within-species variability. The degree of variation in leaf expansion rate within a species could have important implications for fitness and resilience in a population. For example, two trees sharing similar 50% DOYs could have very different leaf emergence timings, making one individual more vulnerable to spring frosts and herbivory damage, but potentially able to take better advantage of milder conditions if they occurred. In a variable spring environment, a range of different phenological responses within a population is a likely outcome, since each different response would have some selective advantages and disadvantages, depending on specific conditions at any one time, with no single response displacing all others. The balance between these responses is also likely to be modified by climate change. The opportunity to see this population-level plasticity is one reason why time-series data are preferable to event monitoring data. Considerable intraspecific variation was also observed in leaf expansion timing, in agreement with other studies that have monitored multiple individuals of a species at a single site (Capdevielle-Vargas et al. 2015; Cole and Sheldon 2017; Delpierre et al. 2017). The level of intraspecific variation differed between phenophases, further highlighting that snapshot assessments of tree phenology can be misleading. Interestingly, in this study there was no significant difference in leaf expansion timing between ash and sycamore, though ash is typically considered a late-leafing species while sycamore an early-leafing species (Morecroft et al. 2008; Roberts et al. 2015; Sparks and Carey 1995). The high variability among the ash trees in this study, if typical, could increase this species' resilience to climate change. The fact that such variability exists within species, confirms the value of methods that facilitate high levels of within-site and within-species replication. While ten individuals is the recommended minimum sample size by the USA-NPN (Denny et al. 2014), we recommend that larger

379

380

381

382

383

384

385

386

387

388

389

390

391

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

412 sample sizes be used initially where possible (Elmendorf et al. 2016) until suitable 413 minimum sample sizes for target species have been proposed based on their inherent 414 variability. 415 Even when the interval between observations was extended, the model still provided 416 very similar estimates of 50% DOY and rate. Our results suggest that for the relatively 417 short time series of individual trees, observations at 3–4 day intervals are sufficient to 418 describe phenological patterns in our study region. Less frequent observations could 419 limit the reliability of the phenological model, especially in warmer years where budburst 420 and leaf emergence could be more condensed. 421 We found that observing three relatively small sections of a tree gives comparable 422 results to whole tree crown estimates. This is promising, as three sections can be 423 assessed relatively quickly, and though more time consuming than a single estimate of 424 a tree crown, observer bias may be reduced by the increase in objectivity (Galloway et 425 al. 2006; Vittoz et al. 2010). However, the trees included in this study were relatively 426 small trees. The comparability between crown sections and whole crowns could 427 decrease as crown size increases, as a smaller proportion of the total crown is 428 assessed—though large trees pose problems for phenology monitoring generally, both 429 in terms of viewing buds in order to make counts, and in terms of making accurate 430 estimates (Fuccillo et al. 2015; Vittoz and Guisan 2007). Trials of count and estimate 431 methods are needed with citizen scientists, to determine levels of error associated with 432 both approaches, and the extent to which this varies with crown size, height and 433 species. 434 Ground-based photography offers potential to supplement data collection on individual 435 tree phenology, though several issues need to be considered. Firstly, in a forest 436 situation, the position from which photographs are taken must be carefully chosen. We 437 had to exclude many of our trees because of the influence of background foliage, 438 despite efforts to choose branch sections that would be unimpeded by surrounding 439 vegetation. Given the potential difficulty in selecting appropriate regions to photograph, 440 the use of fixed camera mounts (University of New Hampshire 2017; Smith and Ramsay 441 2018) might be necessary if this method was to be used with citizen scientists. This 442 would also ensure photos were taken of the same branch sections, and would allow 443 different surveyors to take images.

444 However, image processing costs must be carefully considered before use in a large 445 citizen science project, since the effort involved could be high. A crowd-sourcing 446 approach, where citizen scientists classify and analyse images online, has already been 447 used to validate plant phenology data from webcam images (Kosmala et al. 2016) and 448 to classify images of crown health in tropical rainforests (Zooniverse No date). Another 449 option is to take advantage of the rapidly developing technology in smartphone apps. 450 Tichý (2016) developed an app for calculating canopy cover (i.e., the vertical projection 451 of the tree canopy onto the ground surface) from canopy photos taken with a 452 smartphone or tablet. Image analysis algorithms are able to detect and eliminate poor 453 quality images (e.g., those with lens flare), and select appropriate thresholds for 454 separating canopy and sky pixels (Glatthorn and Beckschäfer 2014). An app for 455 estimating chlorophyll content of individual leaves can be used as a cost-effective 456 alternative to professional chlorophyll meters (Vesali et al. 2015), and carries out an 457 analysis similar to our greenness method. Such an approach could be extended to 458 assess greenness indices for plant canopies, using automatic algorithms to correct for 459 lighting variation (Brown et al. 2016), allowing citizen scientists to track the green-up of 460 the canopy in spring. 461 The greenness index data was comparable to visual observations in terms of 50% DOY 462 but not rate. Previous studies using fixed cameras on canopy towers, found greenness 463 to be closely related to leaf expansion, though in one study greenness identified earlier 464 50% DOY than visual observations (Mizunuma et al. 2011). Greenness is a function of 465 both leaf expansion and pigment changes, so while related, leaf expansion and 466 greenness are different (Keenan et al. 2014). This must be borne in mind when 467 interpreting data from different methods. Greenness indices are an additional gauge of 468 leaf development, and should be seen as complementary to leaf expansion data, rather 469 than a substitute for it.

### 5. Conclusions

470

471

472

473

474

475

476

Citizen science phenology monitoring has the potential to replicate high resolution data, to describe tree leaf phenology in relation to a range of environmental and genetic factors. However, time-series data to track the development of individual tree crowns is necessary. Reliance on first event dates can mislead on the order of leaf development among species, and does not provide a rate of leaf development. Fixed mount photography from the ground could be used to supplement data on canopy greening

477 currently collected through projects such as Phenocams. Low-cost digital cameras and 478 smartphone cameras are becoming increasingly advanced, which could enhance 479 prospects for obtaining reliable data on canopy greening. Nevertheless, visual 480 observations remain the most viable option for widespread data collection on individual 481 tree phenology at present. Further research is needed to assess volunteer accuracy 482 using counts and percentage estimates of expanded leaves, along with further 483 refinement of photographic approaches. 484

#### Acknowledgements 6.

485 The authors would like to thank Hayley Partridge for collecting the data used in this 486 study, and Nicola Steer for providing advice on the logistic growth model. This research 487 did not receive a grant from funding agencies in the public, commercial, or not-for-profit 488 sectors.

#### **7**. References

489

505

506

507

- 490 Ahl DE, Gower ST, Burrows SN, Shabanov NV, Myneni RB, Knyazikhin Y (2006) Monitoring spring 491 canopy phenology of a deciduous broadleaf forest using MODIS. Remote Sensing of 492 Environment 104 (1):88-95. doi:10.1016/j.rse.2006.05.003
- 493 Arend M, Gessler A, Schaub M (2016) The influence of the soil on spring and autumn phenology 494 in European beech. Tree Physiology 36 (1):78-85. doi:10.1093/treephys/tpv087
- 495 Basler D (2016) Evaluating phenological models for the prediction of leaf-out dates in six 496 temperate tree species across central Europe. Agricultural and Forest Meteorology 497 217:10-21. doi:10.1016/j.agrformet.2015.11.007
- 498 Bison M, Yoccoz NG, Carlson BZ, Delestrade A (2019) Comparison of budburst phenology trends 499 and precision among participants in a citizen science program. International Journal of 500 Biometeorology 63 (1):61-72. doi:10.1007/s00484-018-1636-x
- 501 Brown LA, Dash J, Ogutu BO, Richardson AD (2017) On the relationship between continuous 502 measures of canopy greenness derived using near-surface remote sensing and satellite-503 derived vegetation products. Agricultural and Forest Meteorology 247:280-292. 504 doi:10.1016/j.agrformet.2017.08.012
  - Brown TB, Hultine KR, Steltzer H, Denny EG, Denslow MW, Granados J, Henderson S, Moore D, Nagai S, SanClements M, Sánchez-Azofeifa A, Sonnentag O, Tazik D, Richardson AD (2016) Using phenocams to monitor our changing Earth: toward a global phenocam network. Frontiers in Ecology and the Environment 14 (2):84-93. doi:10.1002/fee.1222
- 509 Buitenwerf R, Rose L, Higgins SI (2015) Three decades of multi-dimensional change in global leaf 510 phenology. Nature Climate Change 5 (4):364-368. doi:doi:10.1038/nclimate2533
- 511 Calders K, Schenkels T, Bartholomeus H, Armston J, Verbesselt J, Herold M (2015) Monitoring 512 spring phenology with high temporal resolution terrestrial LiDAR measurements. 513 Agricultural and Forest Meteorology 203:158-168. doi:10.1016/j.agrformet.2015.01.009

514 515 516	Capdevielle-Vargas R, Estrella N, Menzel A (2015) Multiple-year assessment of phenological plasticity within a beech ( <i>Fagus sylvatica</i> L.) stand in southern Germany. Agricultural and Forest Meteorology 211-212:13-22. doi:10.1016/j.agrformet.2015.03.019
517 518 519	Chmielewski FM (No date) International Phenological Gardens in Europe. Humboldt-University of Berlin, Faculty of Agriculture and Horticulture, Institude of Crop Sciences, Subdividion of Agricultural Meteorology
520 521	Chmura DJ, Rozkowski R (2002) Variability of beech provenances in spring and autumn phenology. Silvae Genetica 51 (2-3):123-127
522 523 524	Chuine I (2010) Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B-Biological Sciences 365 (1555):3149-3160. doi:10.1098/rstb.2010.0142
525 526 527	Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22 (7):357-365. doi:10.1016/j.tree.2007.04.003
528 529 530	Cole EF, Sheldon BC (2017) The shifting phenological landscape: Within- and between-species variation in leaf emergence in a mixed-deciduous woodland. Ecol Evol 7 (4):1135-1147. doi:10.1002/ece3.2718
531 532 533	Collinson N, Sparks T (2008) Phenology—Nature's Calendar: an overview of results from the UK Phenology Network. Arboricultural Journal 30 (4):271-278. doi:10.1080/03071375.2008.9747506
534 535 536	Crabbe RA, Dash J, Rodriguez-Galiano VF, Janous D, Pavelka M, Marek MV (2016) Extreme warm temperatures alter forest phenology and productivity in Europe. Science of the Total Environment 563:486-495. doi:10.1016/j.scitotenv.2016.04.124
537 538 539	Delpierre N, Guillemot J, Dufrene E, Cecchini S, Nicolas M (2017) Tree phenological ranks repeat from year to year and correlate with growth in temperate deciduous forests.  Agricultural and Forest Meteorology 234:1-10. doi:10.1016/j.agrformet.2016.12.008
540 541 542 543 544	Denny EG, Gerst KL, Miller-Rushing AJ, Tierney GL, Crimmins TM, Enquist CAF, Guertin P, Rosemartin AH, Schwartz MD, Thomas KA, Weltzin JF (2014) Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. International Journal of Biometeorology 58 (4):591-601. doi:10.1007/s00484-014-0789-5
545 546 547 548	Elmendorf SC, Jones KD, Cook BI, Diez JM, Enquist CAF, Hufft RA, Jones MO, Mazer SJ, Miller-Rushing AJ, Moore DJP, Schwartz MD, Weltzin JF (2016) The plant phenology monitoring design for The National Ecological Observatory Network. Ecosphere 7 (4). doi:10.1002/ecs2.1303
549 550 551	Elmore AJ, Stylinski CD, Pradhan K (2016) Synergistic use of citizen science and remote sensing for continental-scale measurements of forest tree phenology. Remote Sensing 8 (6). doi:10.3390/rs8060502
552 553 554	Feldman RE, Žemaitė I, Miller-Rushing AJ (2018) How training citizen scientists affects the accuracy and precision of phenological data. International Journal of Biometeorology 62 (8):1421-1435. doi:10.1007/s00484-018-1540-4

555 556 557	Finn GA, Straszewski AE, Peterson V (2007) A general growth stage key for describing trees and woody plants. Annals of Applied Biology 151 (1):127-131. doi:10.1111/j.1744-7348.2007.00159.x			
558 559 560	Fisher JI, Mustard JF, Vadeboncoeur MA (2006) Green leaf phenology at Landsat resolution: Scaling from the field to the satellite. Remote Sensing of Environment 100 (2):265-279. doi:10.1016/j.rse.2005.10.022			
561 562	Fox J, Weisberg S (2011) Nonlinear Regression and Nonlinear Least Squares in R. An R Companion to Applied Regression, 2nd edn. SAGE, Thousand Oaks, CA			
563 564 565 566	Fu YH, Zhao HF, Piao SL, Peaucelle M, Peng SS, Zhou GY, Ciais P, Huang MT, Menzel A, Uelas JP, Song Y, Vitasse Y, Zeng ZZ, Janssens IA (2015) Declining global warming effects on the phenology of spring leaf unfolding. Nature 526 (7571):104-107. doi:10.1038/nature15402			
567 568 569	Fuccillo KK, Crimmins TM, de Rivera CE, Elder TS (2015) Assessing accuracy in citizen science-based plant phenology monitoring. International Journal of Biometeorology 59 (7):917-926. doi:10.1007/s00484-014-0892-7			
570 571 572	Galloway AWE, Tudor MT, Vander Haegen WM (2006) The reliability of citizen science: A case study of Oregon white oak stand surveys. Wildlife Society Bulletin 34 (5):1425-1429. doi:10.2193/0091-7648(2006)34[1425:trocsa]2.0.co;2			
573 574 575	Glatthorn J, Beckschäfer P (2014) Standardizing the Protocol for Hemispherical Photographs: Accuracy Assessment of Binarization Algorithms. PLOS ONE 9 (11):e111924. doi:10.1371/journal.pone.0111924			
576 577	Hamunyela E, Verbesselt J, Roerink G, Herold M (2013) Trends in spring phenology of Western European deciduous forests. Remote Sensing 5 (12):6159			
578 579 580 581	Inoue T, Nagai S, Saitoh TM, Muraoka H, Nasahara MN, Koizumi H (2014) Detection of the different characteristics of year-to-year variation in foliage phenology among deciduous broad-leaved tree species by using daily continuous canopy surface images. Ecological Informatics 22:58-68. doi:10.1016/j.ecoinf.2014.05.009			
582 583 584 585	Keenan TF, Darby B, Felts E, Sonnentag O, Friedl MA, Hufkens K, O'Keefe J, Klosterman S, Munger JW, Toomey M, Richardson AD (2014) Tracking forest phenology and seasonal physiology using digital repeat photography: a critical assessment. Ecological Applications 24 (6):1478-1489			
586 587 588	Kosmala M, Crall A, Cheng R, Hufkens K, Henderson S, Richardson AD (2016) Season Spotter: Using Citizen Science to Validate and Scale Plant Phenology from Near-Surface Remote Sensing. Remote Sensing 8 (9):726. doi:10.3390/rs8090726			
589 590 591	Lapenis AG, Lawrence GB, Buyantuev A, Jiang SG, Sullivan TJ, McDonnell TC, Bailey S (2017) A newly identified role of the deciduous forest floor in the timing of green-up. Journal of Geophysical Research-Biogeosciences 122 (11):2876-2891. doi:10.1002/2017jg004073			
592 593 594	Melaas EK, Sulla-Menashe D, Friedl MA (2018) Multidecadal Changes and Interannual Variation in Springtime Phenology of North American Temperate and Boreal Deciduous Forests. Geophysical Research Letters 45 (6):2679-2687. doi:10.1002/2017gl076933			
595	Menzel A, Fabian P (1999) Growing season extended in Europe. Nature 397 (6721):659-659			

596 597 598 599 600 601	Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kubler K, Bissolli P, Braslavska O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl A, Defila C, Donnelly A, Filella Y, Jatcza K, Mage F, Mestre A, Nordli O, Penuelas J, Pirinen P, Remisova V, Scheifinger H, Striz M, Susnik A, Van Vliet AJH, Wielgolaski FE, Zach S, Zust A (2006) European phenological response to climate change matches the warming pattern. Global Change Biology 12 (10):1969-1976. doi:10.1111/j.1365-2486.2006.01193.x		
602 603 604	Miller-Rushing AJ, Inouye DW, Primack RB (2008) How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. Journal of Ecology 96 (6):1289-1296. doi:10.1111/j.1365-2745.2008.01436.x		
605 606 607 608	comparison of several colour indices for the photographic recording of canopy phenology of <i>Fagus crenata</i> Blume in eastern Japan. Plant Ecology and Diversity 4		
609 610 611 612	Morecroft MD, Stokes VJ, Taylor ME, Morison JIL (2008) Effects of climate and management history on the distribution and growth of sycamore (Acer pseudoplatanus L.) in a southern British woodland in comparison to native competitors. Forestry 81 (1):59-74. doi:10.1093/forestry/cpm045		
613 614	Morrison LW (2016) Observer error in vegetation surveys: a review. Journal of Plant Ecology 9 (4):367-379. doi:10.1093/jpe/rtv077		
615 616	Nature's Calendar (2017) <a href="http://naturescalendar.woodlandtrust.org.uk">http://naturescalendar.woodlandtrust.org.uk</a> Accessed December 11, 2017		
617 618	NatureWatch Canada (2017) Plantwatch, University of Ottawa, Canada. <a href="http://www.naturewatch.ca">http://www.naturewatch.ca</a> . Accessed December 11, 2017		
619 620 621	Polgar C, Gallinat A, Primack RB (2014) Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau's Concord. New Phytologist 202 (1):106-115. doi:10.1111/nph.12647		
622 623	Polgar CA, Primack RB (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. New Phytologist 191 (4):926-941. doi:10.1111/j.1469-8137.2011.03803.x		
624 625 626	Primack RB, Miller-Rushing AJ (2012) Uncovering, collecting, and analyzing records to investigate the ecological impacts of climate change: A template from Thoreau's Concord. Bioscience 62 (2):170-181. doi:10.1525/bio.2012.62.2.10		
627 628 629	Project Budburst (2017) Project BudBurst: An online database of plant phenological observations. Boulder, Colorado. <a href="http://www.budburst.org">http://www.budburst.org</a> . Accessed December 11, 2017		
630 631	R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria		
632 633 634	Richardson A, O'Keefe J (2009) Phenological differences between understory and overstory: a case study using the long-term Harvard forest records. In: Noormets A (ed) Phenology of ecosystem processes. Springer Science, Dordrecht, the Netherlands, pp 87–117		
635 636 637	Richardson AD, Anderson RS, Arain MA, Barr AG, Bohrer G, Chen G, Chen JM, Ciais P, Davis KJ, Desai AR, Dietze MC, Dragoni D, Garrity SR, Gough CM, Grant R, Hollinger DY, Margolis HA, McCaughey H, Migliavacca M, Monson RK, Munger JW, Poulter B, Raczka BM,		

638 639 640 641	Ricciuto DM, Sahoo AK, Schaefer K, Tian H, Vargas R, Verbeeck H, Xiao J, Xue Y (2012) Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site Synthesis. Global Change Biology 18 (2):566-584. doi:10.1111/j.1365-2486.2011.02562.x
642 643 644	Richardson AD, Bailey AS, Denny EG, Martin CW, O'Keefe J (2006) Phenology of a northern hardwood forest canopy. Global Change Biology 12 (7):1174-1188. doi:10.1111/j.1365-2486.2006.01164.x
645 646 647	Richardson AD, Jenkins JP, Braswell BH, Hollinger DY, Ollinger SV, Smith M-L (2007) Use of digital webcam images to track spring green-up in a deciduous broadleaf forest.  Oecologia 152 (2):323-334. doi:10.1007/s00442-006-0657-z
648 649 650	Roberts AMI, Tansey C, Smithers RJ, Phillimore AB (2015) Predicting a change in the order of spring phenology in temperate forests. Global Change Biology 21 (7):2603-2611. doi:10.1111/gcb.12896
651 652	Rueden C, Dietz, C., Horn, M., Schindelin, J., Northan, B., Berthold, M., Eliceiri, K. (2016) ImageJ Ops [Software]. <a href="http://imagej.net/Ops">http://imagej.net/Ops</a> .
653 654	Schaber J, Badeck FW (2005) Plant phenology in Germany over the 20th century. Regional Environmental Change 5 (1):37-46. doi:10.1007/s10113-004-0094-7
655 656 657	Smith AM, Ramsay PM (2018) A comparison of ground-based methods for estimating canopy closure for use in phenology research. Agricultural and Forest Meteorology 252:18-26. doi:https://doi.org/10.1016/j.agrformet.2018.01.002
658 659 660 661 662 663	Soudani K, Hmimina G, Delpierre N, Pontailler JY, Aubinet M, Bonal D, Caquet B, de Grandcourt A, Burban B, Flechard C, Guyon D, Granier A, Gross P, Heinesh B, Longdoz B, Loustau D, Moureaux C, Ourcival JM, Rambal S, Saint Andre L, Dufrêne E (2012) Ground-based network of NDVI measurements for tracking temporal dynamics of canopy structure and vegetation phenology in different biomes. Remote Sensing of Environment 123:234-245. doi:10.1016/j.rse.2012.03.012
664 665 666	Sparks TH, Carey PD (1995) The responses of species to climate over two centuries - an analysis of the Marsham phenological record, 1736-1947. Journal of Ecology 83 (2):321-329. doi:10.2307/2261570
667 668 669 670 671 672	Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock TIM, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16 (12):3304-3313. doi:10.1111/j.1365-2486.2010.02165.x
673 674	Tichý L (2016) Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. Journal of Vegetation Science 27 (2):427-435. doi:10.1111/jvs.12350
675 676	University of New Hampshire (2017) Picture Post. <a href="https://picturepost.unh.edu/index.jsp">https://picturepost.unh.edu/index.jsp</a> .  Accessed December 18, 2017
677 678 679	Vander Mijnsbrugge K, Janssens A (2019) Differentiation and non-linear responses in temporal phenotypic plasticity of seasonal phenophases in a common garden of <i>Crataegus monogyna</i> Jacq. Forests 10 (4):293

680 681 682	Vesali F, Omid M, Kaleita A, Mobli H (2015) Development of an android app to estimate chlorophyll content of corn leaves based on contact imaging. Computers and Electronics in Agriculture 116:211-220. doi:10.1016/j.compag.2015.06.012
683 684 685 686	Vitasse Y, Delzon S, Bresson CC, Michalet R, Kremer A (2009b) Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Canadian Journal of Forest Research 39 (7):1259-1269. doi:10.1139/X09-054
687 688 689 690	Vitasse Y, Porte AJ, 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
691 692 693 694	Vittoz P, Bayfield N, Brooker R, Elston DA, Duff El, Theurillat JP, Guisan A (2010) Reproducibility of species lists, visual cover estimates and frequency methods for recording highmountain vegetation. Journal of Vegetation Science 21 (6):1035-1047. doi:10.1111/j.1654-1103.2010.01216.x
695 696 697	Vittoz P, Guisan A (2007) How reliable is the monitoring of permanent vegetation plots? A test with multiple observers. Journal of Vegetation Science 18 (3):413-422. doi:10.1658/1100-9233(2007)18[413:hritmo]2.0.co;2
698 699 700	Wang S, Yang B, Yang Q, Lu L, Wang X, Peng Y (2016) Temporal Trends and Spatial Variability of Vegetation Phenology over the Northern Hemisphere during 1982-2012. PLOS ONE 11 (6):e0157134. doi:10.1371/journal.pone.0157134
701 702 703	Wesolowski T, Rowinski P (2006) Timing of bud burst and tree-leaf development in a multispecies temperate forest. Forest Ecology and Management 237 (1-3):387-393. doi:10.1016/j.foreco.2006.09.061
704 705 706	White K, Pontius J, Schaberg P (2014) Remote sensing of spring phenology in northeastern forests: A comparison of methods, field metrics and sources of uncertainty. Remote Sensing of Environment 148:97-107. doi:10.1016/j.rse.2014.03.017
707 708 709	Wu X, Liu H (2013) Consistent shifts in spring vegetation green-up date across temperate biomes in China, 1982–2006. Global Change Biology 19 (3):870-880. doi:10.1111/gcb.12086
710 711 712	Zhang X, Friedl MA, Schaaf CB, Strahler AH, Hodges JCF, Gao F, Reed BC, Huete A (2003) Monitoring vegetation phenology using MODIS. Remote Sensing of Environment 84 (3):471-475. doi:10.1016/S0034-4257(02)00135-9
713 714 715	Zooniverse (No date) Amazon Aerobotany. <a href="https://www.zooniverse.org/projects/rainforestexpeditions/amazon-aerobotany">https://www.zooniverse.org/projects/rainforestexpeditions/amazon-aerobotany</a> .  Accessed 31 March 2018

### **Table**

			Relationship between methods (regression)		Difference in absolute values between methods (paired t-test)		
Method comparison	Metric	R <sup>2</sup>	p	df	t	p	
	50% DOY	0.97	<0.001	39	0.083	0.935	
Counts vs Whole crown percentage estimates	Completion of LE	0.96	<0.001	39	2.811	0.008	
	Rate of LE	0.55	<0.001	39	0.609	0.546	
4-day v 2-day temporal grain	50% DOY	0.99	<0.001	36	1.320	0.195	
(Counts)	Rate of LE	0.88	<0.001	36	-0.921	0.363	
2-day v 4-day observation frequency	50% DOY	0.99	<0.001	39	0.073	0.942	
(Whole crown percentage estimates)	Rate of LE	0.89	<0.001	39	-1.787	0.082	

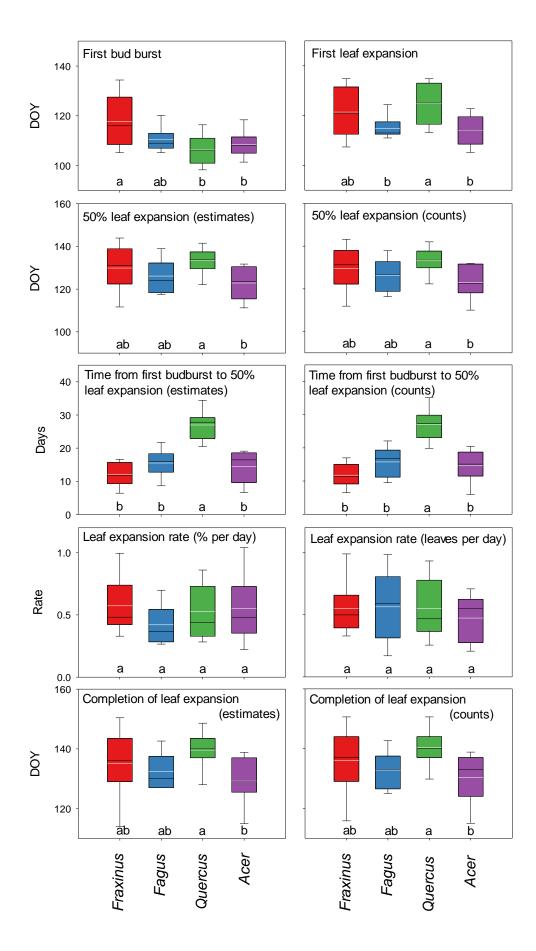
Table 1: Comparison of methods for deriving time-series data on tree leaf development. The relationship between methods is explored with regressions: whether the first variable can be used as a predictor for the second variable. The proportion of variation explained ( $R^2$ ) and statistical significance (p) is shown. Where significant relationships existed, paired t-tests were carried out to assess whether the two methods produced different absolute values (significant p-values in bold).

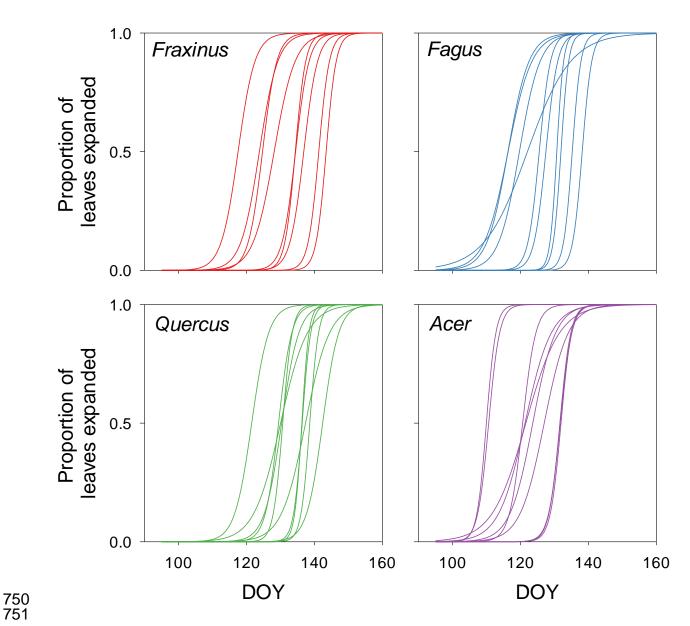
724	<b>Figures</b>

- 725 Fig. 1. Comparison of phenological patterns for four tree species, derived from different
- metrics and methods: first budburst dates; first leaf expansion dates; 50% DOY (from
- 727 percentage estimates); 50% DOY (from counts); time from first budburst to 50% DOY
- 728 (from percentage estimates); time from first budburst to 50% DOY (from counts); leaf
- expansion rate (as percentage estimates per day); leaf expansion rate (as number of
- 730 leaves per day); completion DOY (from percentage estimates); completion DOY (from
- 731 counts). On the box and whisker plots, the horizontal black line shows the median, the
- red line is the mean, the box represents values within the 25–75% guartiles, and the
- 733 whiskers show the 10% and 90% percentiles. In each panel, species sharing the same
- 734 letter above the x-axis were not statistically different.
- 735 **Fig. 2.** Logistic growth models showing model fits for 10 individual trees in each species
- 736 category, based on count data.
- 737 Fig. 3. Relationship between first budburst dates and 50% DOY for the four tree
- species; a = 50% DOY from percentage estimate data; b = 50% DOY from count data.
- For each species, a second-order polynomial fit ( $R^2 = 0.64-0.93$ , p>0.05) shows a
- 740 curved relationship.

- 741 Fig. 4. Comparison of 50% DOY values from visual counts of leaf expansion on tree
- sections and 50% DOY values from photo-derived greenness index on tree sections.
- 743 Data are from counts and photos of eight different trees (each a combined value from
- three different sections of the canopy). The line of best fit is shown.

746 Fig. 1





752 Fig. 3

