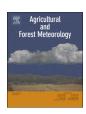
ELSEVIER

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet



Estimating tree phenology from high frequency tree movement data





^b Department of Plant Biology, University of Vermont, Burlington, VT, USA

^c Department of Electrical and Computer Engineering, University of Iowa, Iowa City, IA, USA



Keywords:
Bud flush
Citizen science
Forests
Phenotyping
Populus balsamifera
Tree phenology

ABSTRACT

Shifts in forest tree phenology are one of the most important and conspicuous plant responses to climate variability. However, systematically documenting changes in phenology of individual trees across large areas at high temporal frequency is often prohibitively labor- and resource-intensive. Here we present a new method that uses accelerometers to overcome challenges of measuring high-frequency tree phenology in the field. Accelerometers are small, portable devices that can be attached to trees to record movement due to forcing by wind. Time series analyses of tree movement data recorded by accelerometers can yield an approximation of tree mass. Because leaf emergence and leaf drop alter aboveground tree mass, these phenological events are expected to be detectable from accelerometer data. To test how well accelerometers can be used to measure phenological dates, we deployed 20 accelerometers on balsam poplar (Populus balsamifera) trees across a variety of sites during the 2016 growing season and assessed how well phenology derived from accelerometers matched visual observation of phenology recorded by citizen scientists. We found that accelerometer measurements fit the theoretical expectation for the seasonal change in tree mass associated with leaf phenology; specifically, an increase in tree mass in the spring, and a decline in the autumn. Furthermore, we found that accelerometerderived phenology matched visual observations for leaf emergence, with a strong correlation between the dates of first observed full leaves and accelerometer-derived phenology (r = 0.82, p < 0.01). Estimates of leaf drop from accelerometers and visual observations, however, were not significantly correlated (r = 0.16, p = 0.69). Our work shows that accelerometers can reliably be used to detect spring phenology of forest trees, and have the potential to overcome some of the challenges related to documenting spring tree phenology at high spatial and temporal resolution in the field.

1. Introduction

Changes in plant phenology, the timing of periodic life-cycle events, are among the most prominent biological signals of climate change (Parmesan and Yohe, 2003). Temperate forests in particular have exhibited extreme sensitivity to climate variability, with the timing of spring onset fluctuating from days to weeks on an inter-annual basis in response to recent warming (Schwartz et al., 2006). Because forest phenology mediates interactions between climate and the biosphere (Fitzjarrald et al., 2001; Peñuelas et al., 2009), it plays an important role in ecosystem processes such as carbon and nutrient cycling (Elmore et al., 2016a; Richardson et al., 2009), and can be diagnostic of ecosystem responses to climate change. Phenology is also known to be genetically variable, with many species showing strong heritability and quantitative genetic differentiation for vegetative phenology among

locally adapted populations (Keller et al., 2011; Savolainen et al., 2007). At the scale of individual plants, phenology has been shown to influence fitness and reproductive success (Ehrlén and Münzbergová, 2009; Inouye, 2008), thereby playing a role in limiting species distributions (Chuine, 2010). Ultimately, changes in phenology can have far-reaching consequences, from exposing individuals to detrimental abiotic conditions and disrupting species interactions (Visser et al., 2006) to altering the carbon cycle and even global climate itself.

While forest phenology undisputedly responds to climate variability, our understanding of phenology has been limited by the ability to document phenological processes that operate across spatial and temporal scales that span orders of magnitude—from individuals to biomes and from days to seasons. Repeated visits to individual plants by observers recording phenophases through direct visual observations are one means of monitoring phenology (e.g., Jeffree, 1960; Sparks and

E-mail address: agougherty@umces.edu (A.V. Gougherty).

^{*} Corresponding author.

Carey, 1995). While direct observations have improved our understanding of how organisms in particular locations have responded to climate over time, high frequency monitoring is often too labor- and resource-intensive to be implemented systematically across geographically widespread field sites. While other approaches have been developed to monitor forest phenology over larger spatial areas, including via satellites, near-surface web cameras (Richardson et al., 2007), and publicly available traffic cameras (Graham et al., 2010), there is often a trade-off between spatial-temporal coverage and resolution among these systems. Satellite-derived phenology, for instance, can provide broad spatial coverage, but has limited utility in discerning the phenology of individual plants. In short, methods that overcome the challenge of spatial coverage are often too coarse-grained to quantify phenology of individual plants (Polgar and Primack, 2011), except when phenology of individual plants correlates with surface phenology of forests (Elmore et al., 2016b).

Another approach to monitoring phenology of individual trees is with on-tree sensors. Recent work has shown the utility of a variety of on-tree sensors to estimate phenology, including light emitting/detecting sensors focused on individual leaf buds (Kleinknecht et al., 2015) and sensors that measure changes in light transmitted through the tree canopy during the growing season (Schwartz et al., 2013). Other studies have explored the idea that phenological events, such as leaf emergence and leaf drop, will affect aboveground tree mass, which in turn will alter patterns of acceleration when the tree is subjected to forcing (e.g., by wind) (Selker et al., 2011; H. Lintz, unpublished). These studies show that accelerometers – a sensor that detects changes in tree acceleration related to changes in mass - can be used to detect changes in tree mass before and after leaf emergence and may offer a way to detect phenological dates without relying on intensive ground observations. However, it remains uncertain if accelerometers can be used to detect the actual dates of phenological events, and how well accelerometer-derived phenology compares to direct human observations.

Here we present and validate the use of on-tree accelerometers to derive high temporal resolution measurements of individual tree phenology. With the help of citizen scientists, we deployed accelerometers over an entire growing season, in order to: (i) determine if accelerometers can be used to derive a season-length phenological signal and (ii) compare accelerometer-derived phenology with visual observations made by citizen scientists. We demonstrate that accelerometers represent a promising way of measuring the dates of phenological events, and possibly other biological processes, of individual trees.

2. Materials and methods

2.1. Study species

We focused on the phenology of balsam poplar (*Populus balsamifera* L.), a northern broad-leaf tree species, distributed throughout much of Canada and the northern United States (*Zasada and Phipps*, 1990). Poplars are a model system for understanding the genetic and physiological basis of climate adaptation in trees (*Soolanayakanahally et al.*, 2009), and previous studies have shown that both spring and autumn vegetative phenology in *Populus* has a genetic basis and is adapted to local climate conditions (*Keller et al.*, 2012, 2011; *Soolanayakanahally et al.*, 2013). High resolution field phenology data may be particularly useful to research in model systems such as *Populus*, and other well-studied tree species, seeking to understand the relationship between phenology, climate, and genetics.

2.2. Principles of accelerometer operation

Accelerometers detect movement by measuring acceleration in three dimensions and, when attached to a tree, detect movement caused by wind or other forces (Selker et al., 2011). When forced by wind, a

tree will vibrate at a particular frequency, similar to how a bell vibrates at its resonant frequency when struck. The resonant frequency of a tree, when treated simply as a mass spring with damping, is inversely related to its mass:

$$f_0 \propto \sqrt{\frac{k}{mb}} \Rightarrow T_0 \propto \sqrt{\frac{mb}{k}}$$
 (1)

where f_0 is the dominant resonant frequency, T_0 is the corresponding period, k is stiffness, m is mass, and b models the effect of damping. As Eq. (1) shows, changes in mass will have a direct effect on tree resonant period (T_0) . In the context of phenology, when leaves emerge, the aboveground mass of the tree will increase, causing the resonant period to increase, while the opposite will occur during leaf drop (i.e., a decrease in mass, and a decrease in the resonant period). Because the dominant resonant period/frequency can be estimated from an acceleration signal, it is possible to derive a phenology signal from accelerometer data. It is worth emphasizing that there is no need to estimate the actual mass of the tree over the growing season to document phenology, as only the relative percent change in mass, approximated by a changing dominant period, is needed. Hence, our use of dominant period should be interpreted as a proxy measure, proportional to the percent change in tree mass, and this change in dominant period should be associated with phenological shifts such as leaf out, leaf drop, and other large-scale influences on tree mass.

It is important to note that the change in dominant period is affected by additional factors, such as changes in stiffness (e.g., by the growth and hardening of xylem, or hydraulic conductance of stem water) and damping (e.g., altering air resistance by growing or losing leaves). We consider these changes to be of secondary importance relative to the change in mass associated with leaf emergence, though potentially interesting topics for follow-up study. Furthermore, we note that a portion of the mass in newly expanding leaves is already present in trees before leaf emergence (before leaves become autonomous from stored carbon) in the form of non-structural carbohydrates (Hoch et al., 2003). Hence, a change in tree mass during leaf emergence and expansion is likely due to a combination of new leaf material and new water mass in the leaves and woody tissue. Partitioning the sources of mass increase would be an interesting topic for future study.

In this study, we used Oregon Research Electronics (Tangent, OR, USA) AL100 Acceleration Loggers (Fig. 1). The AL100 devices use STMicro LIS3DSH MEMS accelerometers with supporting electronics. AL100 loggers operate on one or two C cell batteries and record daily (24-h) data files to a microSD card inside the unit, which can be uploaded to a computer for processing. The AL100 devices incorporate a real-time, temperature-compensated clock that provides time-stamps for the recorded data. The electronics are enclosed in a robust weather-resistant plastic case that can be attached to trees around the primary trunk using rope or zip ties. These devices are the same as those used in van Emmerik et al. (2017).

2.3. Citizen scientists & accelerometer deployment

To validate accelerometer-derived phenology with direct estimates of tree leaf out and leaf drop, we partnered with citizen scientists to monitor phenology of individual poplar trees across our study region. Observational data (including phenology) from trained volunteers is particularly useful when sampling is required across a broad geographic area and established and reliable protocols are employed to yield high-quality data (e.g., Bonney et al., 2014). Such an approach has recently been shown in *Populus* to correlate well with phenological estimates at larger spatial scales estimated from satellite remote sensing data (Elmore et al., 2016b; Vanbeveren et al., 2016). In the present study, we trained eight citizen scientists to deploy accelerometers and record phenological observations during the 2016 growing season. This diverse group consisted of adults with various experiences monitoring



Fig. 1. Accelerometer attached to a balsam poplar (Populus balsamifera) tree.

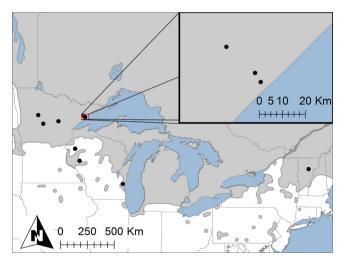


Fig. 2. Location of accelerometers (black points) deployed on balsam poplar trees and monitored for visual observations of phenology by citizen scientists. Gray shading indicate balsam poplar's geographic range (Little, 1971).

phenology through other volunteer programs. Our training workshop was held at the University of Vermont in October 2015, where volunteers learned to identify the species of interest, monitor tree phenology using a standardized protocol, and deploy accelerometers on native balsam poplar trees near their home locales. Four volunteers were located in Minnesota, three in Wisconsin, and one in Vermont (Fig. 2).

Citizen scientists selected focal trees based on the following characteristics: (i) near their location for ease of obtaining frequent direct phenology observations, (ii) diameter at breast height (dbh) of less than approximately 30.5 cm to standardize the effects of tree girth on measurements, and (iii) direct exposure of the tree to wind and/or proximity to the forest edge to ensure a strong acceleration signal. Each volunteer received two accelerometers (one volunteer was given three sets of two accelerometers, see extent box in Fig. 2) to be placed at different heights on the same tree. We instructed volunteers to attach one accelerometer at approximately eye level and the other at

approximately 1 m above the ground to determine if placement height affected the phenology signal. While accelerometers will likely perform best when attached to trees where wind displacement is greatest (i.e., high in the tree; van Emmerik et al., 2017), eye level was chosen because AL100 loggers have a coded light system which can be used to check that the loggers are functioning properly and recording data. Volunteers deployed accelerometers in February or March of 2016, and removed them at the end of the growing season, several weeks after leaf drop. Prior to deployment, accelerometers were set to record measurements continuously at a frequency of 10 Hz along all three spatial dimensions. Data collection at this frequency will yield approximately 864,000 samples/day (10 samples/s \times 60 s/min \times 60 min/h \times 24 h/ day) per axis dimension (Fig. A1). Citizen scientists used protocols developed by the National Phenology Network (https://www.usanpn. org/) to record phenological observations at least twice weekly during leaf emergence and leaf drop, and approximately weekly during the remainder of the growing season.

2.4. Data processing, outlier removal, and phenology model fitting

Transforming raw accelerometer data to phenological estimates proceeded in three main steps: (1) processing the raw daily acceleration data to derive the spectral density and identify the dominant period for each day; (2) outlier removal; and (3) fitting a phenology model to the cleaned data to estimate the dates of spring and autumn onset. We detail each of these steps below.

We used an autoregressive (AR) modelling approach to determine the spectral density and dominant period along each spatial dimension, for each 24-h data file. We tested other approaches to derive the spectral density (e.g., Welch's method; Welch, 1967) and found they were consistent with the AR approach. We chose the AR method as it tended to create smooth periodograms, which facilitated identifying the dominant frequency/period. To calculate the dominant period, we first fit an autoregressive model to the detrended daily acceleration series for each axis individually. The order of the autoregressive model was selected by minimizing AIC, using orders between 1 and an upper threshold of 10*log₁₀(N) (where N is the total number of observations in the daily series, set internally by the 'ar' function in the stats package in R). For our data, this yielded a typical range of autoregressive orders of 1 to ~60. The model that minimized AIC was then used to estimate the spectral density using the 'spec.ar' function in the stats package (R Core Team, 2017), and peaks in the periodograms were identified using the 'findpeaks' function in the pracma package (Borchers, 2017). Next, we identified the frequency with the highest density and calculated the dominant period as 1/f. We calculated the difference between the spectral density of the dominant and second-most dominant period (spectra_{dominant} - spectra_{2nd dominant}/spectra_{dominant}), and used this metric as a weight when fitting the phenology models described below (i.e., a greater weight was placed on dominant period values that had a spectral density much higher than the second most dominant period). We repeated this process for each 24-h data file and for each spatial axis. Dominant period values were assigned the day-of-year that the 24h data file was created.

Before fitting the phenology model, we removed outlying dominant period values, as outliers were found to strongly affect the parameter estimates and fit of the phenology model used in subsequent analyses. To remove outliers, we fit all dominant period values with a LOESS (locally weighted regression; Cleveland and Devlin, 1988) curve with a 'symmetric' option, with points weighted by the squared difference in spectra between the dominant and second-most dominant periods (described above). The 'symmetric' option further reduces the influence of outlying data when fitting the curve, compared to a least-squares approach. Next, we calculated the interquartile range of the residuals from the LOESS curve and determined which data points had residuals beyond $1.5\times$ the interquartile range. Any data points with residuals that exceeded this threshold were removed. This approach is similar to

identifying outliers using a Tukey box-and-whisker plot.

After removing outliers, we fit a seven parameter phenology model (described in Elmore et al. (2012)) to the dominant period values for each accelerometer. The model is a dual-logistic curve with an additional parameter that controls the slope of the line between the spring and autumn logistic curves. The model is given as follows:

$$T_0 = m_1 + (m_2 - m_7 \cdot t) \cdot \left(\frac{1}{1 + e^{(m_3 - t)/m_4}} - \frac{1}{1 + e^{(m_5 - t)/m_6}}\right)$$
 (2)

where T_0 is the dominant period, t is the day of year, m_1 is the dominant period during the winter, m_2 is the difference between the summer and winter dominant period, m_3 and m_4 affect the shape of the spring logistic curve, m_5 and m_6 affect the shape of the autumn logistic curve, and m_7 controls the slope of the curve during the summer. We fit model parameters using an iterative non-linear least-squares algorithm, requiring an initial estimation of parameter values. Initial starting parameters were estimated by visually inspecting the plots of dominant period over time. The starting parameters were chosen as [23, 26, 148, 6, 200, 3, 1] for parameters m_1 through m_2 , respectively, for all models. Using this set of starting parameters, only one model for an accelerometer with an apparent phenological signal failed to converge. To attain convergence for this unit, we changed the starting values of the parameters to the fitted estimates for the complementary accelerometer mounted on the same tree. Additionally, two accelerometers malfunctioned early in the season and therefore recorded only spring phenology. For these accelerometers, the data were fit with only the spring portion of the phenology model. As with the LOESS curve, the squared difference between the spectra of the dominant and second dominant periods was used as weights in the phenology models. We provide code to conduct the analyses above, as well as example data, in an R package hosted at https://github.com/agougher/accel.

2.5. Statistical analyses

We assessed how well visual phenological observations from citizen scientists related to modeled phenology from the accelerometers using correlation analyses and major axis (MA) regression. For spring phenology, we assessed the relationship between the date volunteers first observed unfolded leaves and the associated m_3 parameter of the phenology models for the two accelerometers on each tree. The m_3 parameter indicates the time during the growing season when the dominant period is increasing the fastest (the spring inflection point), and can be interpreted as the onset of spring (Elmore et al., 2012), when full leaves are emerging. For fall phenology, we compared the date full leaves were last observed and the m_5 parameter (i.e., onset of autumn). Unless otherwise specified, we performed correlation and regression analyses using phenology parameters averaged across the upper and lower placed accelerometers on each tree. However, we also explored if accelerometers attached at different heights on the same tree differed from each other in terms of data quality (frequency of outliers) and signal strength (magnitude of correlation with observed phenology).

We also sought to determine the effect of sampling frequency and daily sampling duration on deriving phenology estimates from accelerometers. Decreasing sampling frequency and duration will extend battery life, while also decreasing data storage requirements and processing time. Knowing the minimum sampling frequency and duration needed to derive a phenology signal will help guide future accelerometer studies. To simulate different sampling frequencies and daily durations, we subsetted the accelerometer data in various ways. Reduced sampling frequencies were simulated by removing every second and fourth acceleration record from the daily data files to yield an approximate 5 and 2.5 Hz sampling frequency, respectively. To assess the effects of different daily sampling durations, we extracted and analyzed the accelerometer recordings (at 10 Hz) for only the first approximately 30 min, 60 min, 6 h, and 12 h of each daily data file. Times were estimated using time stamps recorded every 5 s in the 24 h data

file. Results from the three sampling frequencies (10, 5, and 2.5 Hz) and five daily sampling durations (30 min, 60 min, 6 h, 12 h, and 24 h) were compared for their relative ability to derive a phenology signal. Results were visually inspected and, when the phenology model could be fit, parameter estimates were compared across sampling frequencies and durations. Because we expected the shape of the phenology curves for the subsetted frequencies and durations to be similar to that of the full dataset (10 Hz, 24 h), and to maximize the probability of models converging, we used the fitted parameter estimates for the full models as the starting parameters for the phenology models fit to the subsetted data.

3. Results

Of the 20 accelerometers deployed, the phenology model could be fit to the data from 18. Data from the two remaining accelerometers originated from the same tree and exhibited a weak and sparse phenology signal (i.e., reduced difference between winter and summer dominant period, and many outliers). We suspect that this was due to the tree chosen at this particular site, and not a malfunction of the two accelerometers (see Discussion). This pair of accelerometers was removed from all subsequent analyses. Furthermore, we found that the axis recording vertical tree movement did not yield a reliable phenological signal on any tree (as expected), and therefore was also excluded from all further analyses.

Dominant period values from accelerometers matched the theoretical expectation of a seasonal change in aboveground tree mass. Generally, the dominant period tended to be stable during the winter, increased abruptly during the spring and decreased in autumn back to winter levels (Figs. 3, A2 & A3). Furthermore, there was good agreement between spring phenology estimated from direct visual observations and accelerometers. Pearson's correlation coefficient between the date of first observed full leaves and the m_3 model parameter (representing the spring inflection point) was 0.82 (p < 0.01). MA regression between the average m_3 parameter and date of first observed full leaves revealed a slope of 1.37 (95% CI: 0.75–2.93), and a y-intercept of -41.09 (95% CI: -249.45 -42.84) (Fig. 4a). Thus, our estimates of spring phenology derived from accelerometers had a significant relationship with direct visual observations of leaf out.

In contrast to the strong correspondence between accelerometers and spring leaf out, there was no significant relationship between the date of last observed leaves and the m_5 parameter representing the autumn inflection point (Pearson's r=0.16, p=0.69). This may have resulted from the dominant period often decreasing during the summer and autumn (see Fig. 3), sometimes resulting in an indistinct autumn phenology. MA regression between observed autumn phenology and the autumn inflection point was also not significant (Fig. 4b).

The m_3 and m_5 parameters for the upper and lower placed accelerometers were not significantly different (paired t-test; p = 0.45, 0.35for each parameter respectively), indicating height of accelerometers on the trees did not affect estimates for either of these phenological parameters. We also tested for differences in the proportion of data points removed as outliers for the upper and lower accelerometers. While the lower accelerometers tended to yield a greater proportion of outliers, the difference was not significant (p = 0.28). However, for one tree approximately 20% of data points of the upper accelerometer were removed as outliers, while no outliers were identified for the lower accelerometer (Fig. A3f). This was due to an exceptionally large number of outlying data points in the lower accelerometer not being removed because they were partially driving the shape of the LOESS curve and therefore not identified as outliers. If this pair of accelerometers is excluded, the difference in the proportion of outliers between the upper and lower place accelerometers became significant (p < 0.01), with lower placed accelerometers exhibiting a greater frequency of outlier values.

Sampling frequency and duration had differing effects on the ability

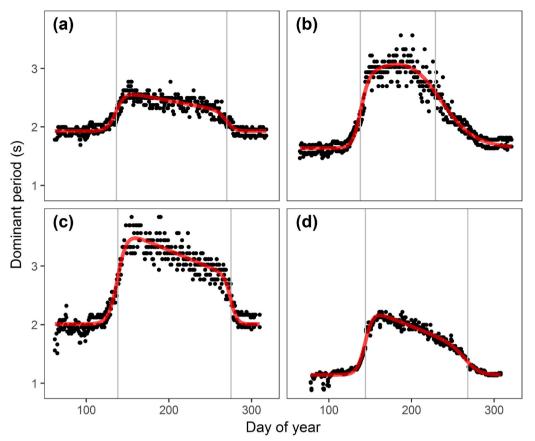


Fig. 3. Examples of processed accelerometer data (black points), with outliers removed, fit with a phenology model (red lines). Vertical gray lines represent the estimated dates of spring and autumn onset derived from the phenology model (m_3 and m_5 parameters, respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) See Fig. A1 for an example of raw data.

to derive a phenological estimate from the accelerometer data. In general, decreasing the sampling frequency resulted in fewer phenology models being fit, while decreasing sampling duration did not have as dramatic an effect (Table 1). For instance, using a simulated sampling frequency of 2.5 Hz, only five of 18 accelerometers could be fit with the phenology model, while reducing the sampling duration to 6 h (approximately equivalent to 25% of the full data) resulted in 14 of 18 accelerometers fit with the phenology model. In addition to affecting model fit, the parameter estimates of the phenology model were more sensitive to decreasing the sampling frequency than sampling duration. For instance, decreasing the duration to six hours resulted in an average shift of < 2 days in the m_3 estimate, while decreasing the sampling frequency to 2.5 Hz resulted in an average shift of > 5 days.

4. Discussion

Forest phenology is a key functional trait of interest in studies of global change and climate adaptation of forests. Yet obtaining high resolution phenology data for individual trees over geographically disparate sites is logistically challenging, and involves either intensive direct observation by networks of observers, or monitoring facilities such as phenocams that can represent a substantial investment at each locality. Here, we report on the feasibility of obtaining high-resolution phenology data for individual trees across landscapes scales using ontree accelerometers. To our knowledge, ours is the first study to describe the use of accelerometers to estimate dates of phenological transitions in trees, representing a promising solution to the challenge

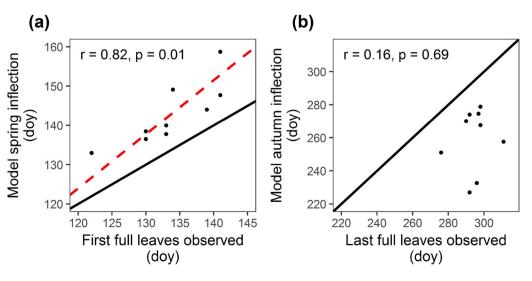


Fig. 4. Relationship between observed leaf phenology and accelerometer-derived phenology for (a) leaf emergence, and (b) leaf drop. Volunteer-observed dates reflect (a) the date unfolded leaves were first observed, and (b) the date full leaves were last observed. The black line is a 1:1 line, and the dashed red line in (a) is a major axis regression line. The regression in (b) was not significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1 Average difference in days between the m_3 parameter of the phenology model based on the full data (10 Hz, 24 H) and models based on subsetted data representing different sampling frequencies and durations. Numbers in parentheses indicate the number of accelerometers that could be fit with a phenology model.

| Accelerometer position | Frequency | | Duration | | | |
|------------------------|-----------|-----------|-----------|-----------|-----------|-----------|
| | 5 Hz | 2.5 Hz | 12 H | 6 H | 1 H | 0.5 H |
| Upper | -0.42 (8) | 5.34 (2) | 0.31 (9) | -0.10 (8) | -0.49 (9) | 0.49 (9) |
| Lower | -0.65 (7) | 11.27 (3) | -1.53 (6) | -1.33 (6) | 0.86 (9) | -0.46 (8) |

of measuring phenology in large, landscape-scale studies.

In general, the accelerometer data agreed well with the theoretical expectation of seasonal tree mass variation as well as with visual observations for spring phenology. Spring phenology was more clearly defined in our data than was autumn phenology, with nearly all the accelerometers detecting an abrupt increase in the dominant period early in the growing season, which coincided closely with observed leaf emergence. These results indicate that accelerometers can be used to accurately estimate the timing of spring leaf emergence for individual trees. The decline in dominant period at the end of the season tended to be less abrupt and more difficult for the phenology models to fit. In some cases, the expected decrease in dominant period, coincident with leaf drop, was entirely absent, contributing to the poor relationship between observed leaf drop and modelled phenology. More broadly, however, our results are consistent with remote sensing studies based on spectral reflectance (e.g., Elmore et al., 2016b) which found stronger relationships between ground observations and spring phenology than with autumn phenology. Lack of association between modeled autumn phenology and leaf drop is not surprising, as many processes other than leaf abscission are likely to affect aboveground tree mass during the end of the growing season (e.g., changes in plant water balance or allocation to belowground tissues). Furthermore, the more diffuse nature of leaf drop, which can span many days or weeks, compared to leaf emergence, when many leaves emerge simultaneously, likely contributed to the poor relationship between accelerometers and visual observations of leaf drop.

Interestingly, the dominant period from seven of the nine trees fit with phenology models declined during the summer, as indicated by a positive m_7 model parameter, similar to the oft-observed 'greendown' phenomenon in remote sensing imagery (Elmore et al., 2012) (although the sign of this parameter varied between the upper and lower accelerometers for two of the seven trees). For many of these trees, the decline began almost immediately after trees reached their peak dominant period in early spring. In some trees, this decline was so substantial that the autumn leaf-drop phenophase was not readily apparent from the accelerometer data, which likely contributed to the poor relationship with the visual observations. Although the reason for the decline in dominant period during the growing season is currently unknown, there are multiple possible explanations. One possibility is that the hardening of current year secondary xylem tissues throughout the growing season results in an increase in tree stiffness, which would translate into a more damped frequency of acceleration. Seasonal changes in leaf orientation (e.g., Raabe et al., 2015) could produce a similar effect, by increasing the effect of wind dampening. Seasonal variation in the mass of the leaves (e.g., leaf water content or leaf mass per area) could also interact with the canopy to affect overall mass during the summer (e.g., Coble et al., 2016; Gond et al., 1999; Jurik, 1986; Poorter et al., 2009). Other possibilities include the loss of leaves during the summer, due to weather events (e.g., wind, rain, hail, etc.), disease, herbivorous insects, etc. However, it seems unlikely that leaf loss could result in such a dramatic decline in dominant period across so many sites (see Figs. A2 & A3). Further study is needed to understand the exact cause of the decline in dominant period during the summer; such work could potentially yield information on the timing of other physiological processes of interest to ecologists.

4.1. Practical findings & recommendations

Based on our findings and experience with deploying accelerometers on forest trees to detect leaf phenology, we offer the following recommendations. Because of the currently unknown effects of tree size and canopy obstruction, when choosing a tree for an accelerometer placement, we recommend a tree either in the open, or near the forest edge, where wind exposure can be expected and canopy obstruction (with nearby trees or other structures) is minimized. Furthermore, while both axes recording movement parallel to the ground yielded similar information, we recommend utilizing both axes, as outliers in one axis may be mediated by the true phenological signal in the other axis, ultimately improving the fit of phenology models. Conversely, despite the upper and lower placed accelerometers yielding similar phenological estimates, we propose that higher accelerometer placement should be preferred. Accelerometers should be placed high enough on the tree to minimize the effects of ground attenuation, while still being easily accessible for maintenance (van Emmerik et al., 2017). A higher accelerometer placement may reduce the need to locate a tree in the open or along the forest edge. Finally, our results suggest that the daily sampling duration can be reduced considerably, with minimal effect on the phenological estimates; however, the same is not true for sampling frequency (Table 1). Hence, if there is a need to balance a tradeoff in sample duration and frequency, we recommend a higher sampling frequency and a shorter duration. (See Oregon Research Electronics, 2016 for information regarding sampling rate error.)

Like other studies (e.g., Fuccillo et al., 2015), we found that citizen scientists can provide high-quality phenology data. In addition to providing a needed ground-truthing for phenological dates used to confirm phenology estimated from accelerometer data, our study further demonstrates that the role of citizen scientists can be expanded beyond data collection. Specifically, our volunteers played an active and productive role in development and refinement of this methodological research. This aligns with other studies that promote and highlight the broader range of contributions that can be made by citizen scientists (Shirk et al., 2012). Although the use of citizen scientist data has sometimes been questioned because of perceived inaccuracies and/or biases in data collection, highly organized and well-established groups such as the National Phenology Network have helped to standardize data collection and submission protocols to help ensure high quality data is consistently collected.

4.2. Future research needs

Although the accelerometers deployed in our study reliably produced a phenology signal, there are several unknown factors that may affect the ability of accelerometers to derive phenology, such as tree size, and leaf/flower/fruit characteristics. While we attempted to control for tree size by instructing volunteers to select moderately sized trees with a dbh < 30.5 cm, we do not know if a phenological signal can be similarly detected from accelerometers attached to much larger or smaller trees. For example, if the change in tree mass due to leaf emergence/drop is low relative to the woody mass of the tree, the seasonal change in mass may not be detectable by an accelerometer. Effects of canopy obstruction (e.g., by nearby trees), flower and fruit

characteristics (e.g., whether flowers and/or fruit emerge before leaves, or if species produce relatively heavy fruit), or marcescent foliage could each also affect the ability of accelerometers to detect leaf phenology or may affect the shape of the resultant phenology curve. Additional studies are needed to quantify the effect of these variables on using accelerometers to derive tree leaf phenology.

It also remains unclear what caused outlying dominant period values on some days. Closer inspection of the spectral density plots for these days showed no clear peaks in the periodograms, indicating lack of a clear signal on these days. This sporadic lack of signal could have multiple causes. Lack of sufficient forcing by wind, for instance, could result in the tree sway pattern being dominated by noise. Although we tried to minimize these effects by asking volunteers to choose trees with direct exposure to the wind, it is unclear if this would have a meaningful impact on windless (or nearly windless) days. A non-stationary dominant period during the day could also obscure the signal. If the dominant period varies throughout the day (e.g., due to weather events or diurnal water dynamics), it could obscure peaks in the periodogram when using a 24 h sampling duration. However, it is worth noting that shorter sampling durations still required outliers to be removed - suggesting that a non-stationary dominant period is likely not the sole cause of the outliers. Identifying the reason why some days do not generate a clear signal, and minimizing these effects, would likely further facilitate the use of accelerometers for measuring tree phenology.

4.3. Additional uses of accelerometer data

In addition to monitoring phenology, accelerometer data may be useful in addressing a variety of other interesting ecological questions. For instance, the devices we used in this study (Oregon Research Electronics AL100 units) include an integrated temperature sensor which could be used to calculate winter chilling and spring heat sum accumulation prior to leaf emergence. This temperature data, combined with phenological estimates, could offer very fine-scale understanding of how individual trees respond to local climatic conditions. The remote deployment and high temporal precision of accelerometers could also allow estimation of the timing of phenology, or other tree characteristics, for many individual trees across large geographic scales and in multiple remote locations. This opens up possibilities for phenology experiments that would be challenging, if not impossible, using other methods such as direct visual monitoring or satellite imagery. Furthermore, because the accelerometers effectively capture temporal change in tree mass at very fine temporal scales, they can provide information on other ecological process contributing to mass change. For example, like other studies, we've observed evidence of daily mass fluctuations associated with precipitation events (results not shown). This suggests the possibility that accelerometer data could inform studies on plant water balance and precipitation interception (e.g., van Emmerik et al., 2017). The varied uses of acceleration data should encourage the further development of accelerometers as a flexible plant sensor that can be used to quantify multiple plant and environmental traits of interest to plant scientists.

In sum, our work shows that high resolution acceleration data can be used to accurately quantify spring phenology of forest trees. Because of their portability and low cost, accelerometers have the potential to be a pragmatic solution when high spatial and temporal resolution tree phenology data is required, contributing to the ongoing development of high-resolution plant sensors for field phenotyping (Li et al., 2014).

Conflicts of interests

The authors declare no conflicts of interests.

Authors' contributions

SK, CS, AG, AK, MF organized the volunteer workshop; AG analyzed the data with assistance from MF, AE, and AK; AG led the writing with all authors contributing critically to the drafts and giving final approval for publication.

Acknowledgements

This work was supported by the National Science Foundation (IOS-1461868). We thank the eight citizen scientists, Paul Conklin, Dallas Hudson, John Latimer, Emily Lind, Erika Mitchell, Joe Walewski, and two anonymous participants, who volunteered many hours to advise on the study design, deploy accelerometers, and diligently recorded phenological observations. We also thank Jim Wagner (Oregon Research Electronics) for developing the accelerometers for this application and providing valuable technical support during the length of the study, Heather Lintz for her help in facilitating this study, and two anonymous reviewers for feedback that improved the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.08.020.

References

- Bonney, R., Shirk, J.L., Phillips, T.B., Wiggins, A., Ballard, H.L., Miller-Rushing, A.J., Parrish, J.K., 2014. Next steps for citizen science. Science 343, 1436–1437. https://doi.org/10.1126/science.1251554.
- Borchers, H.W., 2017. pracma: Practical Numerical Math Functions. R Package. Chuine, I., 2010. Why does phenology drive species distribution? Philos. Trans. Biol. Sci. 365. 3149–3160.
- Cleveland, W.S., Devlin, S.J., 1988. Locally weighted regression: an approach to regression analysis by local fitting. J. Am. Stat. Assoc. 83, 596–610. https://doi.org/10.2307/2289282.
- Coble, A.P., VanderWall, B., Mau, A., Cavaleri, M.A., 2016. How vertical patterns in leaf traits shift seasonally and the implications for modeling canopy photosynthesis in a temperate deciduous forest. Tree Physiol. 36, 1077–1091. https://doi.org/10.1093/ treephys/tpw043.
- Ehrlén, J., Münzbergová, Z., 2009. Timing of flowering: opposed selection on different fitness components and trait covariation. Am. Nat. 173, 819–830. https://doi.org/10.
- Elmore, A.J., Guinn, S.M., Minsley, B.J., Richardson, A.D., 2012. Landscape controls on the timing of spring, autumn, and growing season length in mid-Atlantic forests. Glob. Change Biol. 18, 656–674. https://doi.org/10.1111/j.1365-2486.2011. 02571.x
- Elmore, A.J., Nelson, D.M., Craine, J.M., 2016a. Earlier springs are causing reduced nitrogen availability in North American eastern deciduous forests. Nat. Plants 2, 16133. https://doi.org/10.1038/nplants.2016.133.
- Elmore, A.J., Stylinski, C., Pradhan, K., 2016b. Synergistic use of citizen science and remote sensing for continental-scale measurements of forest tree phenology. Remote Sens. 8, 502. https://doi.org/10.3390/rs8060502.
- Fitzjarrald, D.R., Acevedo, O.C., Moore, K.E., 2001. Climatic consequences of leaf presence in the eastern United States. J. Clim. 14, 598–614. https://doi.org/10.1175/1520-0442(2001)014<0598:CCOLPI>2.0.CO;2.
- Fuccillo, K.K., Crimmins, T.M., de Rivera, C.E., Elder, T.S., 2015. Assessing accuracy in citizen science-based plant phenology monitoring. Int. J. Biometeorol. 59, 917–926. https://doi.org/10.1007/s00484-014-0892-7.
- Gond, V., De Pury, D.G., Veroustraete, F., Ceulemans, R., 1999. Seasonal variations in leaf area index, leaf chlorophyll, and water content; scaling-up to estimate fAPAR and carbon balance in a multilayer, multispecies temperate forest. Tree Physiol. 19, 673–679. https://doi.org/10.1093/treephys/19.10.673.
- Graham, E.A., Riordan, E.C., Yuen, E.M., Estrin, D., Rundel, P.W., 2010. Public Internet-connected cameras used as a cross-continental ground-based plant phenology monitoring system. Glob. Change Biol. 16, 3014–3023. https://doi.org/10.1111/j.1365-2486.2010.02164.x.
- Hoch, G., Richter, A., Körner, C., 2003. Non-structural carbon compounds in temperate forest trees. Plant Cell Environ. 26, 1067–1081. https://doi.org/10.1046/j.0016-8025.2003.01032.x.
- Inouye, D.W., 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89, 353–362. https://doi.org/10.1890/ 06-2128.1.
- Jeffree, E.P., 1960. Some long-term means from the phenological reports (1891–1948) of the Royal Meteorological Society. Q. J. R. Meteorol. Soc. 86, 95–103. https://doi.org/ 10.1002/qj.49708636710.

- Jurik, T.W., 1986. Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. Am. J. Bot. 73, 1083–1092. https://doi.org/10. 2307/2443788.
- Keller, S.R., Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Olson, M.S., Tiffin, P., 2011. Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). Am. J. Bot. 98, 99–108. https://doi.org/10.3732/ aib.1000317
- Keller, S.R., Levsen, N., Olson, M.S., Tiffin, P., 2012. Local adaptation in the floweringtime gene network of Balsam Poplar, *Populus balsamifera* L. Mol. Biol. Evol. 29, 3143–3152. https://doi.org/10.1093/molbev/mss121.
- Kleinknecht, G.J., Lintz, H.E., Kruger, A., Niemeier, J.J., Salino-Hugg, M.J., Thomas, C.K., et al., 2015. Introducing a sensor to measure budburst and its environmental drivers. Front. Plant Sci. 6.
- Li, L., Zhang, Q., Huang, D., 2014. A review of imaging techniques for plant phenotyping. Sensors 14, 20078–20111. https://doi.org/10.3390/s141120078.
- Little, E.L., 1971. Atlas of United States Trees. U.S. Dept. of Agriculture, Forest Service, Washington, D.C., USA.
- Oregon Research Electronics, 2016. Application Note: AL100 Sample Rate Errors and Error Correction [WWW Document]. Status. URL. (Accessed 21 April 2017). https://sites.google.com/site/oregonresearchelectronics/home/status.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
- Peñuelas, J., Rutishauser, T., Filella, I., 2009. Phenology feedbacks on climate change. Science 324, 887–888. https://doi.org/10.1126/science.1173004.
- Polgar, C.A., Primack, R.B., 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. New Phytol. 191, 926–941. https://doi.org/10.1111/j.1469-8137.2011.03803.x.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytol. 182, 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x.
- R Core Team, 2017. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raabe, K., Pisek, J., Sonnentag, O., Annuk, K., 2015. Variations of leaf inclination angle distribution with height over the growing season and light exposure for eight broadleaf tree species. Agric. For. Meteorol. 214, 2–11. https://doi.org/10.1016/j. agrformet.2015.07.008.
- Richardson, A.D., Jenkins, J.P., Braswell, B.H., Hollinger, D.Y., Ollinger, S.V., Smith, M.-L., 2007. Use of digital webcam images to track spring green-up in a deciduous broadleaf forest. Oecologia 152, 323–334.
- Richardson, A.D., Hollinger, D.Y., Dail, D.B., Lee, J.T., Munger, J.W., O'keefe, J., 2009. Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. Tree Physiol. 29, 321–331. https://doi.org/10.1093/

- treephys/tpn040
- Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene flow and local adaptation in trees. Annu. Rev. Ecol. Evol. Syst. 38, 595–619. https://doi.org/10.1146/annurev.ecolsys. 38.091206.095646.
- Schwartz, M.D., Ahas, R., Aasa, A., 2006. Onset of spring starting earlier across the Northern Hemisphere. Glob. Change Biol. 12, 343–351. https://doi.org/10.1111/j. 1365-2486.2005.01097.x.
- Schwartz, M.D., Hanes, J.M., Liang, L., 2013. Comparing carbon flux and high-resolution spring phenological measurements in a northern mixed forest. Agric. For. Meteorol. 169, 136–147. https://doi.org/10.1016/j.agrformet.2012.10.014.
- Selker, J.S., Lane, J.W., Rupp, D.E., Hut, R., Abou Najm, M.R., Stewart, R.D., et al., 2011.

 The answer is blowing in the wind: using wind induced resonance of trees to measure time varying canopy mass, including interception. AGU Fall Meet. Abstr. 11.
- Shirk, J., Ballard, H., Wilderman, C., Phillips, T., Wiggins, A., Jordan, R., et al., 2012.
 Public participation in scientific research: a framework for deliberate design. Ecol. Soc. 17.
- Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Drewes, E.C., Schroeder, W.R., 2009. Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsa-mifera* L.). Plant Cell Environ. 32, 1821–1832. https://doi.org/10.1111/j.1365-3040. 2009.02042.x.
- Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Song, M., 2013. Timing of photoperiodic competency causes phenological mismatch in balsam poplar (*Populus balsamifera* L.). Plant Cell Environ. 36, 116–127. https://doi.org/10.1111/j.1365-3040.2012. 02560.x.
- Sparks, T.H., Carey, P.D., 1995. The responses of species to climate over two centuries: an analysis of the Marsham Phenological Record, 1736–1947. J. Ecol. 83, 321–329. https://doi.org/10.2307/2261570.
- van Emmerik, T., Steele-Dunne, S., Hut, R., Gentine, P., Guerin, M., Oliveira, R., et al., 2017. Measuring tree properties and responses using low-cost accelerometers. Sensors 17, 1098.
- Vanbeveren, S.P.P., Bloemen, J., Balzarolo, M., Broeckx, L.S., Sarzi-Falchi, I., Verlinden, M.S., Ceulemans, R., 2016. A comparative study of four approaches to assess phenology of Populus in a short-rotation coppice culture. IForest Biogeosci. For. 9, 682. https://doi.org/10.3832/ifor1800-009.
- Visser, M.E., Holleman, L.J.M., Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147, 164–172. https://doi.org/10.1007/s00442-005-0299-6.
- Welch, P., 1967. The use of fast Fourier transform for the estimation of power spectra: a method based on time averaging over short, modified periodograms. IEEE Trans. Audio Electroacoust. 15, 70–73. https://doi.org/10.1109/TAU.1967.1161901.
- Zasada, J.C., Phipps, H.M., 1990. Populus balsamifera L. Silv. N. Am. 2, 518–529.