

Interspecific and interannual variation in the duration of spring phenophases in a northern mixed forest

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ABSTRACT

A wide range of intra- and interspecific variation occurs in spring leaf phenology as a result of biotic factors such as, life strategy, ecological niche and genetic adaptation, and abiotic factors such as environmental condition. Whereas knowing when the start of bud-burst occurs is necessary for determining the beginning of the growing season, and the subsequent start of carbon uptake, the duration of phenophases is equally important (to estimate the rate of carbon uptake, for example), but rarely reported. Here, we investigate variation in the timing and duration of 3 key phenophase categories (bud-open, leaf-out, full-leaf unfolded) from a range of 8 broadleaf and 2 conifer species in a mixed forest in northern Wisconsin, USA over a 5-year period. As expected, the start of each phenophase category varied across species and years and an earlier start to one phenophase did not necessarily result in an earlier start to subsequent phenophases nor did it mean a faster or slower progression. Ecological niche was not always a useful predictor of the timing or duration of the spring phenology season. The spring phenology season from bud-burst to full leaf open for the entire forest community took an average of 13 days ranging from 12 to 18 days across species. Bud-open and leaf-out lasted an average of 4 days whereas, full-leaf unfolding lasted 5 and again there were variations among species. Full leaf unfolded for *A. incana* lasted significantly ($p < 0.001$) longer than other species. Variation in the duration of the spring phenology season among years closely tracked local seasonal air-temperature based on growing degree hours (GDH). These results could be used to help determine the relationship between phenology and the potential for carbon storage in early spring in a mixed forest and highlight the value of direct field observation data at species level, the detail of which cannot, at present, be captured by satellite remote sensing.

1. Introduction

The spring season in temperate forests is marked by the phenological development of leaves, from dormant buds, to leaf emergence through to full leaf expansion and canopy development. This annual progression is primarily driven by an increase in temperature in spring although a lengthening of the photoperiod and other environmental parameters (such as precipitation and soil moisture availability) may also influence the rate of leaf development (Downs and Borthwick 1956; Myking and Heide 1995; Stevens et al., 1995; Murray et al., 1989; Bertin, 2008; Caffarra et al., 2011; Pletsers et al., 2015; Shen et al., 2015; Liu et al., 2016). Therefore, when environmental conditions are

suitable bud-burst, leaf-out and leaf expansion will occur but because these conditions vary from one year to the next so too does the timing and duration of the phenology season. Furthermore, not all forest species respond to the same environmental stimulus e.g., rising spring temperature, at the same rate (Lechowicz, 1984; Donnelly et al., 2006; Lopez et al., 2008; Caffarra and Donnelly 2011; Vitasse et al., 2009; Yu et al., 2015) and given the wide range of tree species that make-up a forest community the greening process tends to vary over space and time. Both biotic and abiotic factors combine to influence the overall timing of green-up, making predictions of the timing and the rate of phenological progression a challenging task.

Nevertheless, it is important to be able to determine both the timing

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and rate of leaf development due to its functional significance in overall ecosystem dynamics. Leaf phenology is pivotal to a range of forest processes as, for example, it determines the start, end and length of the growing season which in turn determines the annual amount (and rate) of CO₂ removal from the atmosphere by photosynthesis and subsequent storage in biomass (White et al., 1999; Piao et al., 2007; Richardson et al., 2013; Keenan et al., 2014; Hufkens et al., 2016). Furthermore, leaves are an important element in many food-webs and changes in timing and progression may impact resource availability for herbivores and higher trophic level organisms (Harrington et al., 1999; Visser and Holleman, 2000; Visser et al., 2004; Both et al., 2009; Donnelly et al., 2011, 2014). The timing of the start and end of the phenology season has been successfully determined at a range of scales from the individual tree by direct *in situ* observation (Peñuelas and Filella, 2001; Menzel et al., 2006; Donnelly et al., 2006; Fu et al., 2015; Zheng et al., 2016) to landscape and continental scales by remote sensing using either satellites (Myneni et al., 1997; Justice et al., 1985; Moulin et al., 1997; Zhang et al., 2001; Liang et al., 2011; Li et al., 2015) or digital cameras (Huete et al., 2002; Richardson et al., 2011; Sonnentag et al., 2012; Zhang et al., 2014) capable of recording the greening process. In recent years, much attention has been given to capturing the timing of bud-burst and leaf fall to establish if changes have occurred over time due to climate change and for determining the start and end of the carbon uptake period. Equally important, but much less reported, is knowing the rate at which these events progress. Establishing the timing and duration of subtle transitions from one phenophase to another may not, at present, be captured by remotely sensed means due to the coarseness of both spatial and temporal resolution, cloud contamination and sensor technology limitations. Whereas temporal resolution and cloud cover may be addressed using the geostationary ABI with 5-min observations the spatial resolution is still too coarse to accurately detect subtle transitions in phenophases. Therefore, continuous *in situ* monitoring is necessary to observe how changes in environmental condition, such as rising temperature, impact the timing and rate of progression of leaf phenology which, in turn, may have wider reaching consequences for overall forest dynamics. However, since continuous *in situ* monitoring cannot be accomplished universally, a balance must be reached between spatially extensive *in situ* surveys and remote sensing approaches.

Given the large variation in the timing and duration of leaf-out among different species, populations of the same species, individuals of the same species and even on different locations on the same plant it is challenging to estimate the overall characteristics of spring phenology in a forest community. Therefore, we wanted to test the hypothesis that particular ecological characteristics (opportunistic vs late successional, determinate vs indeterminate growth, ring porous vs diffuse porous wood) of individual species would be reflected in the timing and duration of key phenophases that, in turn, could be used to predict the overall duration of the spring phenology season in a mixed northern forest community. Furthermore, since phenological progression is driven by rising temperature we tested a range of temperature parameters (average temperature and Growing Degree Hours) as potential drivers of the timing and duration of individual species' spring phenology. In order to test these hypotheses we examined the timing and duration of 3 key phenophase categories (bud-open, leaf-out, full-leaf unfolded) from a range of 8 broadleaf and 2 conifer species in a mixed forest in northern Wisconsin over a 5-year period from 2006 to 2010. Subsequently, we correlated the results with temperature parameters derived from a nearby flux-tower.

2. Materials and methods

2.1. Study site

The study area has been extensively described in Schwartz et al. (2013). In brief, the study site is located in a mixed deciduous (70%)

Table 1

Scientific and common names of the tree species used in this study together with the number (range across years) of individuals with sufficient data, ecological niche (US Forest Service) and wood anatomy type. Not all species present at both sites some only found in the North Study Area (NSA) and some in the South Study Area (SSA). Growth habit D – determinate (single growth flush in spring) and I indeterminate (several spurts during growing season).

Species	Number	Wood anatomy type	Adaptation	Growth habit
<i>Broadleaf, late successional</i>				
<i>Acer saccharum</i> Sugar Maple	81–121 NSA 7–12 SSA	Diffuse porous	Shade tolerant	D
<i>Acer rubrum</i> Red Maple	38–79 NSA 19–82 SSA	Diffuse porous	Moderately shade tolerant	D
<i>Tilia Americana</i> American Basswood	9–22 NSA	Diffuse porous	Moderately shade tolerant	D
<i>Broadleaf, early successional</i>				
<i>Populus tremuloides</i>	10–17 NSA	Diffuse porous	Shade intolerant	I
Quaking Aspen	29–114 SSA	Diffuse porous	Shade intolerant	I
<i>Populus grandidentata</i> Big-toothed Aspen	5–7 NSA	Diffuse porous	Shade intolerant	I
<i>Alnus incana</i> Speckled Alder	5–29 SSA	Diffuse porous	Moderately shade intolerant	I
<i>Betula papyrifera</i> White Birch	8–24 SSA 5 NSA	Diffuse porous	Shade intolerant	I
<i>Betula alleghaniensis</i> Yellow Birch	6 NSA 6–7 SSA	Diffuse porous	Shade intolerant	I
<i>Needle</i>				
<i>Abies balsamea</i> Balsam Fir: Late successional	24–51 SSA 7 NSA	Non-porous	Shade tolerant	D
<i>Larix laricina</i> Tamarack: Early successional	11 NSA	Non-porous	Shade intolerant	D

and coniferous (30%) forest community near Park Falls (45.9347° N, 90.4486° W) in northern Wisconsin, USA. There were two (the North and the South) 625 m x 625 m study areas each containing 144 plots and 3 individual trees at each resulting in 864 trees. In addition, 24 *Tilia americana* (American Basswood) trees were included in the observation campaign bringing the total number of trees being monitored to 888. Details of the individual species number, wood anatomy type, adaptation and growth habit are presented in Table 1.

2.2. Phenological data

Spring phenology monitoring was carried out from 2006 to 2010 (see Schwartz et al., 2013 for a detailed description). For the purposes of the current study we used data from three phenophase categories; bud-burst (300–390), leaf-out (400–490) and full leaf unfolded (500–590) (Table 2). Each category was subdivided into 4 percentage classes (< 10%, 10–50%, 50–90% and > 90%) representing progressively more advanced stages of development. Each category and appropriate subdivision were combined to give a phenophase value on a particular day. For example, a tree assigned a phenophase value of 350 meant that between 50 and 90% of the buds were open whereas, a value of 500 indicated that < 10% of the leaves on the tree were fully unfolded. The reason for omitting phenological stages prior to bud-burst e.g., dormant buds and buds swollen, was due to the high number of missing values in these categories as a result of the difficulty of observing these stages accurately in the upper canopy. Furthermore, we only used individual trees for which a complete set of observations i.e., all phenophase categories from 300 to 590, was available in any particular year and we only used species which had a minimum of five individuals with a complete record at a particular site. This resulted in the number of individuals and species varying from year to year. We

Table 2

Phenological observation categories, for example, a value of 300 means that less than 10% of the buds on a tree are open.

Code	Deciduous phenophase	Category	Conifer phenophase	Code
300	Bud open	< 10%	Bud open (candle visible)	300
310	Bud open	10–50%	Bud open (candle visible)	310
350	Bud open	50–90%	Bud open (candle visible)	350
390	Bud open	> 90%	Bud open (candle visible)	390
400	Leaf-out (not fully unfolded)	< 10%	Candle out (not unfolded)	400
410	Leaf-out (not fully unfolded)	10–50%	Candle out (not unfolded)	410
450	Leaf-out (not fully unfolded)	50–90%	Candle out (not unfolded)	450
490	Leaf-out (not fully unfolded)	> 90%	Candle out (not unfolded)	490
500	Full leaf unfolded	< 10%	Needles unfolding from candle	500
510	Full leaf unfolded	10–50%	Needles unfolding from candle	510
550	Full leaf unfolded	50–90%	Needles unfolding from candle	550
590	Full leaf unfolded	> 90%	Needles unfolding from candle	590

determined community-level phenophase categories to be the average of all individual species.

2.3. Species classification

In order to identify any consistent patterns in late and early leafing species we determined a number of categories by which to classify each species (Table 1). We first categorized the trees as either deciduous or coniferous. These were subsequently sub-divided according to wood anatomy type (diffuse- or ring-porous), adaptation strategy (shade tolerant or intolerant) and growth habit (determinate or indeterminate).

2.4. Temperature data

Ambient air temperature (30m) at a nearby AmeriFlux tower (US-PFa, Park Falls, WI, 45.9459°N; 90.2723°W) was sampled (Vaisala, Inc. HMP45C) at one-minute intervals and averaged to hourly intervals and gap-filled with nearby station data. These data were available for download from <http://flux.aos.wisc.edu/twiki/bin/view/Main/ChEASData> (Desai, 2014). Subsequently, we used these data to determine average daily temperature and forcing accumulation. Daily mean temperature was used to calculate (i) average spring temperature (February – April), (ii) average temperature from February 1 to the start of each phenophase and (iii) average temperature for the duration of each phenophase, for each species and year. Since, trees were approximately 10–15 m in height we considered air temperature measurements at 30 m were appropriate for our purposes.

2.5. Determining forcing

Accumulated temperature (Growing Degree Hours) was calculated as follows:

$$\text{cumHeat} = \sum_{i=\text{DOY}_1}^{\text{DOY}_2} \sum_{j=1}^{24} \begin{cases} T_{i,j} & \text{for } T_{i,j} > 0^\circ\text{C} \\ 0 & \text{for } T_{i,j} \leq 0^\circ\text{C} \end{cases}$$

where, DOY_1 is January 1st and DOY_2 is DOY at which phenophase level occurs, T is temperature, j are the hours within a day and i are the days between DOY_1 and DOY_2 .

2.6. Anomaly calculations

Phenological anomalies were determined by calculating the difference between the annual average DOY of each phenophase and the 5-year mean. Similarly, temperature anomalies were calculated for all temperature parameters; average spring temperature, average temperature from February 1 to the start of each phenophase and cumulative heat from January 1 to the start of each phenophase. This analysis was restricted to 4 species (*P. tremuloides*, *A. rubrum*, *A. incana* and *B. papyrifera*) at the South Study Area for which a full set of data for phenophases and years was available. Only 3 years' data were available at the North Study Area which was considered insufficient to determine meaningful anomalies.

2.7. Statistical analysis

Univariate analysis of variance, with species, site and year as fixed factors, was used to determine statistically significant differences in (i) the timing of each phenophase category and (ii) the duration of each phenophase category between species, sites and years. Linear regression was also used to examine trends in (Growing Degree Hours) GDHs to the start of each phenophase category and in the duration of the phenophase categories. All statistical tests were carried out using IBM SPSS version 20.0.

3. Results

3.1. Timing of spring phenology

The median day of the year on which bud-opening, leaf-out and full leaf unfolded began (phenophase category 300, 400 and 500) and ended (phenophase category 390, 490 and 590) for each species, site and year is presented in Fig. 1. Clearly there was a lot of variation between years and species. The start of bud-opening, leaf-out and full leaf unfolded (phenophase categories 300, 400 and 500) for the entire forest community (median across all species and sites) followed a similar pattern and was earliest in 2010 (DOY 121, 124, 132) followed by 2006 (DOY 124, 128, 137), 2007 (DOY 125, 128, 131), 2009 (DOY 131, 134, 138) and latest in 2008 (DOY 131, 136, 140) apart from full leaf unfolded which was earlier in 2007 than 2006 (Supplementary Table 1). The end of each of these categories followed a similar pattern (Fig. 1). In general, *Alnus incana*, only present in the South Study Area (SSA), showed a tendency towards earlier bud-opening than other species but this pattern did not hold true for subsequent phenophase categories. Furthermore, both *Betula papyrifera* and *B. alleghaniensis* tended towards later bud-opening and leaf-out particularly in the SSA.

3.2. Duration of bud-opening: phenophase category 300–390

The duration of bud-opening (2.9d) of *Acer rubrum* exhibited a significantly (ranging from $p < 0.044$ to $p < 0.001$) shorter duration of between 1 and 3 days than all other species except *P. tremuloides* (Fig. 2). In contrast, bud-opening for *A. incana* (5.7d) lasted 1–3 days longer ($p < 0.001$ to $p < 0.05$) for 6 out of 9 species examined. In 2008, this phenophase category for *A. incana* and *B. alleghaniensis* in the SSA and *Tilia americana* and *P. grandidentata* in the NSA lasted 9, 10, 8 and 7 days respectively which was significantly longer than other species. This contributed to 2008 (5.8d) having a significantly ($p < 0.001$) longer (1–3 days) bud-opening duration than other years. For all other species and years this phenophase category lasted 5 days or under with an overall average for the community of 3.9 days (Supplementary Results S2).

3.3. Duration of leaf-out: phenophase category 400–490

On average, the duration of leaf-out (2.5 d) of *Betula papyrifera* was

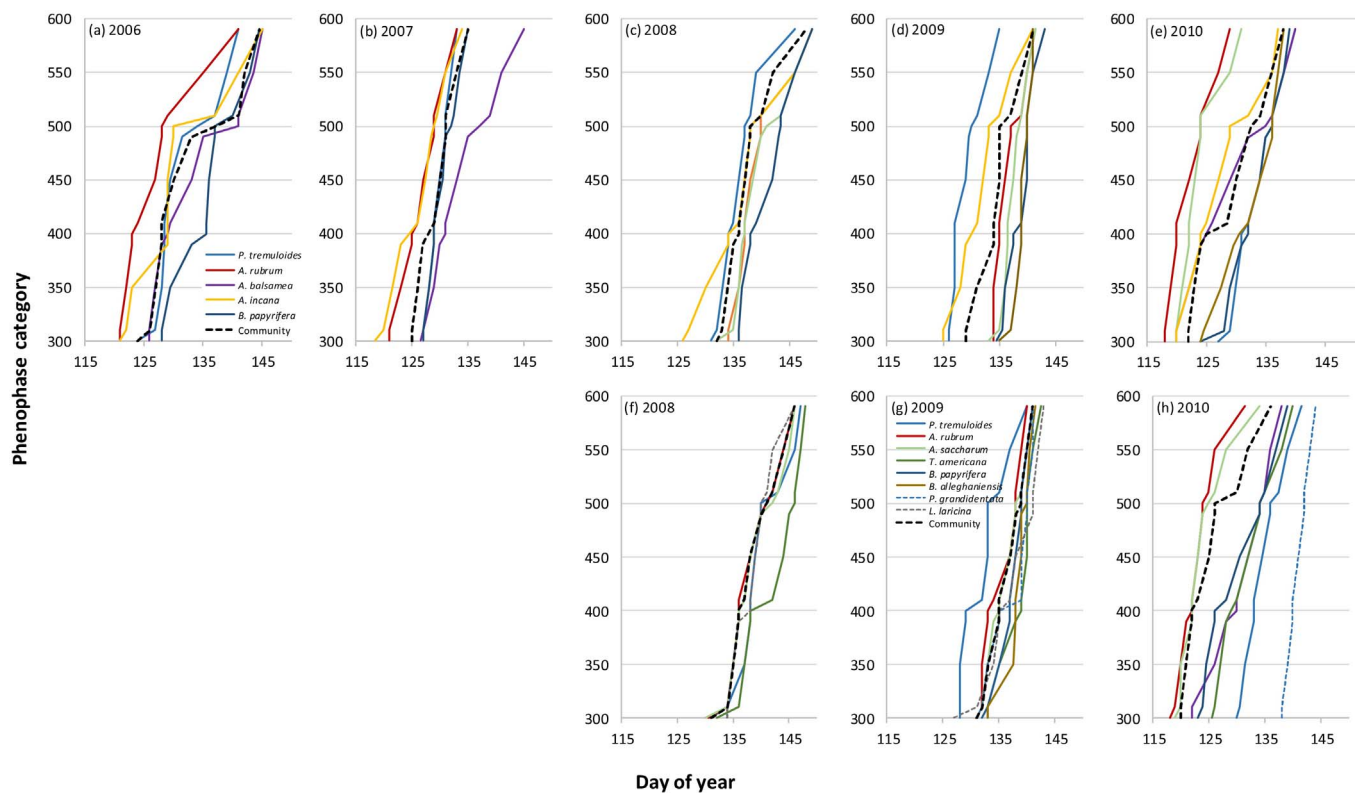


Fig. 1. Median day of year for each phenophase category (300: bud-open; 400: leaf-out; 500: full-leaf unfolded) at the South Study Area 2006–2010 (a–e) and the North Study Area 2008–2010 (f–h) for a range of broadleaf and conifer species and the community (overall median) as a whole in a mixed forest in northern Wisconsin, USA.

between 1 and 2 days shorter than all other broad-leaf species (Fig. 2) but this trend was not statistically significant for *P. grandidentata* and *A. rubrum* (Supplementary Results S2). In contrast, this phenophase category was significantly ($p < 0.001$) 1–2 days longer for *A. balsamea* than all other species except *Tilia americana* and *A. incana*. Leaf-out duration was significantly ($p < 0.001$) shorter in 2009, by approximately 1d, than all other years apart from 2007 whereas, the longest durations (*P. tremuloides* (6d), *T. americana* (5d), *A. rubrum* (4d), *A. saccharum* (5d), *A. incana* (5d)) tended to occur in 2008. In general, leaf-out lasted under 5 days with an overall average for the community of 3.7 days.

3.4. Duration of full leaf unfolded: phenophase category 500–590

The overall length of time for full leaf unfolded to occur for *A. incana* (SSA only) was 7.8 days which was consistently 2–4 days longer ($p < 0.001$) than for all other species (Fig. 2; Supplementary Results S2). In addition, both *P. tremuloides* and *A. rubrum* took 1–2 days longer than the majority of other species. The duration of full leaf unfolded was consistently longer ($p < 0.001$) by 3–6 days in 2006 (9 days) than in all other years and consistently shorter ($p < 0.001$) in 2009 (3.4 days) by 2–6 days. In general full leaf unfolded lasted under 10 days with an overall average for the community of 5.3 days.

3.5. Duration of the spring phenology season: 300–590

The spring phenology season of *A. incana* (SSA only) lasted 18 days on average which was 2–7 days longer ($p < 0.001$) than for any other species (Fig. 2; Supplementary Results S2). In addition, *A. balsamea* showed a similar trend as its spring season lasted 16 days which was longer ($p < 0.001$) than 7 out of the 9 species examined. The average spring duration of *P. tremuloides* and *B. papyrifera* was approximately 12 days which was between 1 and 7 days ($p < 0.001$ to $p < 0.05$) shorter than the majority of other species. The duration of spring in

2006 was 18 days which was consistently ($p < 0.001$) longer by between 2 and 7 days than any other year whereas, spring lasted only 11 days in 2009 which was consistently ($p < 0.001$) shorter (Fig. 1; Supplementary Results S2). In general the duration of the spring phenology season from bud-opening to full leaf unfolded for the community as a whole lasted approximately two weeks (13 days).

The contribution of each species to overall green-up is illustrated in Fig. 3. It is interesting to note that no species or group of species was consistently early or late indicating considerable variation across years. However, there tended to be less variation between species in a particular year in the NSA (Fig. 3f–h) compared to the SSA (Fig. 3a–e).

3.6. Timing of phenophase categories and spring temperature parameters

A number of temperature parameters were tested to determine their effectiveness as drivers of the timing of spring phenology. Accumulated Growing Degree Hours (GDHs), from January 1 with a base temperature of 0 °C, to the start of each phenophase category proved ineffective as heat accumulation naturally increased as the season progressed. For example, if bud-burst occurred on DOY 115 for one individual and DOY 140 for another (*Populus tremuloides* Fig. 4a) there could be as much as 4000 GDHs difference between the two dates. Therefore, heat accumulation from January 1 was not an effective predictor of the timing of spring phenology as it showed high correlation with date of phenophase occurrence. We found a similar pattern for all other species, phenophases and years, and when examining chilling accumulation (data not shown).

In an attempt to overcome the issue of increasing heat accumulation with the later timing of phenophase categories e.g., Fig. 4a, we explored anomalies i.e., differences in the annual timing from the 5-year mean. This analysis was restricted to 4 species (*P. tremuloides*, *A. rubrum*, *A. incana* and *B. papyrifera*) at the South Study Area for which a full set of data for phenophases and years was available. Phenology anomalies varied across species and phenophases (Table 5), but tended to be

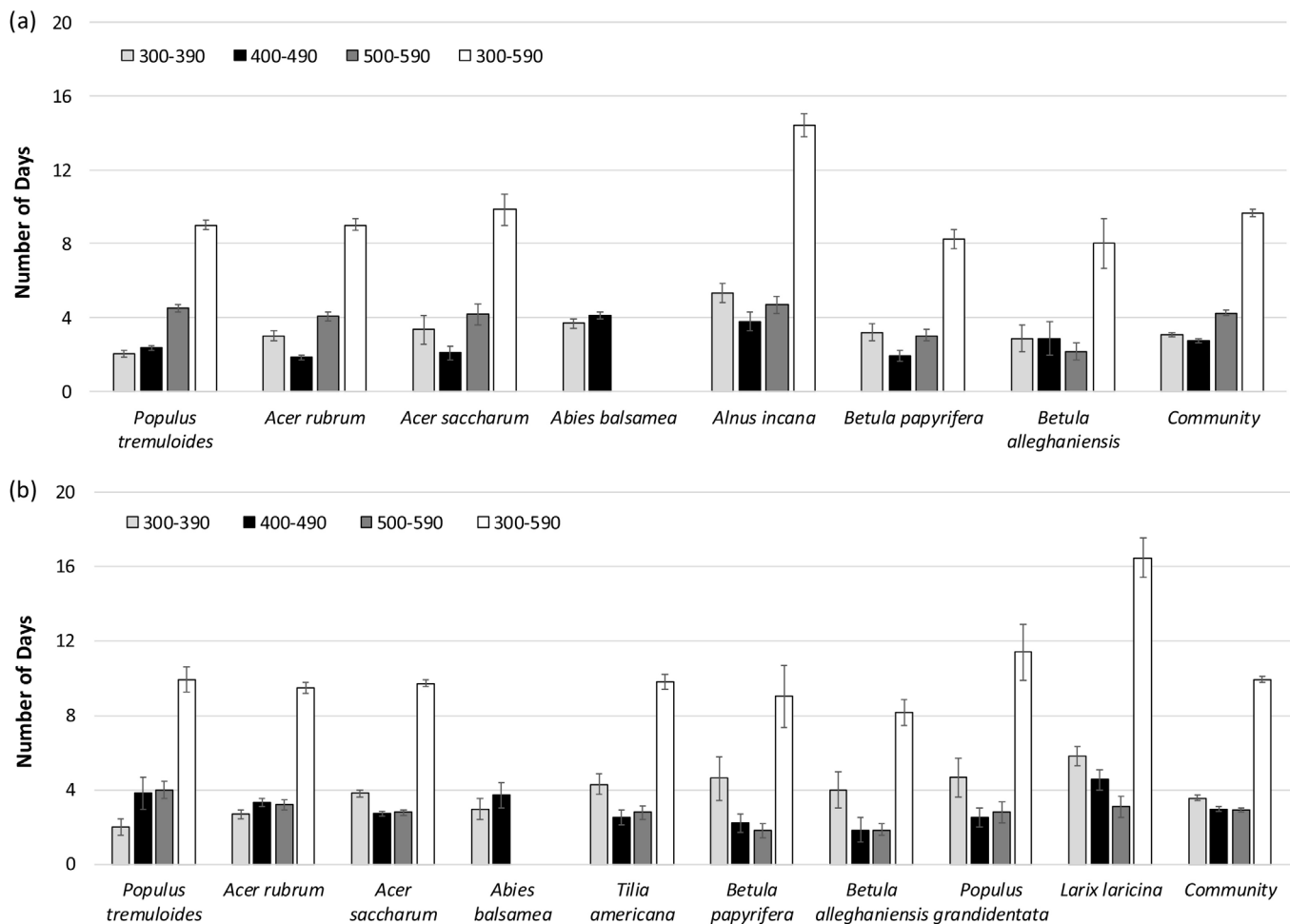


Fig. 2. Duration (number of days) of each phenophase (300: bud-burst; 400: leaf-out; 500: full leaf unfolded) for a range of tree species and the forest community in (a) the South Study Area and (b) the North Study Area in a mixed forest in Northern Wisconsin. Data are for 2009 and error bars represent the standard error of the mean.

greatest in the warmest (2010) and the coldest (2008) years for the community as a whole (Fig. 5). The two years in which overall spring phenology was later than the 5-year mean corresponded to the years with the coldest average spring temperatures (Fig. 5). However, in years when overall spring phenology was earlier than average, spring

temperature tended to be warmer than the 5-year mean except in 2007 when the temperature was cooler than average even though phenology was earlier. The temperature parameter that best reflected the phenology anomaly was GDH because it is highly correlated with time. When GDH was greater than average, phenology was earlier and vice versa

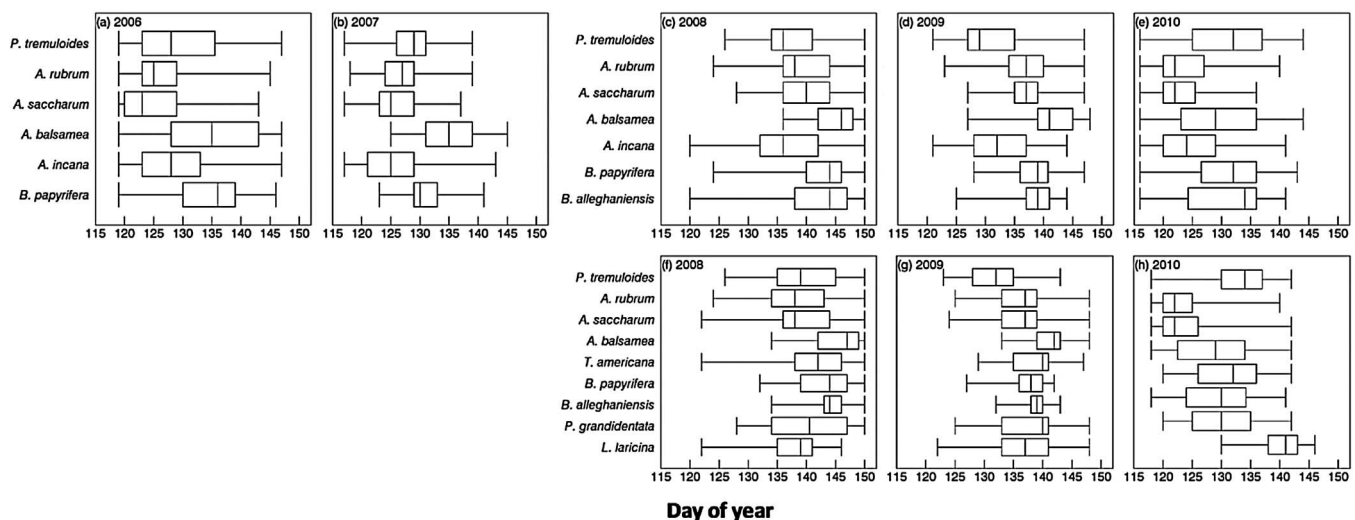


Fig. 3. These plots illustrate the contribution of each species to overall green-up showing day of year (DOY) for the start (phenophase category 300) and end (phenophase category 590) of the phenology season at the South Study Area 2006–2010 (a–e) and the North Study Area 2008–2010 (f–h) for a range of broadleaf and conifer species in a mixed forest in northern Wisconsin, USA.

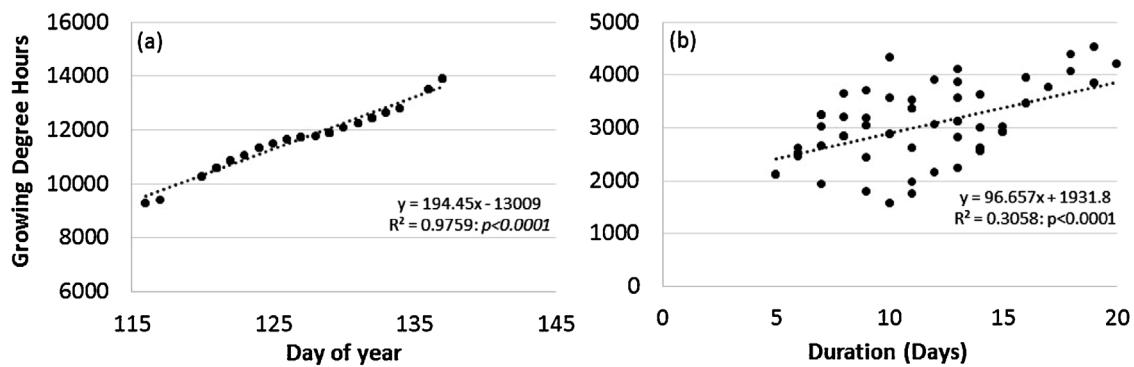


Fig. 4. Growing Degree Hours (GDHs) from January 1 (a) to the start of phenophase category 300 (bud-burst) and (b) for the duration of the spring season (number of days from phenophase category 300–590) for *Populus tremuloides* (Quaking Aspen) at the South Study Area. Data are for 2010.

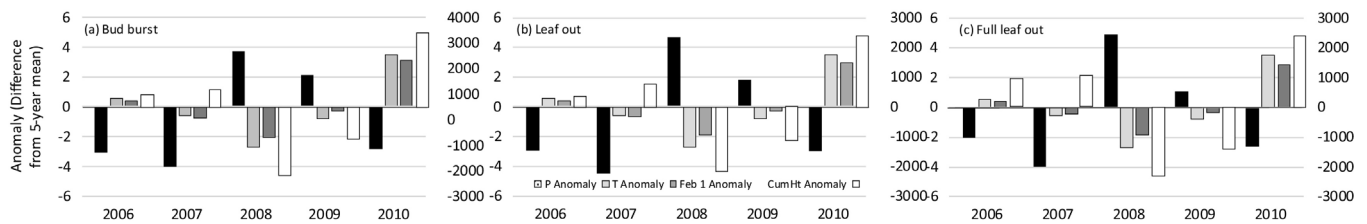


Fig. 5. Timing of phenophase categories (P Anomaly (days)), average spring (FMA) temperature (T Anomaly (°C)), average daily temperature from February 1 to the start of each phenophase (Feb 1 Anomaly (°C)) and Growing Degree Hours (base °C) from January 1 to the start of each phenophase (CumHt Anomaly) anomalies for phenophase categories (a) 300 (bud-burst), (b) 400 (leaf-out) and (c) 500 (full leaf unfolded). Cumulative Heat Anomalies (GDHs) should be read from the secondary y-axis. Data represent the mixed forest community (averaged across all species) at the South Study Area.

(Table 5; Fig. 5). This trend was similar across all species, phenophases and for the subset of the community used to determine anomalies with minor exceptions in 2006 for *A. rubrum* (300, 400 & 500), *P. tremuloides* (500), *B. papyifera* (500), 2009 for *P. tremuloides* (300, 400 & 500) and *P. tremuloides* (500) (Table 5). In these few cases when GDH was less than average, phenology was slightly earlier.

3.7. Duration of phenophase categories and spring temperature parameters

The average temperature during bud-burst (300–390), leaf-out (400–490) and full leaf unfolded (500–590) was 11 °C, 11 °C and 13 °C respectively (Tables 3 and 4; Supplementary Results S3). During bud-burst average temperature did not significantly vary between species or sites but did vary somewhat between years (Tables 3 and 4; Supplementary Results S3) being roughly 3–5 °C warmer in 2007 than other years and 1–2 °C cooler in 2008. Average temperature during leaf-out was 1–5 °C warmer than other years in 2007 and 3–4 °C warmer in 2009. *P. grandidentata* required significantly warmer (2–4 °C) than average temperature for leaf-out to occur than the majority (6 out of 9) of other species (Tables 3 and 4; Supplementary Results S3). In contrast, and to a slightly lesser extent leaf-out for *L. laricina* required significantly cooler (1–4 °C) temperatures than 6 other species. The average temperature during full leaf unfolded varied to a greater extent than the earlier two phenophase categories with respect to species and years. On average, *A. rubrum*, *A. saccharum* and *A. incana* required significantly cooler (1–4 °C) temperatures than the majority other species whereas, *P. grandidentata*, *T. americana*, and *B. alleghaniensis* required warmer temperatures (1–4 °C).

The average temperature during the entire spring phenology season (300–590) was approximately 11 °C which varied between species and years (Tables 3 and 4; Supplementary Results S3). *P. grandidentata* (13 °C) required a significantly warmer (2 °C) temperature than most other species while both *Acer* species (10.6 °C) required less (0.6 – 2 °C). There was considerable interannual variation in average temperature during the spring phenology season. 2008 was significantly cooler (1–4 °C) than all years except 2006, whereas, 2007 was consistently significantly warmer (2–4 °C).

The average Growing Degree Hours (GDHs) during bud-burst was 861 GDHs which varied significantly between species and years (Tables 3 and 4; Supplementary Results S4). However, the heat requirement of *A. incana* (1396 GDH) during bud-burst was consistently greater by between 319 and 674 GDHs than for all other species except *A. balsamea*. In contrast, the heat requirement of *A. rubrum* (753 GDH) and *A. saccharum* (820 GDH) was significantly lower (117–643 GDH) than for the majority of other species. Furthermore, the heat requirement during 2006 was significantly less than during other years except 2010. The average heat requirement during leaf-out was 856 GDHs, similar to bud-burst. Even though there were significant differences between species no one species was consistently different from all others although *A. saccharum* (731 GDH) and *B. papyifera* (692 GDH) had a significantly lower heat requirement (210–370 GDH) than 5 other species (Tables 3 and 4; Supplementary Results S4). The heat requirement during 2007 was consistently greater than for other years. The GDHs for full leaf unfolded was 1377 which was much greater than for either of the previous phenophase categories. Again, *A. incana* (2195 GDH) required significantly more heat of between 635 and 1093 GDHs compared to all other species. The heat requirement during 2006 was significantly greater than during other years whereas, GDHs in 2009 was significantly less than other years.

The average heat accumulation during the entire phenology season (300–590) was approximately 3272 GDHs which varied by species and year (Supplementary Results S4; Tables 3 and 4). *A. incana* (4722 GDH) required significantly more GDHs (400–1644) than all other species and whereas, *A. balsamea* (4322 GDH) also required significantly more heat accumulation than 7 species, the range was slightly less (377–1245 GDHs). In contrast, both *P. tremuloides* (3089 GDH) and *B. papyifera* (3078 GDH) required significantly less heat accumulation than most other species. The number of GDHs required for the entire spring phenology season varied significantly from year to year (Tables 3 and 4; Supplementary Results S4) but 2009 was the only year to require consistently less heat accumulation than all other years.

Accumulated Growing Degree Hours (GDHs) were strongly correlated ($p < 0.0001$) with the duration of each phenophase category e.g., Fig. 4b, a similar pattern was found for all species and years (data

Table 3

Average duration (days \pm SE) of each phenophase category for each individual species and the community as a whole at the South Study Area, together with average temperature (Ave T. \pm SE) and Growing Degree Hours (GDH \pm SE) during each phenophase category. NA not enough data. Only species with five or more individuals are included and only individuals with a full set of phenophases are included.

			<i>Populus tremuloides</i>	<i>Acer rubrum</i>	<i>Acer saccharum</i>	<i>Abies balsamea</i>	<i>Alnus incana</i>	<i>Betula papyrifera</i>	<i>Betula alleghaniensis</i>	Community
2006	300–390	Days	3.21 \pm 0.5	1.95 \pm 0.6	NA	3.67 \pm 0.3	5.33 \pm 1.1	3.80 \pm 0.8	NA	3.08 \pm 0.4
		Ave T.	10.69 \pm 0.3	11.33 \pm 0.4	NA	10.10 \pm 0.3	10.52 \pm 0.2	10.93 \pm 0.4	NA	10.57 \pm 0.2
		GDH	791 \pm 68	524 \pm 69	NA	712 \pm 65	1433 \pm 377	939 \pm 130	NA	755 \pm 44
	400–490	Days	4.16 \pm 0.4	3.67 \pm 0.4	NA	6.36 \pm 0.3	4.15 \pm 0.5	3.30 \pm 0.7	NA	4.74 \pm 0.3
		Ave T.	9.85 \pm 0.4	10.61 \pm 0.2	NA	9.11 \pm 0.3	10.57 \pm 0.7	10.73 \pm 0.7	NA	9.80 \pm 0.2
		GDH	881 \pm 84	847 \pm 100	NA	1308 \pm 116	778 \pm 267	723 \pm 118	NA	1031 \pm 62
	500–590	Days	9.20 \pm 0.4	11.38 \pm 0.5	NA	4.32 \pm 0.4	10.77 \pm 0.6	7.00 \pm 0.8	NA	7.41 \pm 0.4
		Ave T.	10.61 \pm 0.4	9.26 \pm 0.2	NA	14.30 \pm 0.3	10.34 \pm 0.8	12.11 \pm 0.7	NA	12.02 \pm 0.3
		GDH	1968 \pm 101	2685 \pm 230	NA	1520 \pm 100	3137 \pm 374	1967 \pm 159	NA	1966 \pm 82
	300–590	Days	15.90 \pm 0.6	18.21 \pm 0.7	NA	19.64 \pm 0.5	22.00 \pm 1.4	15.20 \pm 1.1	NA	1807 \pm 0.3
		Ave T.	9.94 \pm 0.2	9.61 \pm 0.1	NA	10.49 \pm 0.1	10.15 \pm 0.4	10.61 \pm 0.4	NA	10.18 \pm 0.1
		GDH	3740 \pm 139	4174 \pm 223	NA	4947 \pm 70	5413 \pm 670	3823 \pm 140	NA	4400 \pm 88
2007	300–390	Days	1.90 \pm 0.1	2.97 \pm 0.5	NA	4.24 \pm 0.4	4.44 \pm 0.7	2.30 \pm 0.8	NA	2.69 \pm 0.1
		Ave T.	14.81 \pm 0.3	12.54 \pm 0.2	NA	16.04 \pm 0.2	13.04 \pm 0.3	16.77 \pm 0.4	NA	14.45 \pm 0.2
		GDH	694 \pm 28	868 \pm 66	NA	1440 \pm 71	1362 \pm 159	960 \pm 134	NA	934 \pm 37
	400–490	Days	3.30 \pm 0.3	3.21 \pm 0.4	NA	3.93 \pm 0.3	4.00 \pm 0.5	2.50 \pm 0.7	NA	3.42 \pm 0.1
		Ave T.	14.58 \pm 0.2	14.65 \pm 0.4	NA	12.71 \pm 0.3	13.81 \pm 0.4	15.88 \pm 0.5	NA	14.31 \pm 0.2
		GDH	1142 \pm 62	1141 \pm 69	NA	1170 \pm 59	1350 \pm 135	866 \pm 92	NA	1150 \pm 37
	500–590	Days	3.30 \pm 0.3	4.79 \pm 0.5	NA	7.71 \pm 0.6	5.74 \pm 0.6	3.10 \pm 0.9	NA	4.57 \pm 0.2
		Ave T.	12.68 \pm 0.3	14.09 \pm 0.4	NA	13.00 \pm 0.1	14.14 \pm 0.5	11.84 \pm 0.3	NA	13.13 \pm 0.2
		GDH	970 \pm 46	1577 \pm 69	NA	2477 \pm 72	1941 \pm 204	910 \pm 101	NA	1433 \pm 57
	300–590	Days	8.66 \pm 0.4	12.00 \pm 0.6	NA	17.92 \pm 0.7	16.25 \pm 0.8	8.40 \pm 1.1	NA	11.59 \pm 0.3
		Ave T.	13.76 \pm 0.1	13.66 \pm 0.1	NA	13.43 \pm 0.0	13.46 \pm 0.1	14.25 \pm 0.2	NA	13.69 \pm 0.1
		GDH	2845 \pm 63	3923 \pm 152	NA	5772 \pm 117	5216 \pm 237	2847 \pm 201	NA	3780 \pm 106
2008	300–390	Days	3.74 \pm 0.3	3.78 \pm 0.3	5.50 \pm 0.8	NA	8.79 \pm 0.5	6.30 \pm 0.6	NA	4.11 \pm 0.2
		Ave T.	9.06 \pm 0.1	9.86 \pm 0.2	9.85 \pm 0.8	NA	8.91 \pm 0.2	10.30 \pm 0.8	NA	9.34 \pm 0.1
		GDH	733 \pm 62	978 \pm 93	982 \pm 282	NA	1636 \pm 190	1151 \pm 321	NA	923 \pm 53
	400–490	Days	2.93 \pm 0.2	3.38 \pm 0.2	4.92 \pm 0.6	NA	5.00 \pm 0.4	2.35 \pm 0.5	NA	3.20 \pm 0.1
		Ave T.	9.76 \pm 0.2	10.14 \pm 0.3	9.59 \pm 0.3	NA	9.59 \pm 0.3	10.20 \pm 0.6	NA	9.87 \pm 0.1
		GDH	694 \pm 44	675 \pm 53	1065 \pm 192	NA	1135 \pm 107	637 \pm 118	NA	747 \pm 33
	500–590	Days	6.12 \pm 0.3	8.23 \pm 0.4	6.70 \pm 1.0	NA	9.30 \pm 0.6	6.00 \pm 1.0	NA	7.04 \pm 0.2
		Ave T.	9.99 \pm 0.1	10.30 \pm 0.1	10.61 \pm 0.2	NA	10.27 \pm 0.2	10.61 \pm 0.3	NA	10.16 \pm 0.1
		GDH	1427 \pm 65	1998 \pm 121	1743 \pm 204	NA	2265 \pm 163	1491 \pm 212	NA	1688 \pm 56
	300–590	Days	12.55 \pm 0.6	15.63 \pm 0.5	16.88 \pm 1.1	NA	22.16 \pm 0.7	14.25 \pm 1.1	NA	14.70 \pm 0.4
		Ave T.	9.61 \pm 0.1	9.97 \pm 0.1	9.79 \pm 0.1	NA	9.47 \pm 0.1	10.00 \pm 0.1	NA	9.71 \pm 0.0
		GDH	2921 \pm 103	3779 \pm 140	3989 \pm 275	NA	5104 \pm 136	3405 \pm 425	NA	3451 \pm 88
2009	300–390	Days	2.02 \pm 0.3	3.01 \pm 0.3	3.33 \pm 0.8	NA	5.48 \pm 0.5	3.17 \pm 0.5	2.86 \pm 1.0	2.88 \pm 0.2
		Ave T.	13.01 \pm 0.3	9.98 \pm 0.3	9.71 \pm 0.5	NA	11.39 \pm 0.4	11.12 \pm 0.7	11.98 \pm 1.2	11.57 \pm 0.2
		GDH	606 \pm 44	767 \pm 73	752 \pm 169	NA	1483 \pm 115	860 \pm 112	776 \pm 172	784 \pm 38
	400–490	Days	2.37 \pm 0.2	1.84 \pm 0.2	2.08 \pm 0.6	NA	3.60 \pm 0.4	1.92 \pm 0.4	2.86 \pm 0.8	2.30 \pm 0.1
		Ave T.	12.01 \pm 0.3	11.78 \pm 0.4	11.53 \pm 0.9	NA	10.67 \pm 0.4	14.40 \pm 1.0	13.77 \pm 1.6	12.03 \pm 0.2
		GDH	594 \pm 38	564 \pm 48	635 \pm 146	NA	874 \pm 89	648 \pm 95	875 \pm 162	629 \pm 27
	500–590	Days	4.51 \pm 0.3	4.04 \pm 0.3	4.17 \pm 0.8	NA	5.38 \pm 0.5	3.04 \pm 0.6	2.14 \pm 1.0	4.25 \pm 0.1
		Ave T.	10.83 \pm 0.2	13.77 \pm 0.3	14.74 \pm 0.5	NA	12.55 \pm 0.5	14.57 \pm 0.5	15.23 \pm 1.0	12.54 \pm 0.2
		GDH	1107 \pm 50	1329 \pm 77	1470 \pm 167	NA	1620 \pm 139	1014 \pm 100	778 \pm 167	1230 \pm 39
	300–590	Days	9.02 \pm 0.3	9.02 \pm 0.4	9.83 \pm 0.9	NA	15.07 \pm 0.6	8.25 \pm 0.7	8.00 \pm 1.2	9.62 \pm 0.2
		Ave T.	11.13 \pm 0.1	12.28 \pm 0.2	12.53 \pm 0.3	NA	11.28 \pm 0.2	12.86 \pm 0.4	13.22 \pm 0.8	11.77 \pm 0.1
		GDH	2341 \pm 62	2700 \pm 89	2963 \pm 195	NA	4099 \pm 153	2573 \pm 133	2454 \pm 280	2692 \pm 55
2010	300–390	Days	2.48 \pm 0.3	2.71 \pm 0.4	3.00 \pm 1.0	5.37 \pm 0.4	4.29 \pm 1.0	4.52 \pm 0.6	3.67 \pm 1.1	3.54 \pm 0.3
		Ave T.	9.96 \pm 0.5	9.70 \pm 0.4	11.31 \pm 0.8	9.97 \pm 0.3	9.92 \pm 0.7	8.49 \pm 0.6	9.82 \pm 1.7	9.78 \pm 0.2
		GDH	565 \pm 34	635 \pm 64	798 \pm 112	1150 \pm 90	1066 \pm 225	791 \pm 143	765 \pm 197	772 \pm 36
	400–490	Days	3.32 \pm 0.2	3.25 \pm 0.3	3.00 \pm 0.7	6.51 \pm 0.2	4.23 \pm 0.6	3.67 \pm 0.4	5.71 \pm 0.8	3.94 \pm 0.2
		Ave T.	11.36 \pm 0.5	10.44 \pm 0.5	9.52 \pm 1.0	8.97 \pm 0.5	9.56 \pm 1.8	11.00 \pm 0.7	10.57 \pm 1.8	10.45 \pm 0.3
		GDH	766 \pm 47	602 \pm 35	587 \pm 83	1210 \pm 74	568 \pm 117	965 \pm 112	1122 \pm 321	867 \pm 34
	500–590	Days	6.16 \pm 0.3	6.04 \pm 0.3	5.70 \pm 0.9	5.47 \pm 0.3	8.04 \pm 0.6	4.96 \pm 0.6	3.43 \pm 1.0	5.39 \pm 0.2
		Ave T.	14.37 \pm 0.5	8.49 \pm 0.5	7.39 \pm 0.8	15.25 \pm 0.5	10.84 \pm 1.5	15.10 \pm 1.0	15.94 \pm 1.4	13.39 \pm 0.3
		GDH	1597 \pm 80	1152 \pm 94	1143 \pm 209	1810 \pm 95	2013 \pm 438	1439 \pm 127	1122 \pm 180	1544 \pm 49
	300–590	Days	11.39 \pm 0.4	12.23 \pm 0.5	13.57 \pm 1.2	18.88 \pm 0.5	16.86 \pm 1.2	13.52 \pm 0.7	13.33 \pm 1.3	13.87 \pm 0.3
		Ave T.	11.82 \pm 0.4	8.79 \pm 0.2	8.37 \pm 0.1	10.20 \pm 0.2	9.29 \pm 0.6	10.50 \pm 0.5	11.47 \pm 1.5	10.58 \pm 0.2
		GDH	3033 \pm 74	2536 \pm 112	2666 \pm 148	4636 \pm 147	3777 \pm 505	3336 \pm 179	3288 \pm 401	3391 \pm 76

not shown), the longer the duration the greater the heat accumulation. However, if heat accumulation was driving the duration of the phenophase categories, we would have expected it to be constant across years, for each individual species and each individual phenophase.

4. Discussion

4.1. Timing of spring phenophase categories, bud-burst, leaf-out and full leaf unfolded

The contribution of individual species to the overall spring green-up in a forest community is dependent on a range of biotic (species composition) and abiotic (temperature and photoperiod) factors. It is generally accepted that as spring temperature rises (due to climate

Table 4
Average duration (days \pm SE) of each phenophase category for each individual species and the community as a whole at the North Study Area, together with average temperature (Ave T. \pm SE) and Growing Degree Hours (GDH \pm SE) during each phenophase category. Only species with five or more individuals are included and only individuals with a full set of phenophases are included.

		Populus tremuloides	Acer rubrum	Acer saccharum	Abies balsamea	Tilia americana	Betula papyrifera	Betula alleghaniensis	Populus grandidentata	Larix laricina	Community
2008	300–390	5.94 \pm 0.6	3.54 \pm 0.3	5.62 \pm 0.2	NA	8.42 \pm 0.5	NA	NA	NA	2.36 \pm 0.8	4.50 \pm 0.2
	Ave T.	9.26 \pm 0.4	9.38 \pm 0.2	9.43 \pm 0.1	NA	9.55 \pm 0.4	NA	NA	NA	10.48 \pm 0.5	9.47 \pm 0.1
	GDH	1171 \pm 273	815 \pm 82	1106 \pm 65	NA	1577 \pm 243	NA	NA	NA	600 \pm 82	1035 \pm 50
	400–490	3.59 \pm 0.5	5.05 \pm 0.2	5.20 \pm 0.2	NA	5.00 \pm 0.4	NA	NA	NA	2.27 \pm 0.7	4.74 \pm 0.2
2009	Ave T.	9.14 \pm 0.5	9.45 \pm 0.2	9.47 \pm 0.1	NA	10.17 \pm 0.7	NA	NA	NA	7.23 \pm 0.2	9.35 \pm 0.1
	GDH	710 \pm 120	1141 \pm 88	1121 \pm 61	NA	897 \pm 133	NA	NA	NA	364 \pm 33	1043 \pm 45
	500–590	5.39 \pm 0.8	5.85 \pm 0.4	5.38 \pm 0.3	NA	4.89 \pm 0.9	NA	NA	NA	5.55 \pm 0.8	5.48 \pm 0.2
	Ave T.	10.58 \pm 0.3	10.80 \pm 0.1	10.68 \pm 0.1	NA	10.87 \pm 0.2	NA	NA	NA	10.55 \pm 0.1	10.71 \pm 0.1
2010	300–390	1351 \pm 227	1510 \pm 91	1383 \pm 49	NA	1239 \pm 299	NA	NA	NA	1475 \pm 31	1410 \pm 41
	Ave T.	14.08 \pm 0.9	15.48 \pm 0.5	15.86 \pm 0.3	NA	15.78 \pm 1.1	NA	NA	NA	13.00 \pm 1.0	14.67 \pm 0.5
	GDH	9.66 \pm 0.1	9.82 \pm 0.0	9.79 \pm 0.0	NA	9.93 \pm 0.1	NA	NA	NA	10.11 \pm 0.1	9.82 \pm 0.0
	400–490	3308 \pm 306	3663 \pm 77	3756 \pm 60	NA	3751 \pm 203	NA	NA	NA	3133 \pm 242	3659 \pm 48
2011	300–390	2.00 \pm 0.6	2.68 \pm 0.3	3.82 \pm 0.2	NA	4.29 \pm 0.5	4.60 \pm 1.2	4.00 \pm 1.1	4.67 \pm 1.0	5.82 \pm 0.8	3.56 \pm 0.2
	Ave T.	11.80 \pm 0.6	10.19 \pm 0.2	10.52 \pm 0.1	NA	11.02 \pm 0.5	11.19 \pm 1.8	11.03 \pm 0.7	11.01 \pm 0.9	10.84 \pm 0.2	10.58 \pm 0.1
	GDH	570 \pm 109	649 \pm 62	947 \pm 49	NA	1076 \pm 135	1065 \pm 225	935 \pm 208	1323 \pm 464	1450 \pm 102	886 \pm 36
	400–490	3.82 \pm 0.5	3.29 \pm 0.2	2.72 \pm 0.2	NA	2.50 \pm 0.4	2.20 \pm 1.0	1.83 \pm 0.9	2.50 \pm 0.7	4.55 \pm 0.7	2.97 \pm 0.1
2012	Ave T.	10.79 \pm 0.4	11.77 \pm 0.3	12.32 \pm 0.2	NA	15.78 \pm 0.7	12.92 \pm 1.8	14.28 \pm 4.2	13.40 \pm 1.3	12.33 \pm 0.5	12.40 \pm 0.2
	GDH	926 \pm 229	919 \pm 66	753 \pm 36	NA	876 \pm 109	618 \pm 63	613 \pm 160	1012 \pm 174	1383 \pm 182	832 \pm 31
	500–590	4.00 \pm 0.7	3.19 \pm 0.3	2.78 \pm 0.2	NA	2.77 \pm 0.6	1.80 \pm 1.2	1.83 \pm 1.1	2.80 \pm 1.2	3.09 \pm 0.8	2.92 \pm 0.1
	Ave T.	12.92 \pm 0.8	14.83 \pm 0.3	15.38 \pm 0.2	NA	16.55 \pm 0.5	16.17 \pm 1.2	17.61 \pm 0.8	12.86 \pm 2.0	14.38 \pm 0.2	15.17 \pm 0.2
2013	300–390	9.94 \pm 0.8	9.48 \pm 0.4	9.71 \pm 0.2	NA	9.76 \pm 1.13	719 \pm 177	732 \pm 141	707 \pm 95	1018 \pm 178	965 \pm 33
	Ave T.	11.40 \pm 0.2	11.59 \pm 0.1	11.69 \pm 0.1	NA	9.92 \pm 0.4	9.00 \pm 1.4	8.17 \pm 1.3	11.40 \pm 1.4	16.46 \pm 1.0	11.00 \pm 0.5
	GDH	2744 \pm 199	2660 \pm 83	2737 \pm 54	NA	12.54 \pm 0.2	12.57 \pm 1.1	12.93 \pm 0.6	11.53 \pm 0.8	12.12 \pm 0.1	11.76 \pm 0.1
	400–490	2.80 \pm 0.8	2.74 \pm 0.4	2.82 \pm 0.2	7.14 \pm 1.0	3001 \pm 109	2558 \pm 344	2494 \pm 149	3184 \pm 565	4759 \pm 288	2806 \pm 46
2014	Ave T.	9.74 \pm 0.6	12.10 \pm 0.2	11.44 \pm 0.1	8.26 \pm 0.8	3.29 \pm 0.5	NA	2.83 \pm 1.1	2.11 \pm 0.9	NA	3.01 \pm 0.2
	GDH	650 \pm 74	788 \pm 73	740 \pm 49	1335 \pm 266	560 \pm 54	NA	757 \pm 117	729 \pm 53	NA	738 \pm 33
	500–590	4.10 \pm 0.7	3.09 \pm 0.2	3.44 \pm 0.2	5.47 \pm 0.5	5.42 \pm 0.4	NA	6.00 \pm 0.9	2.22 \pm 0.7	NA	3.42 \pm 0.2
	Ave T.	11.79 \pm 1.3	10.99 \pm 0.5	10.65 \pm 0.4	8.32 \pm 1.3	9.00 \pm 0.7	NA	8.14 \pm 1.3	16.89 \pm 0.5	NA	10.63 \pm 0.3
2015	300–390	6.73 \pm 0.8	5.64 \pm 0.3	5.66 \pm 0.2	916 \pm 69	1093 \pm 96	NA	11.49 \pm 356	982 \pm 91	NA	737 \pm 34
	Ave T.	15.98 \pm 0.9	8.24 \pm 0.5	9.48 \pm 0.4	9.14 \pm 0.6	5.04 \pm 0.6	NA	5.33 \pm 1.2	3.14 \pm 1.0	NA	5.75 \pm 0.2
	GDH	2033 \pm 257	1190 \pm 107	1247 \pm 76	14.61 \pm 0.7	15.63 \pm 0.7	NA	13.94 \pm 1.6	20.78 \pm 0.9	NA	11.26 \pm 0.4
	400–490	13.20 \pm 1.0	12.53 \pm 0.5	12.22 \pm 0.4	1584 \pm 102	1854 \pm 163	NA	17.49 \pm 221	1590 \pm 245	NA	14.09 \pm 0.5
2016	300–390	12.39 \pm 0.7	9.16 \pm 0.2	9.60 \pm 0.2	17.57 \pm 1.2	14.71 \pm 0.7	NA	15.33 \pm 1.3	7.43 \pm 1.2	NA	13.34 \pm 0.4
	Ave T.	3780 \pm 327	2681 \pm 167	2728 \pm 114	9.60 \pm 0.2	10.65 \pm 0.4	NA	9.85 \pm 0.9	17.98 \pm 1.1	NA	10.16 \pm 0.2
	GDH	4055 \pm 314	4055 \pm 314	4055 \pm 314	4055 \pm 314	3712 \pm 153	NA	3657 \pm 530	3187 \pm 280	NA	3019 \pm 82

Table 5

Anomalies for (i) timing of phenophase categories (Phenology anomaly), (ii) average daily temperature from February 1 to the start of each phenophase (February temperature anomaly) and (iii) cumulative heat (Growing Degree Hours) to start of each phenophase (Cumulative heat anomaly) for each species at the South Study Area. 300: bud-burst; 400: leaf-out; 500: full leaf unfolded. Since average spring temperature anomaly did not vary between species the data are displayed in Fig. 4 only.

Species	Year	Phenology anomaly (days)			February temperature anomaly (°C)			Cumulative heat anomaly (GDH)		
		300	400	500	300	400	500	300	400	500
<i>Populus tremuloides</i>	2006	−2.24	−1.48	−0.14	0.47	0.52	0.56	623	751	900
	2007	−2.86	−3.49	−3.18	−0.56	−0.53	−0.34	997	1026	1375
	2008	3.48	4.26	4.22	−2.04	−1.96	−1.94	−2163	−2094	−2165
	2009	−0.20	−0.68	−1.37	−0.53	−0.54	−0.61	−1502	−1553	−1764
	2010	−0.31	−0.24	0.03	3.27	3.15	3.06	3364	3289	3306
<i>Acer rubrum</i>	2006	−6.17	−7.19	−6.39	0.15	0.06	0.12	−71	−306	−199
	2007	−6.16	−5.93	−5.07	−0.98	−0.83	−0.56	195	4.0	924
	2008	5.30	6.34	6.58	−1.77	−1.65	−1.64	−1568	−1378	−1427
	2009	5.03	4.79	3.91	0.12	0.07	−0.01	−2.14	−69	−248
	2010	−8.95	−9.34	−8.86	2.77	2.64	2.54	1735	1589	1503
<i>Alnus incana</i>	2006	−2.37	−2.98	−3.62	1.04	0.91	0.78	1229	1078	848
	2007	−4.05	−4.57	−4.18	−0.38	−0.28	−0.04	970	1093	1588
	2008	2.51	4.04	4.91	−1.65	−1.50	−1.42	−1641	−1542	−1459
	2009	1.69	1.48	0.90	0.18	0.15	0.06	−531	−524	−710
	2010	−2.89	−4.52	−4.90	3.68	3.47	3.16	3557	3088	2664
<i>Betula papyrifera</i>	2006	−0.95	−0.43	0.24	−0.14	−0.09	−0.10	155	265	220
	2007	−2.75	−4.43	−4.46	−1.18	−1.11	−1.00	436	454	583
	2008	4.50	5.52	5.74	−2.62	−2.42	−2.39	−2636	−2426	−2512
	2009	4.50	3.77	2.70	−0.72	−0.71	−0.76	−1040	−1088	−1272
	2010	−4.66	−3.73	−2.98	2.24	2.11	2.11	1745	1666	1851

change) leaf phenology advances (Root et al., 2003; Donnelly et al., 2006; Menzel et al., 2006; Parmesan 2007; Ellwood et al., 2013; Yu et al., 2015) and progresses at a faster rate (Yu et al., 2015). However, not all forest species follow this rule with some species advancing the timing of leaf-out faster than others or not at all. Therefore, it is useful to investigate the role played by different species in contributing to the green-up process. However, many factors influence the timing of bud-burst which results in substantial intra- and inter-specific variation in spring phenology. Variation in the timing of leaf-out is an adaptive trait that maximizes the growing season length while reducing the potential impact of damage from early frost, herbivory or other environmental factors (Lechowicz, 1984; Kramer et al., 2010; Wesolowski and Rowinski, 2008). Several reasons have been proposed that may at least partly explain both intra- and inter-specific differences in phenology. For example, Doi and Katano (2008) reported that species with low genetic diversity showed less variation in the timing of bud-burst than species with high genetic diversity. It has also been shown that wood anatomy type may also play a role in forest phenology timing in that diffuse porous species tend to leaf-out earlier than ring porous (Lechowicz, 1984). Most trees species possess diffuse porous wood (Metcalf and Chalk, 1950) in which small vessel elements (pores) are produced throughout the growing season making it less susceptible to embolism in winter whereas, ring-porous wood produces a range of vessel sizes with larger ones (earlywood) being more susceptible to damage by winter frost. The large vessels are replaced in spring which contributes to delayed leaf-out. Only hardwoods are considered porous with pore size and distribution affecting appearance and hardness of wood. Softwoods do not possess pores (transport of water is conducted in tracheid cells) and, therefore, are referred to as having non-porous wood. Furthermore, species with an opportunistic life strategy tend to resume growth early in spring once the temperature begins to rise, but this leaves them susceptible to potential damage from late frost whereas, late successional species adopt a more cautious approach and tend to resume growth later in the season (Caffarra and Donnelly 2010; Körner and Basler 2010; Yu et al., 2015). In addition, species higher in the canopy tend to leaf-out later than those occupying lower layers (Lopez et al., 2008; Yu et al., 2015). Therefore, the timing of leaf-out in a forest community is influenced by many factors including, species composition, ecological niche, wood type, structural position and genetic makeup but more than likely other factors may also play a

significant role. As different species start to leaf-out at different times and (importantly) progress at different rates, the result is a complex, gradual transition from dormancy to canopy closure during the spring season. In the current study the median timing of the start of 3 phenophase categories (bud-burst, leaf-out and full leaf unfolded) varied over the 5 year study period in line with local spring temperature. In general, community phenology (averaged across all species) was earliest, in 2010 and latest in 2008 which were the warmest and coolest springs respectively. However, as expected, the timing of these phenophases was species specific in agreement with many previous studies (Lechowicz, 1984; Donnelly et al., 2006; Menzel et al., 2006; Lopez et al., 2008; Yu et al., 2015), although an earlier start for one phenophase did not necessarily result in an earlier start to subsequent phenophases.

Numerous factors contribute to early or late leafing species that also appears to be location specific. However, some features do appear related to evolutionary strategies. For example, the start of bud-burst for *A. incana* (Speckled Alder) (SSA), tended to be earlier than other species but this pattern was in contrast to subsequent phenophase categories whereas, both *Betula* species tended to exhibit later spring phenology. Earlier bud-burst of *A. incana* was consistent with the growth strategy of this species as a pioneer which is shade intolerant, has an indeterminate growth habit i.e., can have several ‘spurts’ of growth throughout the growing season when conditions are optimal and occupies a lower layer beneath the main forest canopy. Therefore, we may expect these species to begin bud-burst early in the season before being shaded out by other trees.

Indeed, a similar pattern was reported from a small urban woodland in Wisconsin (USA) whereby *Acer negundo* (Boxelder), an understory shrubby species, leafed out earlier than taller upper canopy species such as *Tilia americana* (Basswood) and *Fraxinus americana* (White Ash) (Yu et al., 2015). Similarly, in the Appalachians Lopez et al. (2008) reported leaf-out being later in upper canopy than lower canopy species. In addition, using cuttings grown under controlled environment conditions, Caffarra and Donnelly (2011) reported a similar pattern in that life strategy of trees influenced the timing of bud-burst whereby opportunistic species (*Betula pubescens* and *Salix smithiana*) were more responsive to high temperature than late successional species (*Tilia cordata* and *Fagus sylvatica*). They concluded that opportunistic pioneer species traded a higher risk of frost damage for vigorous growth early in

the season compared to late successional species.

However, in the current 5-year study, even though *Betula* and *Populus* species have similar growth characteristics (pioneer, shade intolerant, indeterminate) to *A. incana* they did not exhibit a consistently earlier trend to the onset of any of the phenophase categories. This is in contrast to results from Minnesota, USA and Quebec, Canada where *B. papyrifera* in a deciduous forest community was reported to flush earlier than late successional species (Lechowicz, 1984). In addition, Lechowicz (1984) also showed that *P. grandidentata* leafed out later than *P. tremuloides* consistent with the current study and earlier than *T. americana* in contrast to results from the NSA in Wisconsin. These results highlight both the species and location specific nature of phenology in a forest community and that numerous factors contribute to early or late leafing species that also appears to be location specific. Furthermore, care must be taken when comparing results from controlled environment experiments and field studies as recent reports have demonstrated that cuttings and mature trees do not necessarily respond to warming at the same rate (Wolkovich et al., 2012; Vitasse, 2013). Mature trees will evidently be exposed to changes over a much longer time-period than those under experimental conditions and care must be exercised when making comparisons.

The timing of the spring phenophase categories of the late successional, shade tolerant, determinate growth habit i.e., one growth spurt per season, species also varied. Both *Acer rubrum* (Red Maple) and *A. saccharum* (Sugar Maple) tended to be earlier, as regards the timing of the phenophase categories, than the community as a whole while *T. americana* (Basswood) was later. In a study of deciduous forest trees at two locations (Minnesota, USA and Quebec, Canada) Lechowicz (1984) reported a similar pattern with earlier leafing of both early (*B. papyrifera*) and late successional (*A. saccharum*) species while *T. americana* a late successional species tended to flush late. Therefore, he concluded that ecological niche alone could not account for the timing of leaf-out in a deciduous forest.

A. balsamea (Balsam Fir), one of only two conifer species examined, is late successional, shade tolerant and has a determinate growth habit. It generally exhibited later phenology than the community as a whole particularly for the late phenophase categories, which is in line with its growth characteristics. On the other hand, *Larix laricina* (Tamarack) – pioneer, shade intolerant, determinate- showed no consistent pattern in the timing of spring phenology based on only two years of data at the NSA. Some species (*A. incana*) conformed to an expected early spring phenology, based on their growth characteristics, but others (*P. tremuloides*, *B. papyrifera* and *B. alleghaniensis*) did not. In view of the short time period covered by this study it is not wholly unexpected to find such inconsistencies in the onset of spring phenophases and a longer term data set may reveal more consistent patterns.

Trends in the timing of phenology may also reflect wood anatomical characteristics of particular species. Tree species with diffuse porous wood anatomy may be either determinate or indeterminate in growth strategy whereas, ring-porous tend to be determinate only. Tree species that leaf earliest are generally diffuse porous but may be either early successional e.g., *Alnus*, *Betula*, *Populus*, or late successional e.g., *Acer*, whereas, ring porous species tend to be consistently late as vessels damaged by cavitation in winter must be repaired prior to leaf-out in spring which delays the process (Lechowicz, 1984). There were no species with ring-porous wood in the current study however in a woodlot, with similar species to the current forest, Yu et al. (2015) reported ring-porous species (*Fraxinus americana* and *Quercus* spp.) consistently leafed out later than diffuse-porous species.

4.2. Duration of spring phenophase categories: bud-burst, leaf-out and full leaf unfolded

The timing of bud-burst is possibly the most widely observed, recorded and reported phenophase across many regions both *in situ* and by satellite remote sensing (Reed et al., 1994; Schwartz et al., 2002; De

Beurs and Henebry, 2005; Ahl et al., 2006; Julien and Sobrino, 2009). Both methods have successfully shown that spring phenology has become earlier in recent decades and this can be attributed to climate change (Zhang et al., 2004; Menzel et al., 2006; Zhang et al., 2007; Jeong et al., 2011; Zhang et al., 2013). Although the timing of bud-burst is well documented, less had been reported on the duration of spring phenophases and whether or not a change in the rate at which different phenophases progress during the season has occurred in recent years. It has often been reported that changes in the timing of leaf-out has important implications for carbon sequestration (Black et al., 2000; Piao et al., 2007; Richardson et al., 2009; Polgar and Primack, 2011; Keenan et al., 2014), but equally the rate at which leaves develop and mature in early spring will impact the rate at which carbon is removed from the atmosphere and the rate at which water is being removed from the soil. In the current study we found the duration of the bud-opening and leaf-out phases lasted approximately 4 days (each) with some variation across species and years particularly in the bud-opening phase. The notable exceptions were (i) *A. incana*, which exhibited significantly longer bud-opening durations than most other species and (ii) *P. tremuloides* and *A. rubrum* which completed bud-opening in a shorter duration than most other deciduous species. Since, *A. incana* is an opportunistic species it was not surprising that it took a greater (2 days) than average time over which to bud-burst in spring as, being indeterminate, they are not restricted to one growth episode and can respond to environmental cues as they become optimal. However, even though *P. tremuloides* and *A. rubrum* exhibit different life strategies both completed bud-burst quickly, indicating that life strategy cannot always indicate phenological behavior. Therefore, similar to the beginning of each phenophase the duration of these two early phenophases varied among species and only somewhat reflected the growth strategy, location in the canopy and wood anatomy of the individual species.

The last phenophase category, full leaf opening, took just over a day longer than the previous phases i.e., bud-burst and leaf-out, with *A. incana* taking between 2 and 4 days longer than other species, again reflecting the opportunistic nature of this species' growth habit. In general, the spring phenology season from bud-burst to full leaf open for the entire forest community took an average of 2 weeks (13 days) to complete with *A. incana* taking nearly 5 days longer (18 days) than other species whereas, *P. tremuloides* and *B. papyrifera* completed spring phenology in a shorter duration (one day less). The 3 late successional deciduous species (*T. americana*, *A. saccharum* and *A. rubrum*) did not vary greatly from the community average whereas, the more opportunistic pioneer deciduous species showed greater (2–5 days) variation. Both the late successional *A. balsamea* and the early successional *L. laricina* conifer species tended to be later by 3 and 2 days respectively than the community average. Overall, the earlier phenophases progressed more rapidly than the later one which could have implications for future predictions of the rate of carbon sequestration from the atmosphere in early spring.

4.3. The influence of temperature parameters on spring phenology

Interannual variation in the duration of the spring phenology season between years closely tracked local temperature. The progress of the spring phenology season was fastest in 2009 (11 days; 2–7 days shorter than other years) and slowest in 2006 (18 days; 2–7 days longer than other years) which reflected the difference in heat accumulation between these two years. The number of accumulated GDHs (Growing Degree Hours) during the spring phenology season was 3134 (significantly less than all years) in 2009 and 4313 (significantly more than all years except 2007) in 2006 demonstrating the close relationship between forcing temperature and phenophase duration. As chilling requirements and active chilling temperature for these species have not been studied to date, it was not possible to determine the date of chilling fulfillment and verify its relation with variation in green-up timing. However, as the two sites are characterized by cold winters with

temperature falling below 10 °C from October onwards, we assumed that by January, chilling requirements were not limiting for growth resumption. It was interesting to note the wide range of GDHs to the start of bud-opening for individuals of the same species at the same site demonstrating that GDH alone is not a good predictor of the timing of spring phenology but timing tended to track average spring temperature.

In phenological models, growing degree days has often been used as an indicator of the timing of bud-burst and has been shown to be effective especially when only a small number of individuals are being tested which generally reach a particular phenophase at roughly the same time (Cannell and Smith, 1983; Chuine et al., 1998, 1999; Caffarra et al., 2011; Yu et al., 2015). However, when many individuals are observed the timing of a particular phenophase e.g., bud-burst, can occur over an extended time period which subsequently means the heat accumulation may vary considerably. Individuals that bud-burst later in the season will naturally accumulate more heat than those earlier in the season. Similarly, species that exhibit an extended duration for bud-burst will accumulate more heat than those with a shorter duration. In order for heat accumulation to be a useful predictor of bud-burst GDHs should remain constant for each individual and from year to year. We did not find this to be the case and so we could not use this parameter as an effective predictor of either the timing or duration of the phenophases we examined. However, when we examined the relationship between phenology anomalies and 3 temperature parameter anomalies we found that, for the majority of species and phenophases, when cumulative heat anomalies were greater than average the timing of the phenophase categories was earlier than average and vice versa. In contrast, neither average spring temperature anomalies nor average temperature from February 1 to the start of each phenophase category anomalies showed the same pattern. In particular, in 2007 when these 2 temperature parameters were cooler than average spring phenology was earlier. Therefore, whereas, average spring temperature is a good indicator of the start of the phenology season in general, accumulated heat to the start of each specific phenophase category is more accurate. This may be due to the fact that once bud-burst has been reached, warm i.e., not chilling, temperature drives phenology progression.

As the spring season progressed, the later phenophase category (500–590) experienced warmer temperature (13 °C) than the earlier categories (300–390 & 400–490) (11 °C), for 2 possible reasons, (1) it was later in the season and (2) the phenophase lasted longer. Species that tended towards a later start to the phenology season, such as *P. grandidentata* and to a lesser extent *B. alleghaniensis* required warmer temperatures during leaf-out (13 & 11 °C) and full leaf unfolded (15 °C respectively) whereas, *A. incana* and *A. saccharum* which displayed early phenology required cooler temperatures (11 °C & 11.5 °C leaf-out and full leaf unfolded respectively). Overall, *B. alleghaniensis* and *P. grandidentata* tended to complete the spring phenology season in a relatively short time (12–13 days) period but with warmer average temperatures whereas, *A. incana* took almost a week longer (18.5 days) at a cooler temperature. Interestingly, there was little variation between species and years regarding the duration of bud opening but the later phenophase categories showed more variation whereby *A. incana* had longer durations for all categories and *B. alleghaniensis* tended to be shorter for full leaf unfolded. This variation showed that the duration of the spring phenology season is species specific which is reflected in variation of the different phenophase categories. This pattern in phenology timing and duration reflects average spring temperature which naturally increases as the season progresses. Therefore, species that start development early will naturally experience cooler temperatures.

Accumulated heat during the first 2 phenophase categories, bud opening and leaf-out, was approximately 860 GDHs which was consistent with the similarity in (i) average temperature (11 °C) and (ii) duration (4 days) of these phases. Furthermore, the heat requirement during full leaf unfolded was greater (1380 GDHs) that of the

earlier categories reflecting both the extended duration of this category (5 days) and that it occurs later in the season when temperatures are naturally warmer. Again, *A. incana* was notable in that overall its heat requirement was consistently greater than for any other species for bud-burst and full leaf unfolded but not for the second phenophase category, leaf-out, reflecting its longer phenology season and the variation between phenophase categories.

4.4. Implications for monitoring and modeling of spring phenophases

Similar to *in situ* observations, satellite products such as Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) derived from Advanced Very High Resolution Radiometer (AVHRR) and Moderate Resolution Imaging Spectroradiometer (MODIS) for detecting the onset of green-up have become widely used in recent years and have proven to be extremely effective especially across large geographical areas (Zhang, 2001; Huete et al., 2002; Zhang et al., 2003; Stöckli and Vidale, 2004; Delbart et al., 2006; Fensholt and Proud, 2012). However, as yet, these remotely sensed data products do not have the ability to distinguish between very subtle transitions in phenological events, such as the gradual progression from bud-burst to leaf-out, and subsequently to full leaf unfolded. This limitation is due primarily to low spatial resolution and the fundamental difference between specific phenophases of an organism and the gradual progression of land surface phenology (Henebry and de Beurs 2013). In addition, whereas, the return time of an orbiting satellite or sensors on a geostationary satellite may be sufficient to capture rapid day-to-day changes in phenology, issues such as cloud contamination may cause interruptions in the time series during the season of interest in particular at locations with frequent cloud cover such as Western Europe. However, unmanned aircraft systems mounted with suitable sensors may overcome some of these limitations and will probably be used in the not too distant future to monitor near-ground phenology and help bridge the gap between *in situ* observations and satellite data. But, there continues to be a need for high frequency direct field observations to capture subtle changes and variation in key phenophases at the species level in a forest community, the results of which may be useful to more accurately determine carbon uptake rates in early spring, and may also be valuable for ground validation of remotely sensed phenology.

Numerous studies from a range of locations using long-term data sets of the timing of bud-burst from a variety of forest species, have clearly demonstrated an advance in spring phenology in response to local increases in temperature (Myneni et al., 1997; Peñuelas and Filella, 2001; Menzel et al., 2006; Donnelly et al., 2006; Fu et al., 2014). Subsequently, these results have been incorporated into phenological models to make future projections of the timing of the start of the growing season (Morin et al., 2009; Caffarra et al., 2011; Vitasse et al., 2011; Caffarra et al., 2014), a useful parameter for estimating the potential future carbon storage capacity of a forest community. Many of these long-term data sets have been based on a small number of individuals located at a specific site (many of the studies cited above), such as a garden participating in a phenology network, and therefore may not capture the large variation in the timing of phenological events expected in a forest community with many individuals of each species. Furthermore, whereas, knowing when the start of bud-burst occurs is necessary for determining the beginning of the growing season, and the subsequent start of carbon uptake, the duration of phenological events, such as bud-burst, leaf-out, full leaf unfolded, etc. is equally important (to estimate the rate of carbon uptake or the duration of vulnerable periods for plants) but rarely reported. The findings presented here clearly show that in a mixed forest, species specific timing and duration vary greatly.

5. Conclusions

Individual species contribute to the dynamic nature of the timing and duration of leaf-out in spring in a mixed forest community. Whereas the start of spring phenology is widely reported, the duration of key phenophases, such as, bud-burst, leaf-out and full leaf unfolded in a mixed northern forest community, has not previously been reported at the individual species level. Interestingly, it took longer for full leaf unfolded to occur than the earlier phenophase categories and again varied among species. The overall spring season lasted roughly two weeks, but an earlier start to one phenophase did not necessarily result in an earlier start to subsequent phenophases nor did it mean a faster or slower progression. Only one of the pioneer species, *A. incana*, with opportunistic, shade intolerant, indeterminate growth, exhibited greater variation in both the timing and duration of spring phenology than the more ‘conservative’ late successional species, thereby revealing a high capacity to exploit resources earlier in the season and contributing to an extension of the phenology season of the community as a whole. However, in general, ecological niche was not a suitable predictor of the timing or duration of the spring phenology season.

The short length of the time series used in this study was insufficient to determine any long term trends or establish clear temperature or other environmental drivers of individual species’ response and contribution to overall forest phenology. Therefore, it would be inadvisable to extrapolate the current tendencies to a broader spatial or temporal scale due to the limitations of the timeframe. However, this study provided a unique insight into the progression of spring phenology over a variety of species and phases and highlighted how variable the start and duration of these spring phenophase categories are. This study highlights the need for high frequency *in situ* field observations to capture subtle transitions and variation in key phenophases at the species level in a forest community, the results of which may be useful to more accurately determine carbon uptake rates in early spring.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.05.007>.

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