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Calibrating PhenoCam Data with Phenological Observations of a Black Spruce Stand

Étalonnage d'images de PhenoCam avec des observations phénologiques d'un peuplement d'épinette noire

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ABSTRACT

Bud and leaf development are important phenological events and help in defining the growing period of trees. Canopy greenness derived from PhenoCam has been used to investigate leaf phenology. Questions remain on how much the continuous records of canopy greenness represent bud developmental phases, and how growing period boundaries are related to canopy greenness and bud phenology. In this study, we compared bud phenology of black spruce [*Picea mariana* (Mill.) B.S.P.] during 2015, 2017 and 2018 with the canopy greenness, represented by Green Chromatic Coordinate (GCC), derived from PhenoCam images of a boreal stand in Quebec, Canada. Logit models were applied to estimate the probability of observing sequential phenological phases of bud burst and bud set along with GCC. GCC showed a bell-shaped pattern, with a slow increase in spring, a peak in summer and a gradual decrease in autumn. The start and end of budburst, and bud set, occurred when GCC reached 72% and 92% (spring), and 94% (autumn) of its maximum amplitude, respectively. These GCC values are reliable thresholds indicating the growing period boundaries. Our study builds a bridge between phenological observations and automatic near-surface remote sensing, providing a statistically sound protocol for calibrating PhenoCam with field observations.

RÉSUMÉ

L'ouverture des bourgeons et le développement des feuilles représentent des événements phénologiques importants servant à définir la période de croissance des arbres. L'indice du verdissement de la végétation dérivé de caméra captant la phénologie (PhenoCam) est utilisé pour étudier l'ouverture des bourgeons. Par contre, plusieurs interrogations demeurent quant à la capacité de cet indice du verdissement à bien représenter les différentes phases de développement des bourgeons et à bien définir les limites de la saison de croissance. Dans cette étude, nous avons comparé la phénologie des bourgeons de l'épinette noire [*Picea mariana* (Mill.) BSP] en 2015, 2017 et 2018 avec les coordonnées chromatiques vertes (GCC), à partir d'images captées par des PhenoCam d'un peuplement boréal au Québec (Canada). Des modèles de type logit ont été appliqués pour estimer la probabilité d'observer les phases de débourrement et de formation des bourgeons en fonction du GCC. Tout au long de la saison de croissance, le GCC a montré un patron en forme de cloche, avec une augmentation lente au printemps, un pic en été et une diminution progressive en automne. Le début et la fin de l'ouverture des bourgeons au printemps et la formation des bourgeons à l'automne sont survenus lorsque le GCC a atteint respectivement 72%, 92% ainsi que 94% de son amplitude maximale. Ces valeurs de GCC représentent des seuils fiables indiquant les limites de la saison de croissance chez l'épinette noire. Notre étude établit un pont entre les observations phénologiques et la télédétection automatique des changements de la canopée, fournissant un protocole statistique solide pour calibrer les PhenoCam avec des observations mesurées sur le terrain.

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Introduction

Plant phenology characterizes the specific recurrent timings of biological events such as bud development or leaf senescence (Badeck et al. 2004; Lieth 1974). Plant phenology represents a functional adaptation trait of plants to the local environment. In turn, plant phenology affects many aspects of the plant life cycle including growth, reproductive performance and competition, thus strongly affecting species distribution, forest productivity and trophic patterns at both local and global scale (Cleland et al. 2007; Chuine 2010; Bartlam-Brooks et al. 2013). Bud phenology, including bud burst in spring and bud set in summer, plays a pivotal role in modulating seasonal plant phenology. Bud phenology is known to be one of the primary indicators of climate change, due to its sensitivity to environmental changes (Buitenwerf et al. 2015). Many phenology studies focused on spring phenology, while autumn phenological events received less attention and still need to be explored (Gallinat et al. 2015; Richardson et al. 2013; Yang et al. 2017; Deslauriers and Rossi 2019). Monitoring and quantifying both spring and autumn bud phenological events is therefore essential for understanding regional-to-global ecosystem carbon and energy cycling and climate change.

Traditionally, plant phenology data are recorded through human observation, based on direct visual inspection of individual plants in the field (Sparks and Menzel 2002). Data detected by this approach can be used to identify each sequential bud phenological phase (i.e., from bud swelling to leaf out, or from winter bud formation to leaf senescence) (Rossi and Bousquet 2014), which are considered to be well correlated to many physiological mechanisms (e.g., reactivation, vigorous or senescent photosynthesis) (Michailidis et al. 2018; D'Odorico et al. 2015). Because of the simple data collection and fine resolution of field observations, this approach has been applied in tracking plant phenology since the 10th century BCE (Rossi and Bousquet 2014; Silvestro et al. 2019; Menzel and Fabian 1999; Piao et al. 2019). However, direct observations are time-consuming, especially when finer temporal and spatial sampling resolutions are required (Richardson et al. 2013). This limitation hampers plant phenology research at large geographical scales, especially in remote sites or inaccessible areas (Richardson et al. 2013).

In recent decades, the use of PhenoCam based on digital repeated imagery has greatly enhanced plant phenology studies (Richardson et al. 2013). PhenoCam provides an array of high spatial and

temporal resolution information based on a repeated collection of near-ground imagery, and could thus provide continuous and quantitative information of seasonal trajectory in leaf development and senescence (Richardson et al. 2013). Based on the large network available for scientists, the PhenoCam time series can improve understanding of plant phenology from an individual, up to the landscape and even ecosystem level (Richardson et al. 2018).

Previous studies used PhenoCam-derived indices such as green chromatic coordinate (GCC), excess green index (ExG), a normalized difference of the green and red bands (VIgreen), red chromatic coordinate (RCC) and vegetation contrast index (VCI) for vegetation phenology analysis (Liu et al. 2017; Richardson et al. 2018; St Peter et al. 2018; Zhang et al. 2018). Among these, the GCC index is considered as a reliable proxy for tracking the seasonality of plant phenology (Klosterman et al. 2014; Richardson et al. 2018).

In PhenoCam studies, the determination of the phenological transition dates is usually arbitrary or refers to methods applied for imageries from satellite remote sensing (Keenan et al. 2014; Zhang et al. 2003). For instance, plant phenological transition dates were usually calculated and defined by the local minima or maxima of the rate of change in the curvature of GCC, or the 30th or 50th percentile of the amplitude of GCC (Zhang et al. 2003; Keenan et al. 2014). Such transition dates may have limited physiological significance in practical applications of plant growth or vegetation dynamics if they are not validated or confirmed by field observations. For instance, a study in a temperate deciduous forest of the northeastern US showed that canopy greenness in spring rises quickly to its maximum before leaves are even half their final size. Increases of canopy greenness also occurred before spring development of both leaf area index (LAI) and the physiological (e.g., leaf reflectance and transmittance, and chlorophyll fluorescence) and morphological (e.g., leaf area and mass) traits (Keenan et al. 2014). With the spreading network of PhenoCam, this is becoming an alternative to the traditional direct observations (Keenan and Richardson 2015; Richardson et al. 2009). There is, therefore, a need to validate PhenoCam data with the appropriate transition phases of leaf development.

Although PhenoCam studies are now available to monitor canopy phenology on evergreen species (Richardson et al. 2018; Brown et al. 2017; Melaas et al. 2016; Richardson et al. 2009; Saitoh et al. 2012), the accuracy of phenological transitional dates derived from PhenoCam is still unclear due to the elusive

seasonal cycle of the needles and canopy of evergreen species. Evergreen species generally retain their needles for several years, and the older needles then gradually drop off after a number of years that depends on the species (Reich et al. 2014). This characteristic of evergreen species prevents a clear and easy identification of needle and canopy development. Critical assessment and calibrations of the PhenoCam chronologies based on field observations of phenology are therefore essential for verifying plant phenology, but such calibrations are still scarce, mainly for conifers. In this study, the bud phenological phases of black spruce [*Picea mariana* (Mill.) B.S.P.] occurring from spring to autumn that were derived from field observations are compared with PhenoCam data. Black spruce has a wide transcontinental boreal distribution in North America, covering the latitudinal range from Alaska to Labrador. Thus, the study of the growth dynamics in this species could have a huge potential for phenological investigation and application. We aim to test and calibrate the PhenoCam derived GCC index using ordinal logit models based on the longitudinal data represented by the sequential developmental phases of bud phenology. We expect to assess reliable thresholds of GCC index for defining the start and end of the growing period in evergreen species based on PhenoCam images.

Materials and Methods

Study Site

This study was conducted at Simoncouche Research Station (48°22' N, 71°25' W, 338 m.a.s.l.) in Laurentides Wildlife Reserve, Québec, Canada. The study site is located in the balsam fir (*Abies balsamea* L. Mill.)-white birch (*Betula papyrifera* Marsh.) bioclimatic domain, in a mixed forest growing on podzol with a mor-type humus at the southern boreal zone. Black spruce is one of the dominant species in the study area. The site has a typical boreal climate, with a short and cool summer, and cold and harsh winter. The mean annual temperature is 0.9 °C, with absolute minimum and maximum temperatures of −36.7 °C in January–February and 31.1 °C in July, respectively. The mean annual precipitation is 1162 mm (Rossi 2015).

Identification of the Phenological Phases

Bud phenology was recorded weekly from May to October on 105 black spruce saplings during 2015, 2017 and 2018. The saplings were the offspring of

trees planted in a forest gap at a distance of 2×2 m in 2014. We defined the different phenological phases of budburst during spring, and bud set during summer and autumn (Dhont et al. 2010). 6 phases of bud burst were defined: open bud (BB1), with a pale spot at the tip of the bud; elongated bud (BB2), with lengthening brown scales; swollen bud (BB3), with smooth and pale-colored scales but no visible needles; translucent bud (BB4), with needles visible through the scales; split bud (BB5), with open scales but needles still clustered; and exposed shoot (BB6), with needles completely emerged from the surrounding scales and spreading outwards. 5 phases of bud set were defined: white bud (BS1), presence of a white bud; beige bud (BS2), with beige scales around the bud; brownish bud (BS3), with a significant increase in volume; brown bud (BS4), with needles starting to spread outwards; and spread needles (BS5), with the needles in the whorl spreading outwards.

Near-Surface Remote Sensing Data

In a mature black spruce stand close to the plantation, a digital camera (Netcam XL, StarDot Technologies, Buena Park, CA) was placed on the top of the weather station at 8 m from the ground, and pointed north to minimize shadows and lens flare. For minimizing variability from day to day due to scene illumination, automatic white/color balancing was turned off, and exposure adjustment was set to automatic mode (Richardson et al. 2009, 2007). Images of the canopy were collected at 30-minute intervals and stored in memory cards connected to a CR10X datalogger (Campbell Scientific Corporation, Canada).

During data extraction, we defined 10 regions of interest (ROIs) dominated by black spruce on each image to collect data from the canopy of black spruce, and exclude disturbances from the surrounding areas (i.e., the canopy of other species, sky and ground). Green chromatic coordinate (GCC) of the 10 ROIs was extracted using the xROI R package and averaged for each image (Seyednasrollah et al. 2019). Following the data extracting protocol in Richardson et al. (2018), the 90th percentile of GCC across a 1-day moving window was calculated, resulting in 365 GCC observations per year.

Curve Fitting and Statistics

GCC data was fitted with a double-logistic function (1) using the NLIN procedure in SAS (version 9.4, SAS Institute Inc., Cary, NC):

$$f(x) = gcc_{min} + (gcc_{max} - gcc_{min}) \times \left(\frac{1}{1 + \exp(-mS \times (t - S))} \right) + \left(\frac{1}{1 + \exp(mA \times (t - A))} - 1 \right) \quad (1)$$

Where gcc_{min} and gcc_{max} are the minimum and maximum values measured in winter and summer, S and A are the inflection points when the curve rises and falls, and mS and mA are the rates of increase and decrease of the curve at the inflection points (Antonucci et al. 2017; Beck et al. 2006). This function describes asymmetrical patterns, leading to a reliable estimation of the canopy greenness trajectory (Beck et al. 2006).

The estimated double-logistic functions were standardized to the range 0–1 and compared to the observed phenological phases. We applied logit models for bud burst (6 phases, i.e., BB1–BB6) and bud set (5 phases, i.e., BS1–BS5) to estimate the probability of observing each sequential phenological phase along the GCC measurements (Deslauriers et al. 2019). Such a procedure fits the proportional odds model to ordinal response data, represented here by the sequential phases of bud phenology. The ordinal logit models were applied using the LOGISTIC procedure in SAS. We assessed the performance of the model 3 times, each time with 1 of the 3 years, with model training being performed on 2 years and tested on the 3rd. Observations and predictions were compared with a regression and using goodness of fit (R^2) and root mean square error in prediction (RMSE) (Prislan et al. 2019).

Results

Observed Bud Phenology

On average, the process of bud burst began in mid-May (DOY 139 ± 2.67 , mean \pm standard deviation), and ended in mid-June (DOY 165 ± 4.07) (Figure 1). Overall, the process lasted 20–27 days, depending on the year. The duration between one specific bud burst phase and the following phase was shown to be less than a week. Bud set started at the beginning of July (DOY 185 ± 5.41), and ended at the beginning of September (DOY 224 ± 21.8). The duration between one specific bud set phase and the one following gradually increased from 1 to 3 weeks. Standard deviation between years during bud set phases was larger than that in bud burst phases, with values of 5.41–21.83 and 2.67–5.60, respectively. This means that bud set was more variable among years, especially in the last

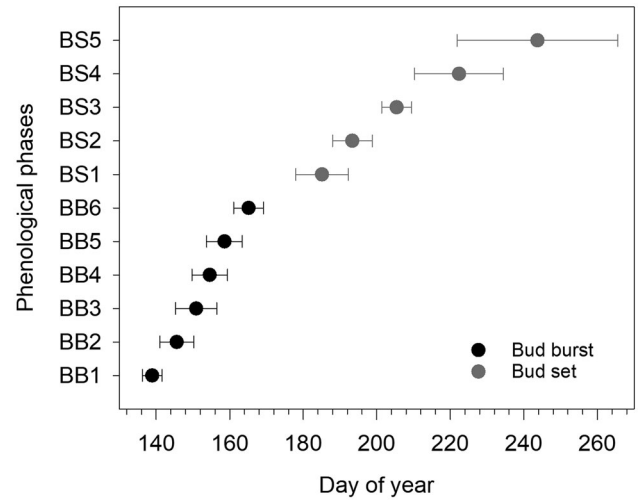


Figure 1. Occurrence of the bud phenological phases of black spruce in a southern boreal stand of Quebec, Canada. Dots and error bars represent average and standard deviation between 3 years.

phases, ranging between 45 days in 2015 and 2018, and 77 days in 2017 (Figure 1).

GCC Patterns Derived from PhenoCam

The GCC showed a bell-shaped pattern, with a slow increase in spring, followed by a rapid increase and culmination in July, gradually decreasing in autumn and winter until reaching the minimum value (Figure 2). The double-logistic function well represented GCC variation during the growing season, including the asymmetric patterns of the curve observed between spring and autumn. The goodness of fit in the curves was confirmed by the distribution of studentized residuals, which uniformly fell within the confidence interval (range between -2 and 2) in 97% of cases, confirming the model reliability (Figure 2). On average, GCC ranged from 0.32 in winter, to 0.43 in summer (Table 1). The fitted minimum GCC is not shown in Figure 2 due to the absence of observations at the beginning of 2015 (until DOY 76). The inflection points of the curves occurred at the beginning of May (DOY 122, coefficient S) and beginning of November (DOY 308, coefficient A) (Table 1). The average increasing (mS) and decreasing (mA) rates were estimated at 0.04 and 0.02, respectively (Table 1), demonstrating that the autumnal reduction in GCC was slower than the spring increase. The difference shown in mS between 2015 and the 2 other years may be due to the missing values in spring 2015 (Figure 2), when the camera was installed. Because of missing observations at the beginning of 2015 and end of 2018, the coefficient gcc_{min} in 2015 and mA in 2018 shown in Table 1 are pure extrapolated

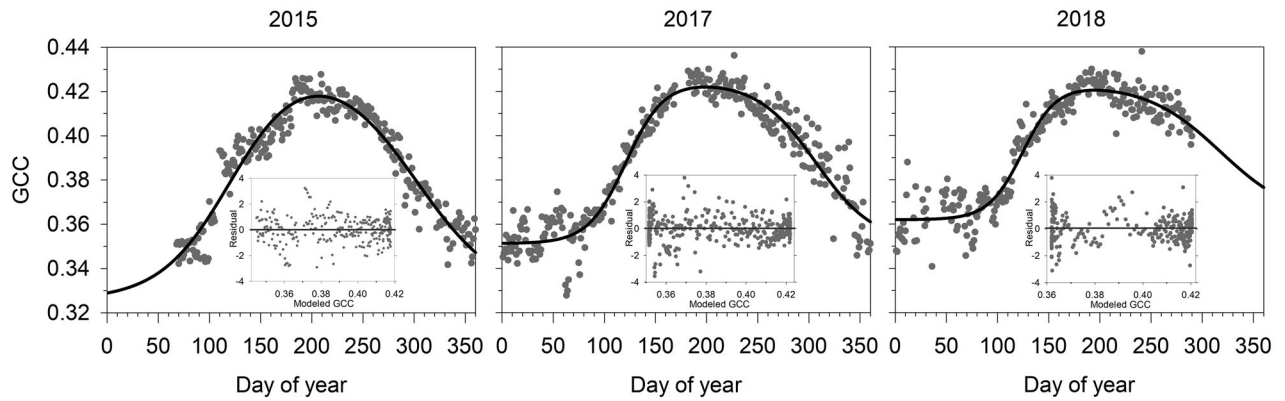


Figure 2. Daily GCC (green chromatic coordinate) fit by double-logistic equations during the 3 study years on black spruce in a southern boreal stand of Quebec, Canada. The small internal figures represent the studentized residuals vs. Modeled GCC from GLM models performed on GCC data of black spruce. The range between -2 and 2 indicates the 95% confidence interval.

Table 1. Coefficients of the double-logistic function fitted for the GCC of black spruce during 2015, 2017 and 2018 in a southern boreal stand of Quebec, Canada.

Year	Coefficients					
	gcc_{min}	gcc_{max}	S	A	mS	mA
2015	0.3258	0.4376	121.61	299.86	0.0290	-0.0238
2017	0.3512	0.4247	121.03	306.59	0.0543	-0.0349
2018	0.3620	0.4233	124.45	317.88	0.0600	-0.0277

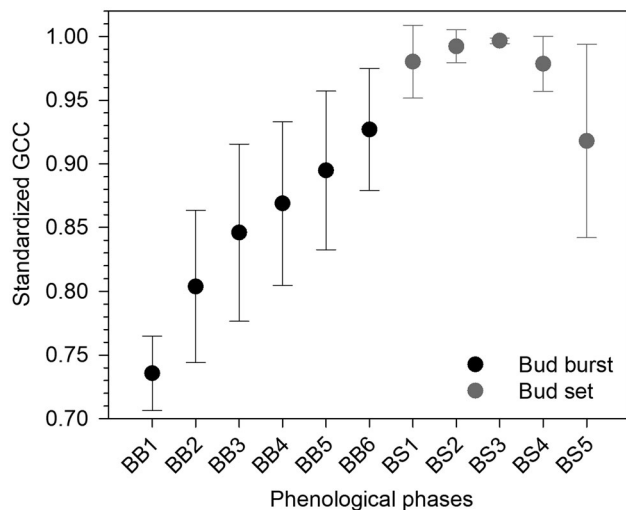


Figure 3. Standardized GCC measured at each bud phenological phase of black spruce in a southern boreal stand of Quebec, Canada. Dots and error bars represent average and standard deviation between 3 years.

values and should be considered with care (Table 1 and Figure 2).

Comparing GCC with Observed Bud Phenology

GCC increased during the whole bud burst process (i.e., BB1–BB6), including part of bud set. GCC culminated when the bud reached phase BS3, while BS4

and BS5 occurred when GCC was decreasing (Figure 3).

Model validation produced satisfying estimations of the timings of phenological phases (Figure 4). The good predictions of the model were indicated by a high R^2 (0.89) and a RMSE of 12.53 days. The regression estimated a slope of 1.03, which was not statistically different from 1 ($F=0.37$, $p>0.05$).

With $GCC < 0.6$, the probability of observing a dormant bud was 0.94, which reduced at increasing GCC (data not shown). BB1 exhibited a probability of 0.2 at GCC of 0.65, exceeded dormant bud at GCC of 0.69, and culminated at 0.52 with GCC of 0.72 (Figure 5). At this value of GCC, BB1 had the highest probability of occurring. BB2 exceeded BB1 at GCC of 0.77, culminating at a probability of 0.43 with GCC of 0.79 (Figure 5). BB3, BB4 and BB5 culminated at GCC ranging between 0.85 and 0.92 (Figure 5). $GCC > 0.92$ corresponded to the highest probability of observing BB6, which represents the end of the bud burst process. BS1–BS3 showed the highest probability of being observed at GCC varying between 1 and 0.98 (Figure 5). In autumn, BS4 occurred with the highest probability at GCC of 0.95 (Figure 5). When $GCC < 0.94$, BS5 was the most likely phase, indicating that bud set was complete (Figure 5).

Discussion

Near-surface remote sensing data are a distinct and growing resource for documentation and interpretation of individual to ecosystem-level phenological responses to climate change (Richardson et al. 2009). However, there is a lack of clear practical-implication guidance regarding how to determine the phenological transition dates in evergreen species due to their unclear seasonal color changes of canopy (Sonnentag

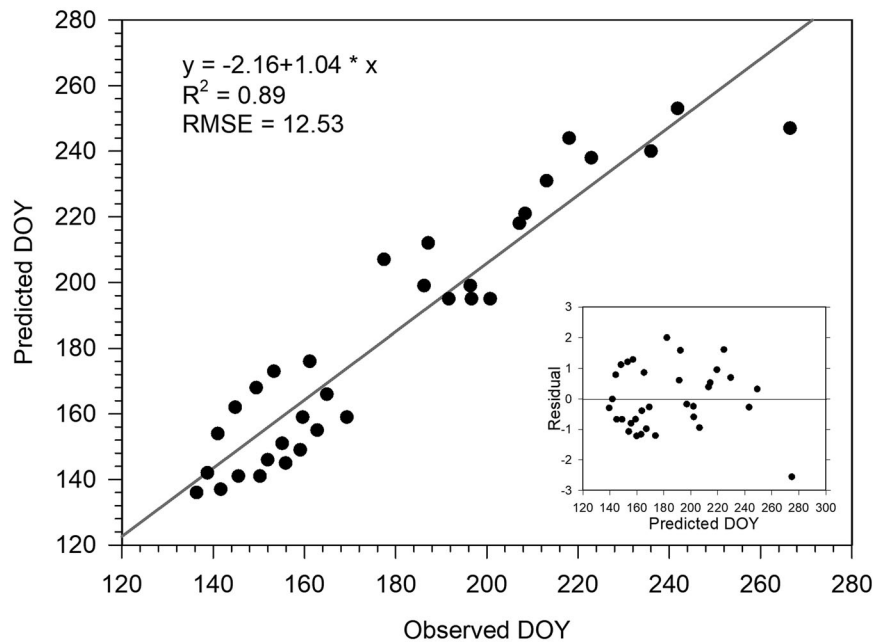


Figure 4. Relationship between observed DOY and simulated DOY in 3 years. The gray line is the regression line between observed DOY and simulated DOY. The small panel shows the distribution of the residuals.

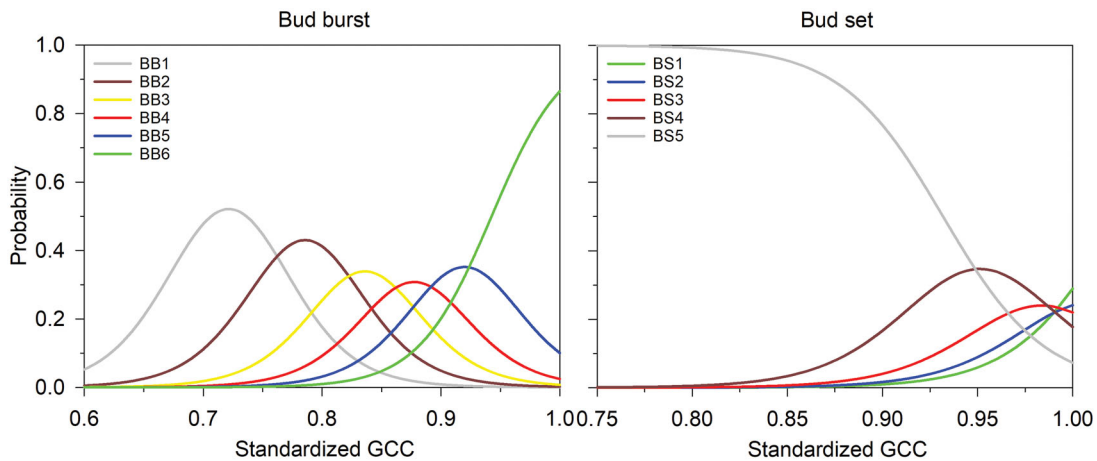


Figure 5. Probability of each bud phenological phase estimated along the standardized GCC of black spruce in a southern boreal stand of Quebec, Canada.

et al. 2012). To offer a solution to this, we investigated the dynamics of canopy greenness (i.e., GCC) in black spruce and timing of the sequential bud phenological phases (i.e., 6 bud burst and 5 bud set phases), and associated the variation in GCC with these phases. Our results confirmed that GCC could be used to identify the intra-annual variability of bud phenology, including both spring bud burst and autumn bud set. Bud burst showed the highest probability of beginning when GCC reached the 72nd percentile of its amplitude in mid-May, and peaked in the middle of bud set at the end of July. The completion of bud set occurred when GCC decreased to the 94th percentile of its amplitude in the beginning of September.

Our results provide a series of options with practical significance for determining vegetation dynamics when using PhenoCam derived phenology data.

Bud Phenological Phases

The processes of bud burst and bud set in black spruce are composed of a distinctive chain of events that could produce effects on the contiguous phases, where the timing of occurrence of each phase influences that of the successive ones (Rossi and Bousquet 2014), resulting in a duration of several weeks for both bud burst and bud set. The timing of bud burst in this study was consistent with that of previous

studies, occurring during mid-May to mid-June (Perrin et al. 2017; Silvestro et al. 2019). During this period, spring warms up and daytime lengthens, frost events are unlikely in boreal regions, so trees can resume growth without the risk of frost damage to developing meristems (Rossi and Bousquet 2014). In our study, bud set began at the beginning of July and was completed at the beginning of September, which would reduce the risk of damage caused by early frost events in autumn to the new formed bud and meristem growth of the next year (Charrier et al. 2015). The timings of bud burst and bud set are an evolutionary adaptation to local conditions, ensuring reproduction and growth by avoiding unfavorable winter conditions (Evans et al. 2016).

During BB1-BB3, although the bud swelled and scales surrounding the bud opened, there was still no visible new formed needle. From BB4 to BB6, new formed needles were gradually visible, and the fresh green needle could be seen (Dhont et al. 2010). Thus, technically, if compared with the generally recorded leaf phenology in broadleaf species (Richardson et al. 2006), the leafing of black spruce began at BB5, when parts of the new needles could be seen.

Phenocam Chronologies

Near surface remote sensing offers a possibility for time series phenology analysis by recording continuous imagery with fine spatial and temporal accuracy (Keenan et al. 2014; Richardson et al. 2009). GCC and other digital index (e.g., RCC, ExG) that were extracted from the continuous imagery were used for identifying transition dates for seasonal trajectory of deciduous species (Keenan et al. 2014; Yang et al. 2014; Klosterman et al. 2014; Sonnentag et al. 2012). In these studies, GCC was used to track the green-up and green-down dynamics to represent the spring and autumn phenology of canopy, while RCC was used to identify the autumnal leaf senescence, especially in deciduous broadleaf species. By comparing the performances of GCC, RCC and ExG on characterizing diurnal and seasonal patterns of canopy greenness in deciduous-dominated and coniferous-dominated forests, Sonnentag et al. (2012) found that GCC was more effective in capturing the trajectory of canopy phenology as it reduces the effects of scene illumination. In our study, GCC from black spruce suitably tracked the seasonal canopy development of both spring and autumnal events, confirming on an evergreen species the observations reported in the literature for deciduous species (Keenan et al. 2014;

Yang et al. 2014; Toomey et al. 2015). Our results indicate that PhenoCam derived GCC can be considered as a reliable proxy for the seasonal development of canopy phenology in evergreen species.

The double-logistic function fitted GCC data well, demonstrating that this could be successfully applied to the time-series greenness data derived from near-surface remote-sensing on black spruce, not just on data of Normalized Difference Vegetation Index (NDVI) or on deciduous species (Hufkens et al. 2012; Zhang et al. 2003). For the culmination of GCC in summer, black spruce showed lower GCC than the previous studies on deciduous species, which could exceed 0.45 in some cases (Toomey et al. 2015). This was probably due to the larger leaf area index (LAI) of broadleaf compared to conifer species with needles.

This study demonstrated the ability of high end PhenoCam (Netcam XL, StarDot Technologies, Buena Park, CA) used for our analysis due to its color channel sensitivity and reliability in detection of seasonal changes in color dynamics of black spruce (Toomey et al. 2015). However, the presence of only visible spectral bands such as red, green and blue limit our observations in the near infrared (NIR) spectral region, which is also an important indicator to study vegetation phenology (Li et al. 2013). This limitation could be overcome in future researches by including NIR enabled PhenoCam (Filippa et al. 2018) or satellite remote sensing data such as moderate resolution imaging spectroradiometer (MODIS), visible infrared imaging radiometer suite (VIIRS) and Landsat, which have NIR band along with the visible bands (ORNL DAAC 2018).

Comparing GCC to Observer-Based Phenology

By comparing bud phenological phases with GCC curves, the peak standardized GCC occurred at BS3, 6 and 3 weeks after the completion of bud burst and start of bud set, respectively. This can be attributed to the increase in content of pigmentation and chlorophyll concentration in needles and LAI of the canopy resulting from the growth and development of the new formed needles after being exposed from the bud scales (Keenan et al. 2014; Brown et al. 2017). After that, a further increase in leaf chlorophyll concentration inducing reduction in reflectance at green wavelengths may be attributed to the decline of GCC during the bud set process (Brown et al. 2017; Richardson et al. 2002). In late summer and autumn, the consequences of needle aging and the associated

declining pigmentation may also result in decreasing GCC (Keenan et al. 2014; Sonnentag et al. 2012).

The adult trees of the boreal forest maintain living branches only in the upper part of the canopy, forcing phenological studies to be conducted with binoculars or on photos at high magnifications (De Barba et al. 2016). However, data collection of bud phenology requires precise observations of changes in the morphological characteristics of the buds. Due to their size and the small morphological variations, reliable observations must be performed directly on the buds. We therefore collected data on saplings growing near the studied trees.

Budburst occurs earlier in young than adult trees, to avoid shading by the dominant canopy and maximize growth in deciduous species. Such an ontogenic pattern in phenology is described in many studies (Augspurger 2004; Augspurger and Bartlett 2003; Gill et al. 1998; Seiwa 1999; Vitasse 2013). Leaf phenology is generally driven by a combination of temperature and photoperiodic cues, and the degree of chilling experienced in winter (Vitasse et al. 2014). In *Acer saccharum*, bud break occurred 5 days earlier in suppressed saplings (i.e., under canopy) than in mature trees. In *Tilia platyphyllos*, seedlings growing in the understory advanced leaf unfolding by 10 days compared to mature trees, but the difference was not significant (Vitasse 2013). Autumn phenology of *Acer saccharum*, that is, leaf senescence and leaf fall, occurred 10 days later in saplings than in mature trees (Augspurger and Bartlett 2003). In our study, seedlings were planted in an open area, which ensured similar growing conditions (i.e., light and temperature). We cannot exclude differences in phenology among young and old individuals of black spruce in our study, although, to our knowledge, no information is available in the literature for this species, and phenological studies on this topic frequently involve deciduous broadleaves. However, a literature review suggests that the potential error in defining bud break and bud set could range within an interval of between 5 and 10 days, which is comparable to the resolution and statistical error of our weekly field observations (Augspurger and Bartlett 2003; Wyka et al. 2012). Besides, while acknowledging such potential errors, our results still remain meaningful and more accurate than an arbitrary selection of growth reactivation set at 50% of the amplitude value of the curve.

Probability of Occurrence of Each Bud Phenological Phase along GCC

The probability of occurrence of each sequential phenological phase along the GCC was predicted by

using an ordinal logit model. The model included all phenological phases by taking into account that each one is sequential and interconnected. Based on our results, the start of bud burst was more likely to occur when GCC was at the 72nd percentile of annual amplitude. This might suggest that, instead of using the empirically applied 33rd or 50th percentile of the annual remote-sensing time-series (Antonucci et al. 2017; Keenan et al. 2014), the 72nd percentile of GCC well represents the start of the growing season in studies related to the resumption of new shoots. Similarly, in the case of studies focusing on exposed needles (e.g., the increment of new formed shoots), the 92nd percentile of GCC is the appropriate threshold for determining the timing of this spring event. Furthermore, bud reactivation does not just represent the beginning of tree growth morphologically, but is also accompanied by a number of endogenous reactivations of regulation processes (Durbak et al. 2012).

The timing of autumn phenology in black spruce is less studied because the changes in leaf coloring and abscission are less evident (Klosterman et al. 2014; Brown et al. 2017; Richardson et al. 2009; Garrity et al. 2011). In autumn, once bud set is finished, shoot apical meristems in most temperate and boreal perennial plants terminate primary growth and form buds consisting of leaf primordia surrounded by protective bud scales (Cooke et al. 2012). Within a few weeks, the buds become dormant and would not be activated even under ideal conditions until spring of the next year (Guy 2014). The completion of bud set closely follows the cessation of primary shoot growth, and generally indicates that the plant is prepared for the harsh conditions in autumn and winter (Gyllenstrand et al. 2007; Rohde et al. 2011). Therefore, based on the findings of this study, we suggest setting the formation of winter buds at the 94th percentile of the GCC amplitude as the threshold to determine the cessation of primary growth in black spruce.

Implication of this Study

Our results provide a possible protocol to investigate canopy phenology of black spruce with new and historical archived camera digital imageries, and would thus have a potential to improve the results of previous studies.

Considering the broad interest in near-ground imagery collection (i.e., PhenoCam data), and the transcontinental range of black spruce, our calibration has a great potential of application to wide areas in northern North America. Bud phenology corresponds

to the period of primary (apical) growth and is closely related to secondary (wood) growth (Antonucci et al. 2017; Huang et al. 2014), the strong sink of the carbon assimilated by photosynthesis. By providing a novel and reliable statistical approach, this study could allow the phenological models for evergreen forests to be improved, as has been achieved for grasslands and deciduous forest (Melaas et al. 2016; Hufkens et al. 2016). Furthermore, by combining with other measurements, such as physiological traits, eddy covariance data of land-atmosphere fluxes and satellite remote sensing data, our results would be valuable for improving the investigations of responses of phenology, carbon sequestration and ecosystem function to climate change (Filippa et al. 2018).

Conclusions

In recent decades, various studies on plant phenology have benefited from open access to an increasing amount of digital camera imagery of the canopy. However, these imageries are unable to capture the specific bud phenological phases, which are closely related to primary growth and of vital significance in defining growing periods. The ability to clarify and calibrate canopy phenology of coniferous species is scarcely known due to the elusive seasonal cycle of the canopy in evergreen species, but it is essential to improve the management of boreal forests and phenological models. In this study, we proposed an innovative protocol to calibrate GCC time series extracted from digital camera imageries with field observed bud phenological phases (i.e., 6 phases of bud burst and 5 of bud set). Our results confirmed that GCC could be used to represent canopy phenological changes in evergreen species and identify the intra-annual variability of phenology, including both spring and autumnal phenological phases (e.g., 72% of GCC amplitude in spring and 94% of GCC amplitude in autumn). Besides, we proposed statistical-based thresholds for the identification of 6 phases of bud burst and 5 of bud set. Our study, based on a statistical model, builds a bridge between direct phenological observations and near-surface remote sensing, providing a statistically sound protocol for calibrating PhenoCam derived data with field observation, as well as for determining canopy phenology. Our approach and biological thresholds present a great potential for testing and investigating canopy phenology of black spruce at large geographical scale.

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Disclosure Statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. All the authors have approved the current version of the manuscript and agreed to submit this manuscript in this journal.

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