

ARTICLE

Climate Ecology

Leaf phenology as an indicator of ecological integrity

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Abstract

Climate change leads to an increased frequency of severe weather events as well as stressful growing conditions. Together these changes may impact the resilience of ecosystems. To keep track of such effects, conservation managers monitor the “ecological integrity” or coherence of ecosystem processes, such as the cycling of carbon and water. Networked phenocams can produce near-continuous observations of leaf function in the context of climate change, capturing declines due to disturbance or stress. Here we explore the application of phenocams to detect responses to disturbance and stress using 14 examples from the PhenoCam Network. We selected these previously published and new examples to include a variety of disturbances in the form of hurricanes, a windstorm, frost, insect defoliation, and stress due to drought. Frost and herbivory disturbances led to both reductions and extensions in the duration of the rising section of the greenness curve, while hurricanes generally led to reductions in the duration of the plateau section and entire leaf-on period. We found that changes of at least $\pm 20\%$ in the duration of the rising section in the seasonal greenness curve, $\pm 20\%$ in the duration of the plateau section following the seasonal greenness peak, and $\pm 10\%$ in the duration of the entire leaf-on period were a reliable signal of leaf functional declines due to disturbance or stress. If such declines become increasingly frequent and severe as a consequence of climate change, this could impact ecological integrity through interruptions to ecosystem processes. Comparing the

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duration of these periods in a given year to the average for other years with these thresholds resulted in average true detection rates of 86% and false-positive detection rates of 11% when sampling from probability density functions of 344 broadleaf and needleleaf PhenoCam site-years. Here we show that phenocams are powerful ecological integrity monitoring tools, which can be efficiently applied to quantify dynamic responses to disturbance or stress.

KEYWORDS

climate change, defoliation, drought, ecological integrity, hurricanes, leaf phenology, phenocams, spring frost

INTRODUCTION

Phenology is the study of recurring biological events and their causes with respect to abiotic forces (Lieth, 1974). “Plant phenology” typically refers to the timing of seasonal changes in leaves and flowers, including spring leaf emergence and fall leaf senescence. Observations show that global warming has advanced leaf emergence for deciduous species over the past five decades (Menzel et al., 2006; Peñuelas & Filella, 2009; Piao et al., 2019) and to a lesser extent delayed leaf senescence (Estiarte & Peñuelas, 2015; Menzel & Fabian, 1999; Peñuelas et al., 2002; Xie et al., 2018). Climate-driven increases in extreme weather and changes in leaf phenology together may lead to an increased risk of damage from disturbance such as frost, ice storms, herbivory, and hurricanes (Allstadt et al., 2015; Augspurger, 2013; Bascietto et al., 2018; Casson et al., 2019; Delpierre et al., 2017; Lechowicz, 1984; Marquis et al., 2022; Pureswaran et al., 2019; Taylor et al., 2020). Climate change has also led to a change in the frequency of stress from drought or excessive precipitation, due to both an extension of the growing season and an alteration of global hydrology (Čehulić et al., 2019; Charlet de Sauvage et al., 2022; Etzold et al., 2022; Lukasová et al., 2020; Meier et al., 2021; Sangüesa-Barreda et al., 2021). The detrimental effects of climate change may lead to reduced carbon uptake, counteracting the potential enhanced uptake afforded by earlier leaf emergence and later senescence (Curtis & Gough, 2018). The unprecedented rate of ongoing climate change challenges the suitability of vegetation strategies for responding to warming and enhanced variability in temperatures, as these were evolved for relatively stable historical climates (Casson et al., 2019; Martin et al., 2010; Norby et al., 2003; Richardson, Hufkens, Milliman, Auerbach, Furze, et al., 2018; Vitasse et al., 2022; Zohner et al., 2020). The combination of increased disturbance and stress in the context of climate change may culminate in impaired ecosystem processes and deteriorated resilience for ecosystems that are susceptible to such

effects (Niinemets, 2010; Price et al., 2013). For example, Stephens et al. (2018) reported the transition from a carbon sink to source for a stand of *Populus tremuloides* during a growing season with insect defoliation, with lower primary production than the previous 20 years of records. Hufkens, Friedl, Keenan, et al. (2012) also reported annual gross productivity was reduced by as much as 14% following a late spring frost in 2010 in more than 8000 km² of forest in the northeastern United States. Along with climate-driven changes in leaf phenology, the effects of increased disturbance and stress have considerable implications ranging from species to ecosystem levels, with potential for alterations to community structure and impaired ecosystem function (Kharouba et al., 2018).

A near-remote sensing technique of leaf phenology monitoring via phenocam employs time-lapse digital cameras installed at the ground level (Brown et al., 2016; Browning et al., 2019; Richardson, 2019; Richardson et al., 2007; Sonnentag et al., 2012). Globally, there are now extensive networks of phenocams including the North American PhenoCam Network (<https://phenocam.nau.edu/webcam/>; Seyednasrollah et al., 2021) and European Phenology Camera Network (<http://european-webcam-network.net/>; Wingate et al., 2015). Phenocams produce near-continuous sub-daily resolution observations of leafing status at the individual tree level in the form of seasonal greenness curves (Delpierre et al., 2020; Liu et al., 2021). Leaf phenology can also be observed at the individual tree level using manual techniques in the field, though this approach can be limiting for conservation managers due to time and financial resource constraints. Phenocams present an automated, affordable, and robust approach to monitoring the timing of seasonal leaf development as well as the effects of disturbance or stress (Parmentier et al., 2021; Toomey et al., 2015).

Ecological integrity is a measure of the viability of an ecosystem based on the cohesion of processes resulting from interactions between its abiotic and biotic components (Jenssen et al., 2021). Disturbance and stress can threaten ecological integrity through interruptions to ecosystem processes and alterations to ecosystem

structure (LaPaix et al., 2009; Ordóñez & Duinker, 2012). Key forest ecosystem processes affected by disturbance or stress include primary production, water cycling, nutrient cycling, and energy flow, among others (Bonan & Shugart, 1989). The composition and structure of forest ecosystems are also impacted by disturbance and stress, as susceptible species may exhibit reduced fitness and reproduction. Alternatively, disturbance and stress may have limited impacts on ecological integrity for resilient forest ecosystems. In order to determine whether or not disturbance or stress has undermined ecological integrity in forest ecosystems, it is necessary to monitor ecosystem processes before, during, and following disturbance and stress. Leaf damage or defoliation during the optimal growing season period can indicate disruptions to ecosystem processes (Stephens et al., 2018). Some approaches to monitoring ecological integrity include the designation of indicator thresholds to differentiate between different levels of integrity in comparison to a reference state (Dubé et al., 2013; Parks Canada Agency, 2011). Phenocams can capture quantitative data of moderate to extensive leaf damage due to disturbance or stress, as well as recovery (Matiu et al., 2017; Nagler et al., 2014; Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018; Stephens et al., 2018). Phenocams can also aid in documenting baseline leaf function prior to disturbance or stress. Together these processes impart important implications for ecological integrity (Chamberlain et al., 2019; Halman et al., 2011; Scheffer et al., 2009; Smith et al., 2022; Taylor et al., 2020). Despite this potential, little work has been done to explore the implementation of phenocam-derived leaf phenology observations as an indicator of ecological integrity for conservation efforts. This may be due in part to the considerable challenge of designating indicator thresholds to convey critical adverse effects on the ecology of an ecosystem (Hansen et al., 2021).

Many factors complicate the development of ecological integrity indicator thresholds in relation to leaf phenology. In the context of disturbance or stress, leaf phenology alone may not provide a pronounced signal of leaf functional decline. For example, the work of Zohner et al. (2020) shows that leaf phenology does not always deviate notably in response to damaging late spring frost events relative to alternative drivers of interannual variability. Given this inherent background variability with multiple drivers of variation in leaf phenology beyond disturbance or stress, an alternative signal of leaf functional declines may be necessary. A promising alternative signal of leaf function is the duration of leaf developmental periods approximated from the canopy greenness time series or greenness curve. Depending upon how leaf developmental periods are defined along the greenness curve, these periods can be stable within a few days for an individual region of interest over time in the absence

of disturbance or stress. Examples of these periods include the greenness rising portion of the greenness curve from 10% to 90% amplitude, the greenness plateau following the seasonal peak in greenness, and the entire leaf-on period from 50% amplitude in the rising portion of the curve to 50% amplitude in the falling portion of the curve. If the duration of leaf developmental periods signals disturbance or stress-related leaf damage more often for a given species than adaptation can overcome, this species may be susceptible to adverse global change impacts, with potential consequences for ecosystem processes, structure, and composition (Cavers & Cottrell, 2015).

Both field studies and phenocam studies indicate that spring disturbances, such as false springs, in which warm spring conditions are followed by a late frost event, can result in an extended greenness rising period due to the time necessary for recovery following disturbance (Augspurger, 2009; Hufkens, Friedl, Sonnentag, et al., 2012; Kaitaniemi et al., 1997; Menzel et al., 2015). These spring-time disturbances may in turn delay the senescence process (Zohner et al., 2019). A reduced period is also possible if anomalously warm springs conducive of frost damage give rise to rapid early leaf development before frost (Hufkens, Friedl, Keenan, et al., 2012). Additionally, frost may lead to reduced seasonal peak greenness values, prompting a reduced greenness rising period. A notable deviation in this period between budburst and leaf maturity in the form of either an extension or reduction can therefore be a signal of disturbance effects having an impact on ecosystem processes. Later in the growing season, the severity of stress or disturbance can translate into commensurately advanced senescence (Bigler & Vitasse, 2021; Xie et al., 2015), which would reduce the leaf maturity period or the entire period between leaf emergence and senescence. Studies have shown with a variety of cameras that following disturbance, which led to leaf damage, there may be a pronounced decline in canopy seasonal maximum greenness, which would impact various leaf stages extracted from the greenness curve (Hufkens, Friedl, Keenan, et al., 2012; Ide et al., 2011; Keenan et al., 2014; Menzel et al., 2015; Mizunuma et al., 2013; Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018). These studies also show such a decline is distinct from the greenness patterns at nearby sites or growing seasons with no recorded disturbance at the same site, suggesting this feature is a promising signal of disruption to ecosystem processes due to disturbance or stress.

Leaf phenology is currently monitored at more than 500 phenocam sites throughout the North American PhenoCam Network, with some site records spanning over a decade (Seyednasrollah et al., 2021). We hypothesized that disturbance or stress associated with an impact on leaf function will be evidenced through one or more

of the following: (1) the time between the onset of leaf growth and the seasonal peak in greenness; (2) the duration of the greenness plateau or slow decline following the seasonal peak in greenness; or (3) the duration of the entire leaf-on period for that site (Figure 1). Additionally, we hypothesized that such deviations would differ substantially from alternative reference growing seasons, allowing the designation of indicator thresholds based on the magnitude of deviation. We will examine these periods from known site-years with disturbance or stress that affected the leafing status of vegetation within the PhenoCam Network. We will then examine how distinct these periods are under circumstances of disturbance or stress in comparison to other years across the PhenoCam Network. Finally, we will develop an approach to detect such anomalous periods. This would allow for the detection of leaf functional declines and associated impacts to ecological integrity within networks such as the PhenoCam Network.

METHODS

PhenoCam Network

For information on PhenoCam Network protocols refer to Seyednasrollah, Young, Hufkens, Milliman, Friedl,

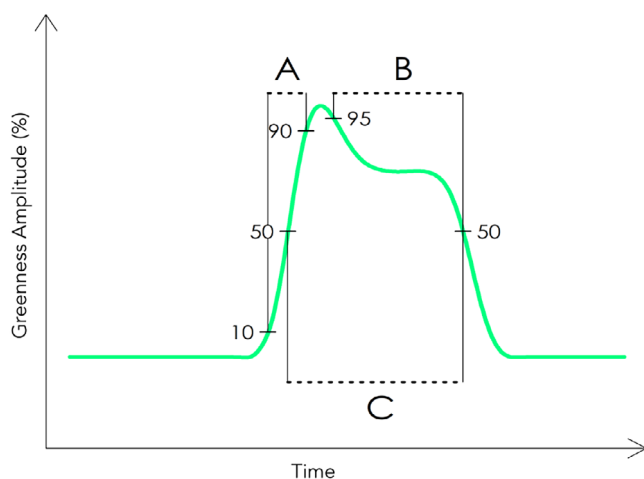


FIGURE 1 The delineation of three periods that may be affected by disturbance or stress: (A) the greenness rising portion of the curve between the onset of leaf growth and the seasonal peak in greenness calculated as the time between the 10% and 90% amplitude, (B) the greenness plateau following the seasonal peak in greenness calculated as the time between 95% and 50% amplitude in the falling portion of the greenness curve, (C) the entire leaf-on period calculated as the time between 50% amplitude in the rising portion and 50% amplitude in the falling portion of the greenness curve.

Frolking, and Richardson (2019) and Richardson, Hufkens, Milliman, Aubrecht, Chen, et al. (2018). Regions of interest (ROIs) from PhenoCam cameras are delineated to characterize the dominant vegetation in each field of view, and in some cases several ROIs are defined to distinguish between different plant functional types such as evergreen needleleaf versus deciduous needleleaf (Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018). The green chromatic coordinate (GCC) is then calculated as shown in Equation (1) from red, green, and blue color channel intensity values within each ROI for each image to produce greenness time series:

$$GCC = B_G / (B_G + B_R + B_B), \quad (1)$$

where B_G corresponds to the intensity (brightness) of the green color channel, B_R refers to the intensity of the red color channel, and B_B refers to the intensity of the blue color channel. The GCC represents the intensity of the green color channel versus the total intensity of all color channels. For examination of the greenness time series from PhenoCam Network cameras, we extracted original and 3-day 50th percentile filtered GCC records from the PhenoCam V2.0 data set, which includes observations up until the end of the 2018 growing season (Seyednasrollah, Young, Hufkens, Milliman, Friedl, Frolking, Richardson, Abraha, et al., 2019). We also downloaded select records for currently active phenocam sites with cases of disturbance or stress that had limited reference growing season observations prior to 2018 from a prerelease of the PhenoCam V3.0 data set (https://phenocam.nau.edu/phenocam_explorer_prerelease/; Hufkens et al., 2018; Richardson, Hufkens, Milliman, Aubrecht, Chen, et al., 2018). Images that were too dark or too bright were removed from these datasets prior to their release using digital number threshold quality control filters. ROIs for PhenoCam Network sites can be accessed online through the PhenoCam Network portal at <https://phenocam.nau.edu/webcam/>, as well as through the PhenoCam V2.0 data set in Seyednasrollah, Young, Hufkens, Milliman, Friedl, Frolking, Richardson, Abraha, et al. (2019).

Exploration of ecological integrity indicators from greenness time series

We selected 14 cases of disturbance or stress captured by phenocams from the PhenoCam Network (Table 1). These cases were selected through visual inspection of images and in some cases ancillary data (Hufkens, Friedl, Keenan, et al., 2012; Keenan et al., 2014; Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018; Stephens et al., 2018; Stephenson et al., 2018), which

TABLE 1 PhenoCam Network sites with recorded instances of disturbance or stress included in our study.

Camera name	Location (latitude, longitude)	Full site name	Disturbance or stress	Reference years
<i>elverde</i>	18.3207, −65.8199	El Verde Field Station, El Yunque National Forest, Northeastern Puerto Rico, USA	Hurricane Maria (September 2017)	2015, 2016, 2019
<i>NEON.D07.GRSM.DP1.00033</i>	35.6890, −83.5020	NEON Site—D07 (Appalachians and Cumberland Plateau) Great Smoky Mountains National Park, TN, USA	Spring windstorm (May 2017), Hurricane Irma (September 2017), Derecho (May 2020)	2018, 2019, 2021
<i>woodshole</i>	41.5495, −70.6432	Woods Hole Research Center, Falmouth, MA, USA	Hurricane Irene (August 2011)	2013–2018
<i>spruceT9P17</i>	47.5060, −93.4527	Marcell Experimental Forest, north of Grand Rapids, MN, USA	Frost (April 2016)	2017 and 2018
<i>arbutuslake</i>	43.9821, −74.2332	Arbutus Lake, Huntington Wildlife Forest, Newcomb, NY, USA	Frost (May 2010)	2011–2014
<i>proctor</i>	44.5250, −72.8660	University of Vermont, Proctor Maple Research Center, Underhill, VT, USA	Frost (May 2010)	2009, 2011–2018
<i>mammothcave</i>	37.1858, −86.1019	Environmental Learning Center, Mammoth Cave National Park, KY, USA	Frost (April 2007)	2004, 2005, 2008, 2009, 2011–2014, 2016–2018
<i>canadaOA</i>	53.6289, −106.1978	BERMS Old Aspen Site, Prince Albert National Park, Saskatchewan, Canada	Herbivory (May 2016)	2012–2015
<i>millhaft</i>	52.8008, −2.2988	Norbury, Staffordshire, UK	Herbivory (April 2018 and 2019)	2016, 2017, 2020, 2021
<i>worcester</i>	42.2697, −71.8428	Worcester State University, Worcester, MA, USA	Herbivory (June 2018)	2014–2017, 2019–2021
<i>harvard</i>	42.5378, −72.1715	EMS Tower, Harvard Forest, Petersham, MA, USA	Ice storm (December 2008)	(2008, 2010–2019)
<i>sequoia</i>	36.5658, −118.7772	Lower Kaweah, Sequoia/Kings Canyon National Park, CA, USA	Drought mortality (2015)	2012–2014

indicated these cases of disturbance or stress were associated with impaired leaf function and thus a decline in ecological integrity. The disturbances we investigated included hurricanes, windstorms, spring frost, insect herbivory, and a winter ice storm. The case of stress we investigated was drought mortality (2015). We used imagery data from the PhenoCam Network to include a spatial and temporally replicated data set of seasonal greenness curve records, in the context of disturbance and stress as well as under normal conditions. This allowed us to examine the stability of our indicator in the absence of disturbance or stress, as well as the detectability of leaf damage from known cases of disturbance or stress.

We calculated the duration of three leaf developmental periods based on the transition time between different amplitude values in the rising and falling portions of the greenness curve as is shown in Figure 1. To ensure our

approach utilized optimal amplitude values, we explored different amplitude thresholds to denote the start and end of each period. Amplitude thresholds that corresponded to the best compromise between signal in response to disturbance or stress and noise in the absence of disturbance or stress were selected. We calculated the duration of the greenness rising period as the time between the first instances of 10% and 90% amplitude in the rising portion of the greenness curve following Klosterman et al. (2018). We also examined the time between the first instances of 25% and 90% amplitude in the rising portion of the greenness curve as the duration of the greenness rising period and found this to fluctuate slightly more across site-years in the absence of disturbance or stress without commensurate increases in signal response to disturbance or stress. We calculated the duration of the apparent greenness plateau as the time between the first instance (if there was more than one instance in a single year) of 95% and the

final instance (if there was more than one instance in a single year) of 50% amplitude in the falling portion of the greenness curve to capture greenness declines potentially due to disturbance or stress (Klosterman et al., 2014). We also tested the time between the first instance of 95% and the final instance of 75% amplitude in the falling portion of the greenness curve as the greenness plateau period, though found variability in this duration in the absence of disturbance or stress to occlude signal responses to disturbance or stress. We calculated the duration of the total nondormancy period or leaf-on period as the time between the first instance of 50% amplitude in the rising portion and the final instance of 50% amplitude in the falling portion of the greenness curve following common approaches (Misra et al., 2018). The duration between these amplitude values was optimal over that of between 25% amplitude in the rising and falling portions of the greenness curve, for which variability in the absence of disturbance or stress was reduced though signal responses to disturbance or stress were also much reduced.

To explore how these leaf developmental periods differed in comparison to a reference state, we then computed the percentage change and ratios of the duration of these periods in years with disturbance or stress to the average duration of these periods in years without evident disturbance or stress. To more broadly establish how this ratio varies in the absence of disturbance or stress for other sites, we computed the probability density function of these ratios for all other sites in the PhenoCam Network, comparing each year to the average of all other years as a reference state proxy. We filtered available data to remove annual data sets, which were less than 300 days in length, multiyear data sets, which were less than four years in length, as well as data sets with observed periods, which were less than the 25% quantile (-1.5 times the interquartile range) or else more than the 75% quantile ($+1.5$ times the interquartile range), to address the influence of potential artifacts associated with field-of-view shifts or data gaps (Richardson, Hufkens, Milliman, & Frolking, 2018; Seyednasrollah, Young, Hufkens, Milliman, Friedl, Frolking, & Richardson, 2019; Tian et al., 2021). It is possible that some of these values may have been associated with disturbance or stress, though we wished to refine our focus to data sets with representative stability from across the PhenoCam Network for this exercise. To examine the likelihood of positively identifying disturbance or stress based upon the duration of these periods in a given year relative to other years, we designated threshold average ratios to serve as indicators of probable disturbance or stress warranting concern regarding ecological integrity. We designated these ratios to achieve an optimal compromise between detection of true cases of disturbance or

stress and the avoidance of false detections. We then computed the probability of correct detections using these threshold average ratios.

RESULTS

Cases of disturbance or stress from the PhenoCam Network

Cases of disturbance or stress from the PhenoCam Network confirmed that disturbance or stress can lead to detectable deviations in one or more of the following in comparison to reference years: (1) the duration of the greenness rising portion of the curve between the onset of leaf growth and the seasonal peak in greenness; (2) the duration of the leaf maturity period greenness plateau following the seasonal peak in greenness prior to the fall decline; and (3) the duration of the entire leaf-on period. Frost and herbivory led to both reductions and extensions in the rising period. Hurricanes and windstorms typically coincided with a reduced plateau or overall leaf-on period. However, in some cases, disturbance effects on these greenness curve developmental periods were mild or not evident. Stress in the form of drought led to reductions in all periods for a site with evergreen vegetation.

Disturbance: Hurricanes and windstorms

Hurricane Maria was a category 4 hurricane that made landfall on September 20, 2017, on the island of Puerto Rico, resulting in widespread forest damage (Zhu et al., 2021). Greenness signals captured by the “*elverde*” phenocam from March to February show a seasonally early decline in greenness immediately following Hurricane Maria relative to previous years (Figure 2). The plateau period was reduced by 58 days (40%) in 2017 relative to the 143-day average from the reference growing seasons 2015, 2016, and 2019. The entire leaf-on period was reduced by 52 days (29%) in 2017 relative to the 177-day average from reference growing seasons. Interpolation with available data and inspection of images from the 2018 growing season suggests there was an extended recovery into the growing season following Hurricane Maria, and that these periods were also affected in 2018. Alternatively, the greenness curve from the 2019 growing season is similar to that of the 2015 and 2016 growing seasons. The rising period in 2018 was lengthened by 39 days (124%) relative to the 32-day average of reference growing seasons. As in 2017, the plateau period was also approximately reduced by 58 days (40%) in 2018 relative to reference years. The leaf-on period in 2018 was 159 days, an 18-day reduction

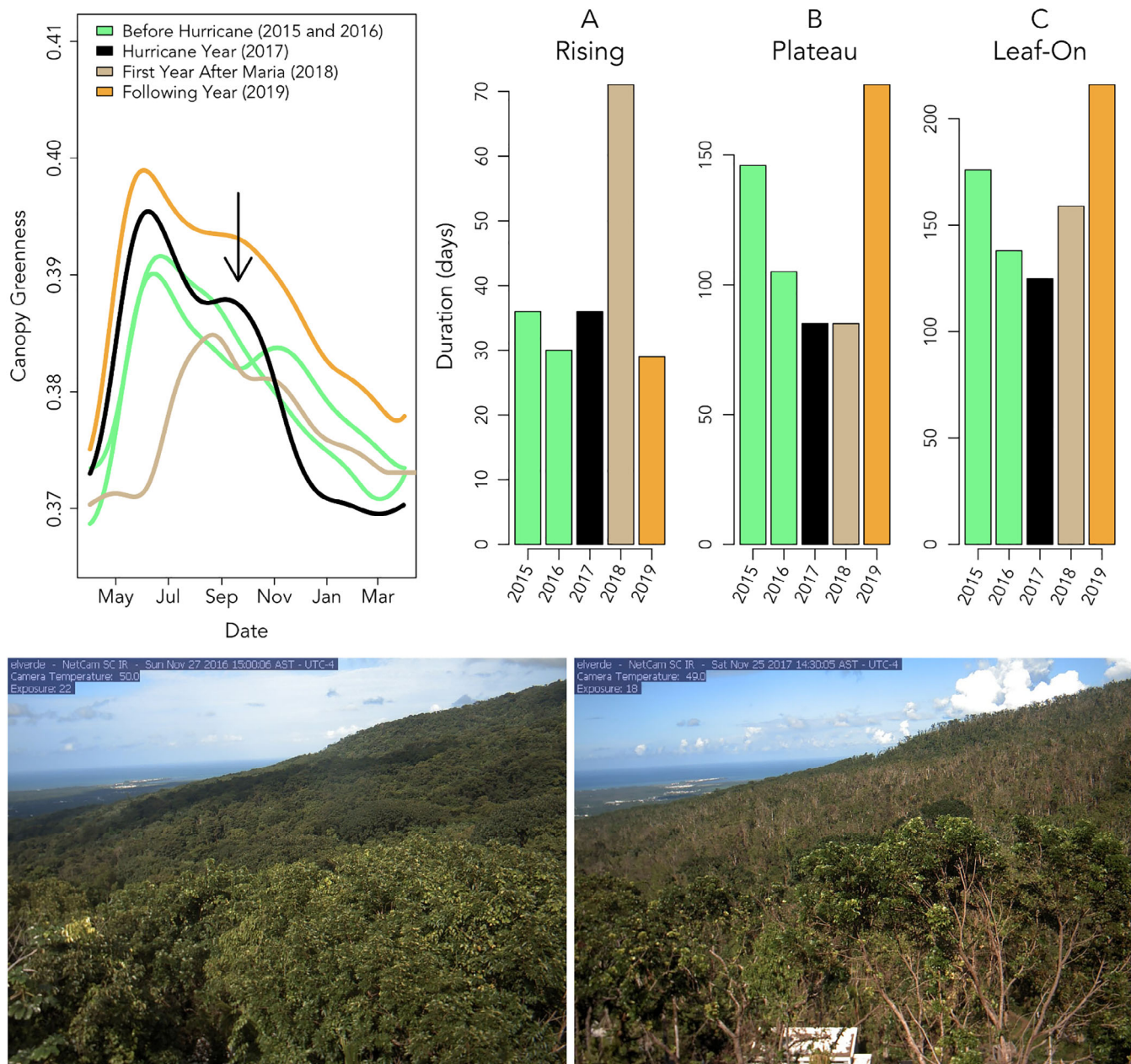


FIGURE 2 Greenness signals from before and after a severe drought during the 2015 growing season as well as following Hurricane Maria (September 20, 2017) captured by the “elverde” phenocam located at the El Verde Field Station, El Yunque National Forest, Northeastern Puerto Rico. The time of year during which Hurricane Maria occurred in 2017 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from before and after Hurricane Maria are shown on the bottom.

(10%) from the 177-day average of reference growing seasons. This suggests that Hurricane Maria led to sufficiently severe damage to impact seasonal leaf developmental periods in the 2017 and 2018 growing seasons. Visual inspection of available images for 2019 onwards suggests a return to pre-storm foliage levels, although a recovery transition in seasonal greenness may have still been underway in 2019. As more complete growing season records become available, the recovery can be further assessed.

A windstorm with wind speeds approaching 160 km/h led to widespread damage in the Great Smoky Mountains National Park on May 4, 2017 (Ahillen, 2017). The storm led to a reversal in the rising greenness signal usually observed in May, with a sudden decline in greenness, which was captured by the “NEON.D07.GRSM.DP1.00033” phenocam at the Great Smoky Mountains National Park, Tennessee (Figure 3). Another disturbance event impacted local vegetation later in the 2017

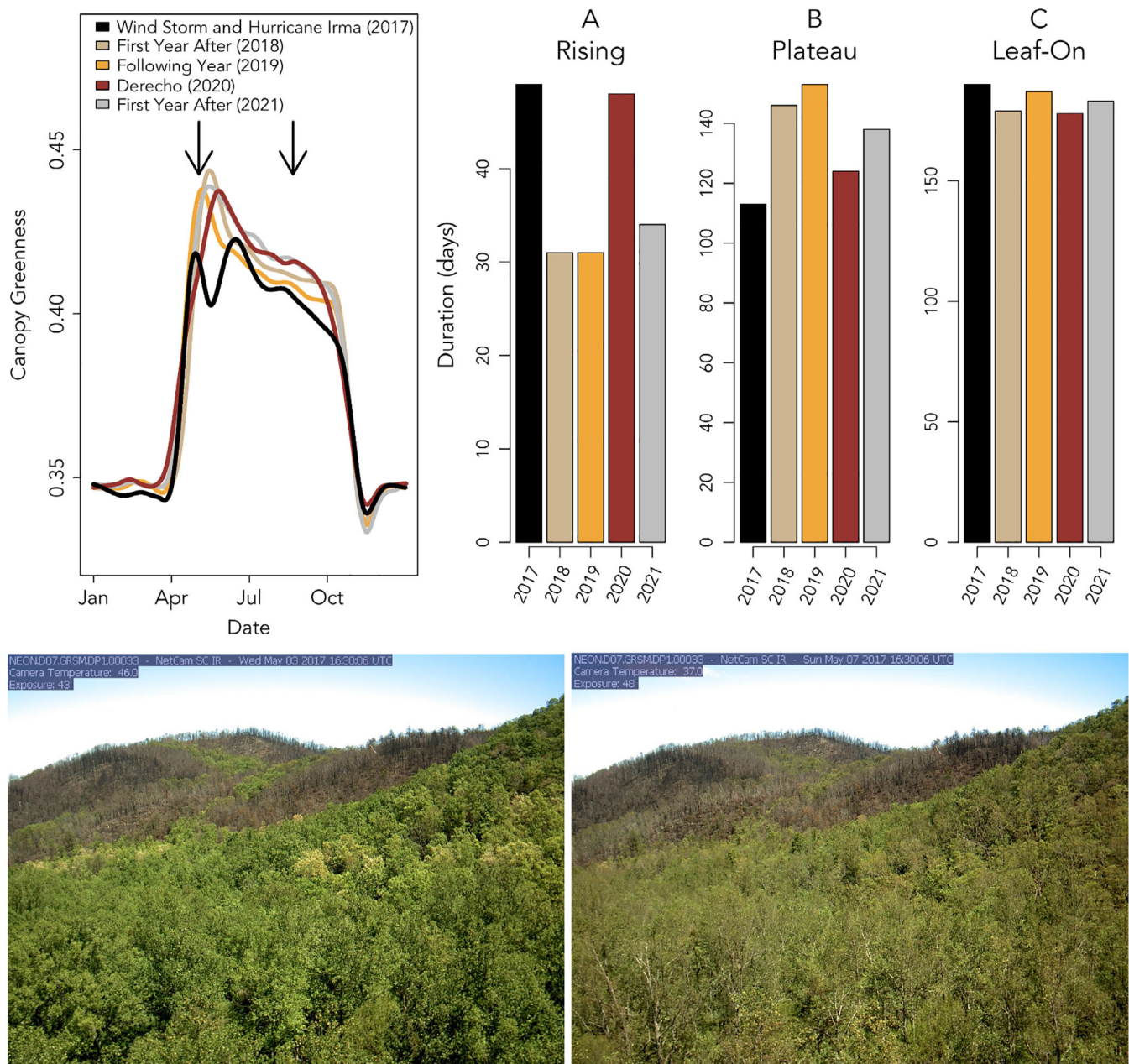


FIGURE 3 Greenness signals from before and after a spring windstorm and Hurricane Irma captured by the “NEON.D07.GRSM.DP1.00033” phenocam. The timings of disturbance events in 2017 and 2020 are denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from immediately before and after the spring windstorm are shown on the bottom.

growing season as Hurricane Irma traveled through eastern Tennessee as a tropical depression on September 12 before dissipating on September 13. The 2020 growing season also saw canopy damage due to wind disturbance. A complex of severe long-lasting thunderstorms designated as a derecho moved across Tennessee on May 3, 2020, with windspeeds approaching ~129 km/h (US Department of Commerce, 2020). In the 2017 growing season, the seasonal greenness peak was both reduced and late relative

to reference years without disturbance (2018, 2019, and 2021). In the fall of 2017, the late-growing season decline in greenness also began notably earlier in 2017 than in reference years. The rising period in 2017 was 17 days longer (53%) than the 32-day average period from reference years. The plateau period was 33 days shorter (22%) than the 146-day average period observed in reference growing seasons, while the leaf-on period was just 7 days longer (4%) in 2017

versus the 183-day average from reference years. Three years later in 2020, the seasonal greenness peak was also late relative to reference growing seasons. In 2020, the rising period was 16 days longer (50%) than the 32-day average from reference years, similar to that of 2017. Additionally, in 2020, the plateau period was 22 days shorter (15%) than the 146-day average period observed in reference years. The leaf-on period in 2020 was only 5 days shorter (3%) than the 183-day average from reference growing seasons. This suggests that these disturbance events led to sufficient damage to

impact leaf developmental periods in both the 2017 and 2020 growing seasons.

Hurricane Irene caused extensive damage due to flooding following excessive rainfall as well as a combination of high winds, tornadoes, and storm surges across the North American Acadian region in 2011 (Matyas, 2017). Hurricane Irene led to a seasonally early and rapid decline in greenness in August of 2011 captured by the “woodshole” phenocam at the Woods Hole Research Center in Massachusetts (Richardson, Hufkens, Milliman, & Froelking, 2018; Figure 4). The length of the plateau and

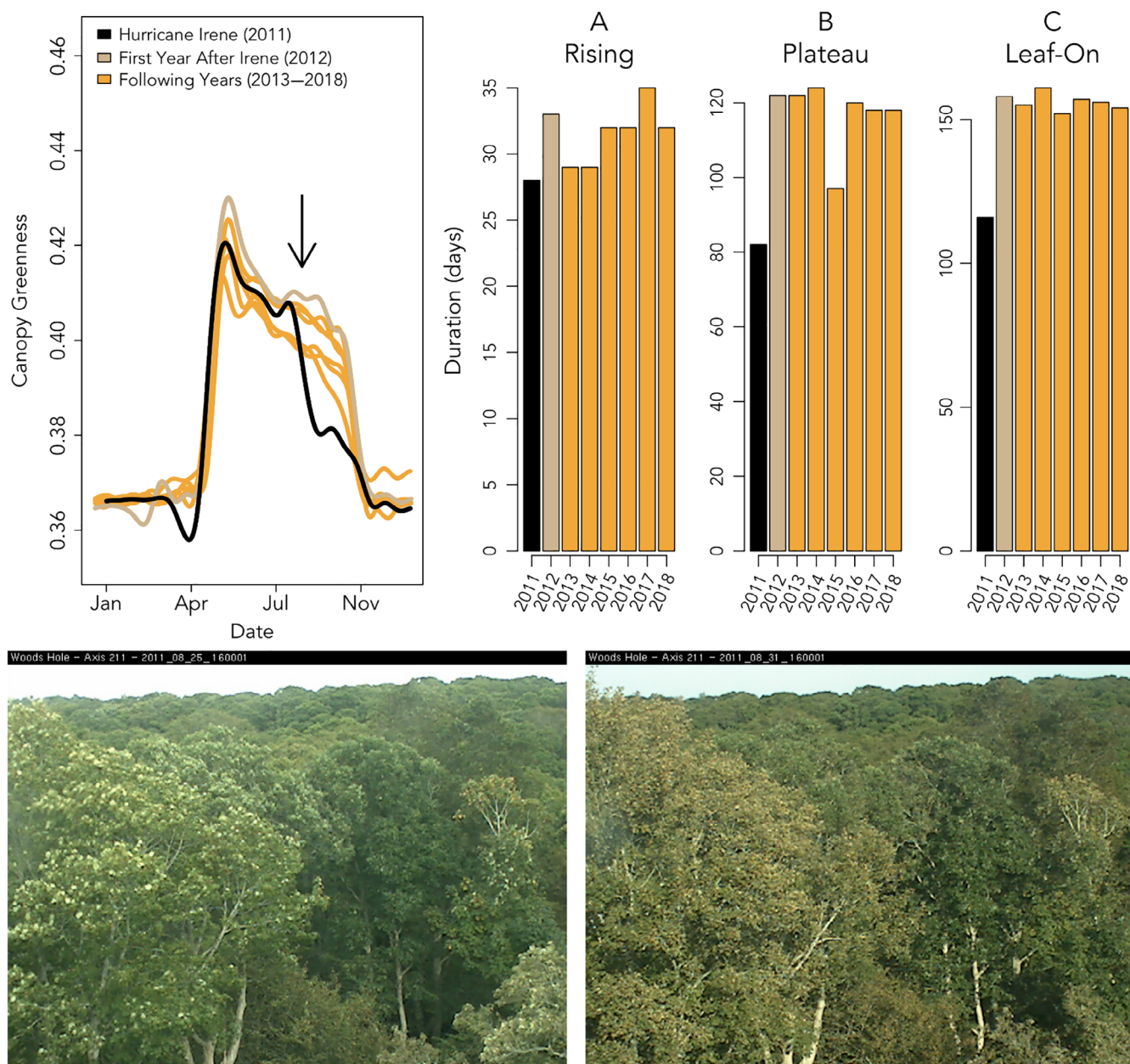


FIGURE 4 Greenness signals from before and after Hurricane Irene captured by the “woodshole” phenocam. The timing of the Hurricane in 2011 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from days before and after Hurricane Irene are shown on the bottom.

leaf-on periods in 2011 was 35 (30%) and 40 days (26%) shorter than the 117-day and 156-day averages from subsequent seasons, respectively. The length of the rising period following Hurricane Irene did not vary beyond the range of subsequent years. This suggests that Irene led to sufficient damage to truncate the plateau and leaf-on periods in the 2011 growing season.

Disturbance: Frost

Warmer than average March temperatures in 2016 were followed by a frost event on April 9, which led to leaf damage in an experimental warming chamber of the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment located in the USDA Forest Service Marcell Experimental Forest (MEF) north of Grand Rapids, Minnesota, captured by the “*spruceT9P17*” phenocam (Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018). The +9°C warming above ambient temperatures in this chamber led to a premature loss of frost hardiness, resulting in damage following this frost event in which ambient temperatures dropped below −15°C. The rising greenness signal usually observed in April was temporarily reversed after reaching a relatively reduced seasonal peak and declined until a local minimum was reached in late April (Figure 5). Following this, the greenness signal once again rose to a local peak in mid-June over approximately a 45-day period. The warming treatment led to both an advanced green-up as well as an advanced peak in greenness prior to the frost event (Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018). Following the frost event, greenness signals remained below the initial peak value. This interruption in the green-up process had the effect of substantially reducing the apparent rising period in comparison to subsequent years. The length of the rising portion of the greenness curve in 2016 was 25 days shorter (47%) than the 53-day average from subsequent seasons. Due to the early green-up, the duration of the apparent plateau period was substantially extended by 112 days (102%) relative to the 110-day average from subsequent years. The leaf-on period was also extended by 86 days (53%) relative to the 163-day average from other years. This suggests that the combined influence of warming and severe frost event in 2016 led to sufficient damage to impact seasonal leaf developmental periods.

An unusually warm spring was followed by a severe frost event in May of 2010 across the northeastern United States. This led to widespread frost damage of newly emerging leaves, part of which was captured by both the “*arbutuslake*” and “*proctor*” phenocams, which are located near Arbutus Lake and the University of

Vermont campus, respectively (Hufkens, Friedl, Keenan, et al., 2012). For the *arbutuslake* phenocam, the combination of this warm spring and late frost event led to a sufficiently early leaf development such that leaves were vulnerable at the time of frost (Figure 6). The rising greenness signal usually observed in May was temporarily reversed on approximately May 8 before increasing once more following May 12. The 2010 growing season greenness curve had an early and reduced seasonal peak greenness value relative to other years. The duration of the rising period in 2010 is intermediate to that of subsequent years. The plateau period was 9 days longer (9%) than the 94-day average of other years, and the leaf-on period was 14 days longer (11%) than the 126-day average of other years. This suggests that the combination of this warm spring and late frost event was of sufficient severity to influence seasonal leaf developmental periods in 2010.

This warm spring and late frost event also affected vegetation captured by the *proctor* phenocam in 2010 (Hufkens, Friedl, Keenan, et al., 2012). For the *proctor* phenocam, the combination of this warm spring and late frost event also led to a sufficiently early leaf development such that leaves were vulnerable at the time of frost, and a reduced seasonal maximum greenness value was observed in 2010 as well as a quicker decline from the seasonal maximum (Figure 7). The calculated length of the rising, plateau, and leaf-on periods was not anomalous in 2010, however, compared with other years. This suggests that despite this warm spring and late frost event leading to visible damage and a reduced seasonal greenness peak value, we were unable to detect anomalous leaf developmental periods with the amplitude thresholds we utilized. If the plateau period is calculated as the time between 95% and 75% amplitude in the falling portion of the greenness curve instead of between 95% and 50% amplitude, there is a notable reduction by 56 days (93%) relative to the 60-day average from other years in 2010. However, this calculation approach leads to pronounced variability in growing seasons without known cases of disturbance or stress, and it produces a similar magnitude of deviation with an apparent 39-day (65%) reduction in the plateau period for the year 2014. In addition, this alternative approach to calculating the plateau period resulted in pronounced variability for other sites across the PhenoCam Network in the absence of disturbance or stress.

In early April of 2007, a widespread frost event following an unusually warm March affected vegetation across much of the eastern United States (Gu et al., 2008; Hufkens, Friedl, Sonnentag, et al., 2012; Richardson, Hufkens, Milliman, & Froelking, 2018). This frost event was captured by the “*mammothcave*” phenocam at the Environmental Learning Center in Mammoth Cave

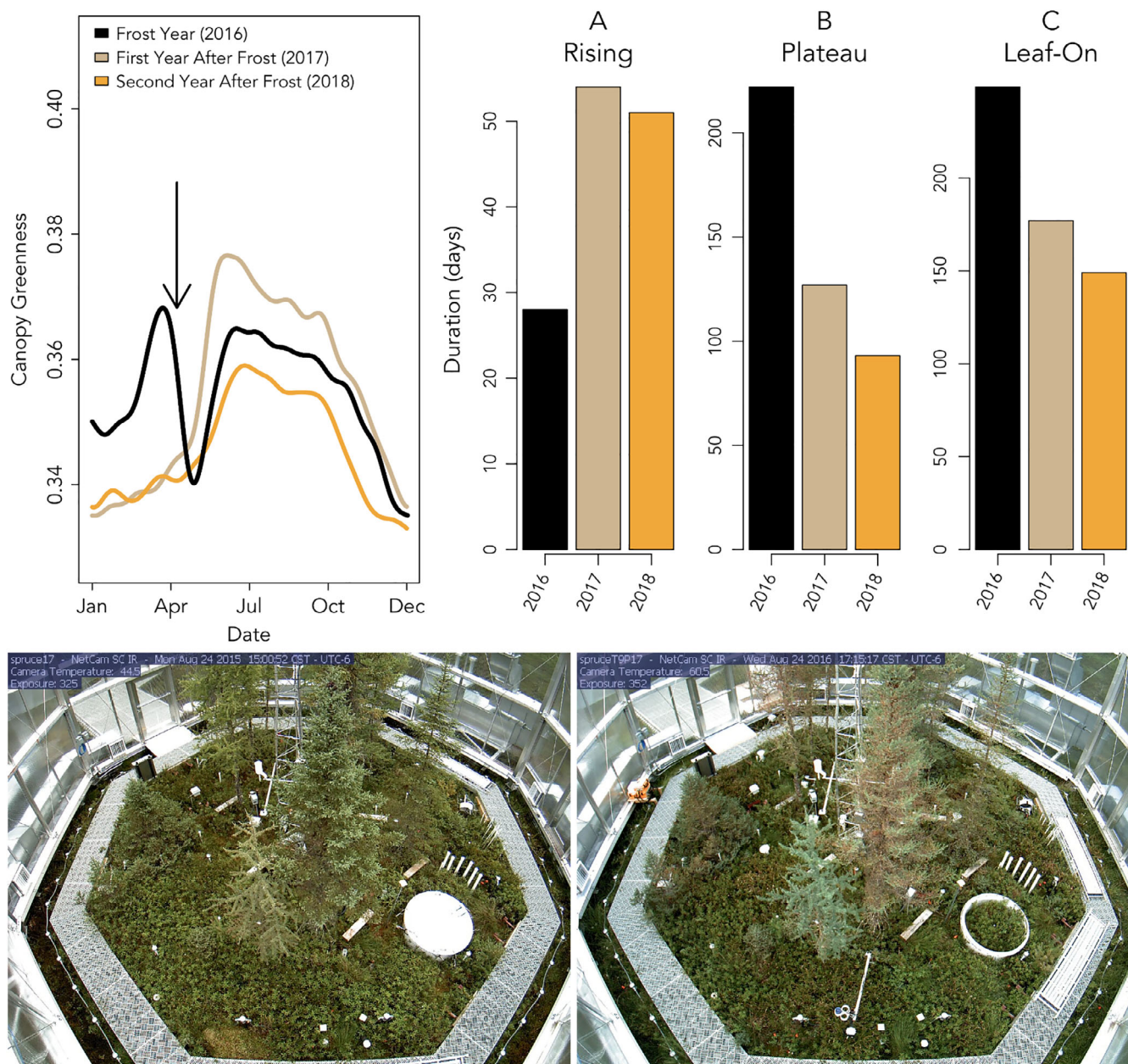


FIGURE 5 Greenness signals from before and after a frost event on April 9, 2016, which led to leaf damage in an experimental warming chamber of the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment captured by the “spruceT9P17” phenocam (Richardson, Hufkens, Milliman, Aubrecht, Furze, et al., 2018). The time of year during which the frost damage occurred in 2016 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from before and after this frost event are shown on the bottom.

National Park, Kentucky. This frost event resulted in a reversal in the rising greenness signal observed in early April until a local minimum was reached shortly after in mid-April (Figure 8). Following this, the greenness signal rose to late seasonal greenness peak in early June. The length of the rising period was 28 days longer (75%) in 2007 than the 37-day average from other years, while the lengths of the plateau and leaf-on periods were not distinct from other years. This suggests that the frost event

led to sufficient damage to impact leaf developmental periods in the 2007 growing season.

Disturbance: Insect defoliation

A forest tent caterpillar (*Malacosoma disstria*) outbreak in the Canadian province of Saskatchewan led to widespread defoliation in 2016, with a defoliation onset date

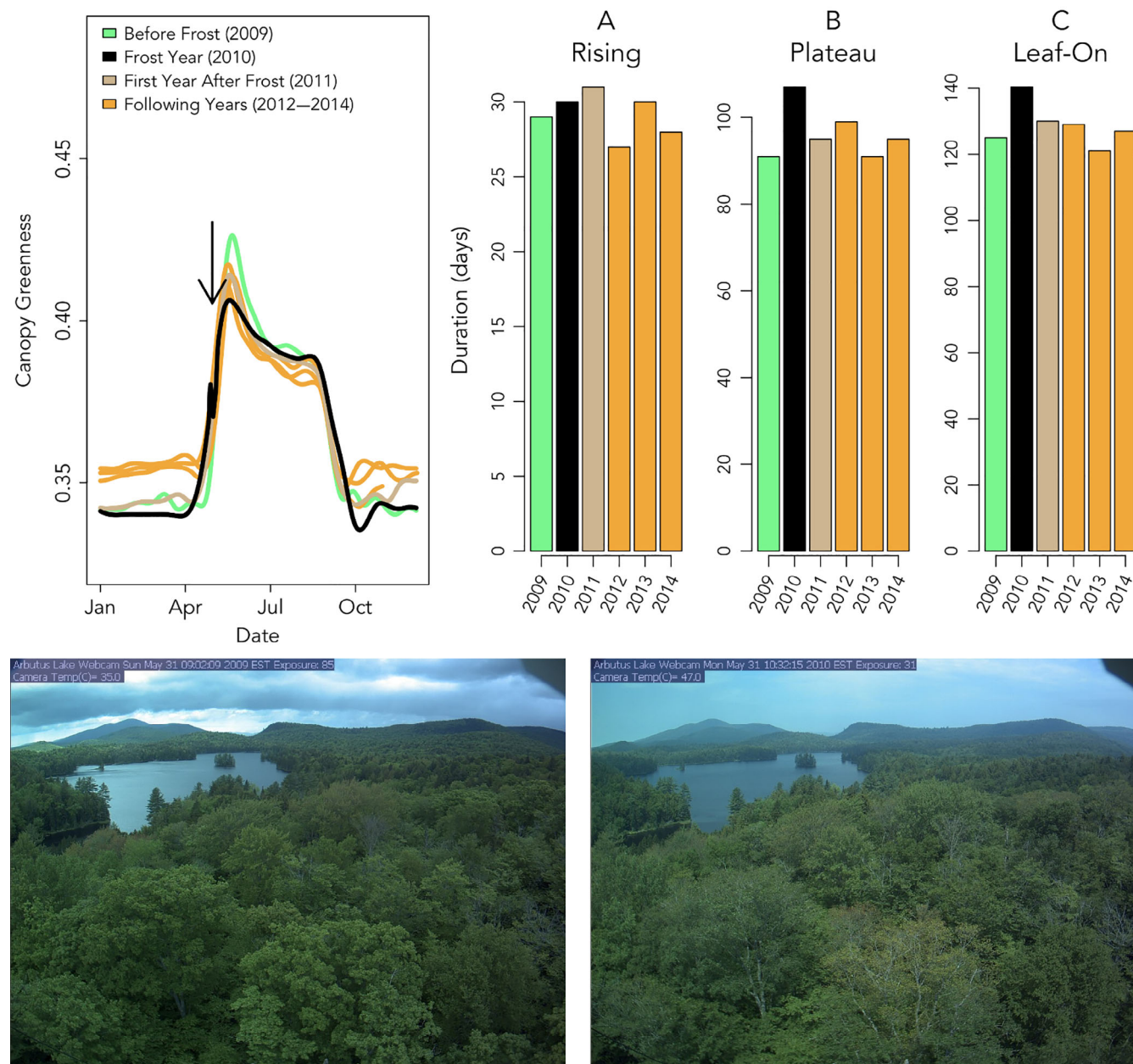


FIGURE 6 Greenness signals from before and after a widespread warm spring and late frost event in 2010 captured by the “arbutuslake” phenocam. The timing of the frost in 2010 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from one year before and immediately after the frost event are shown on the bottom.

of May 13 captured by the “canadaOA” phenocam in Prince Albert, Saskatchewan (Stephens et al., 2018). The rising greenness signal usually observed in May was temporarily reversed immediately following the outbreak and exhibited a decline until a local minimum was reached in mid-June (Figure 9). Following this, the greenness signal rose to a peak in early July over an approximately 24-day period. This seasonal peak in greenness was both reduced and late relative to previous seasons. Insect herbivory by the forest tent caterpillar led

to a rising period that was lengthened by 44 days (149%) in 2016 relative to the previous four-year average of 30 days. The duration of the plateau period was reduced by 34 days (34%) relative to the previous four-year average of 98 days. Additionally, the length of the leaf-on period was reduced by 30 days (23%) relative to the 131-day average of previous years. This suggests that the outbreak of forest tent caterpillar led to sufficient damage to impact seasonal leaf developmental periods in the 2016 growing season.

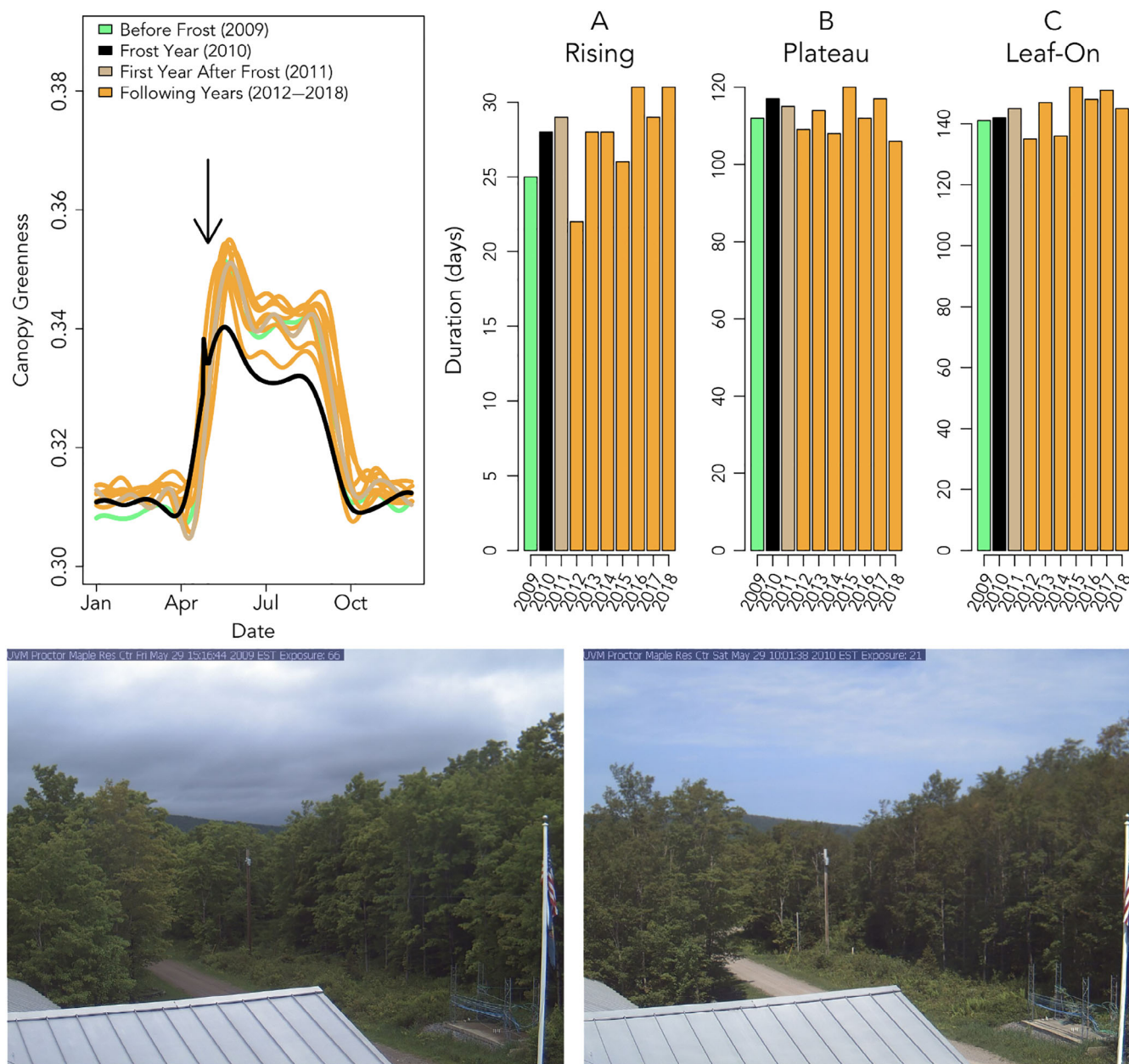


FIGURE 7 Greenness signals from before and after a widespread warm spring and late frost event in 2010 captured by the “proctor” phenocam. The timing of the frost in 2010 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from before and after the frost event are shown on the bottom.

Herbivory primarily by the European winter moth (*Operophtera brumata*) led to visibly evident defoliation in 2018, with an estimated onset date of April 20, captured by the “millhaft” phenocam in Norbury, Staffordshire, UK according to site metadata notes. Herbivory also occurred in 2019, with an estimated onset date of April 25, though to a lesser extent. The rising greenness signal usually observed in April and May was delayed immediately following the outbreak in 2018 (Figure 10). Following this, the greenness signal increased to a peak that was reduced

relative to the disturbance-free reference years of 2016, 2017, 2020, and 2021. Insect herbivory by the winter moth led to a plateau period that was shortened by 46 days (33%) in 2018 relative to the average of 141 days from reference years. The duration of the leaf-on period was reduced by 52 days (29%) relative to the 179-day average from reference years. Conversely, the extent of the rising period was not distinct in 2018 relative to reference years. In 2019, the rising greenness signal was temporarily reversed in early and mid-May until it rose over a 33-day

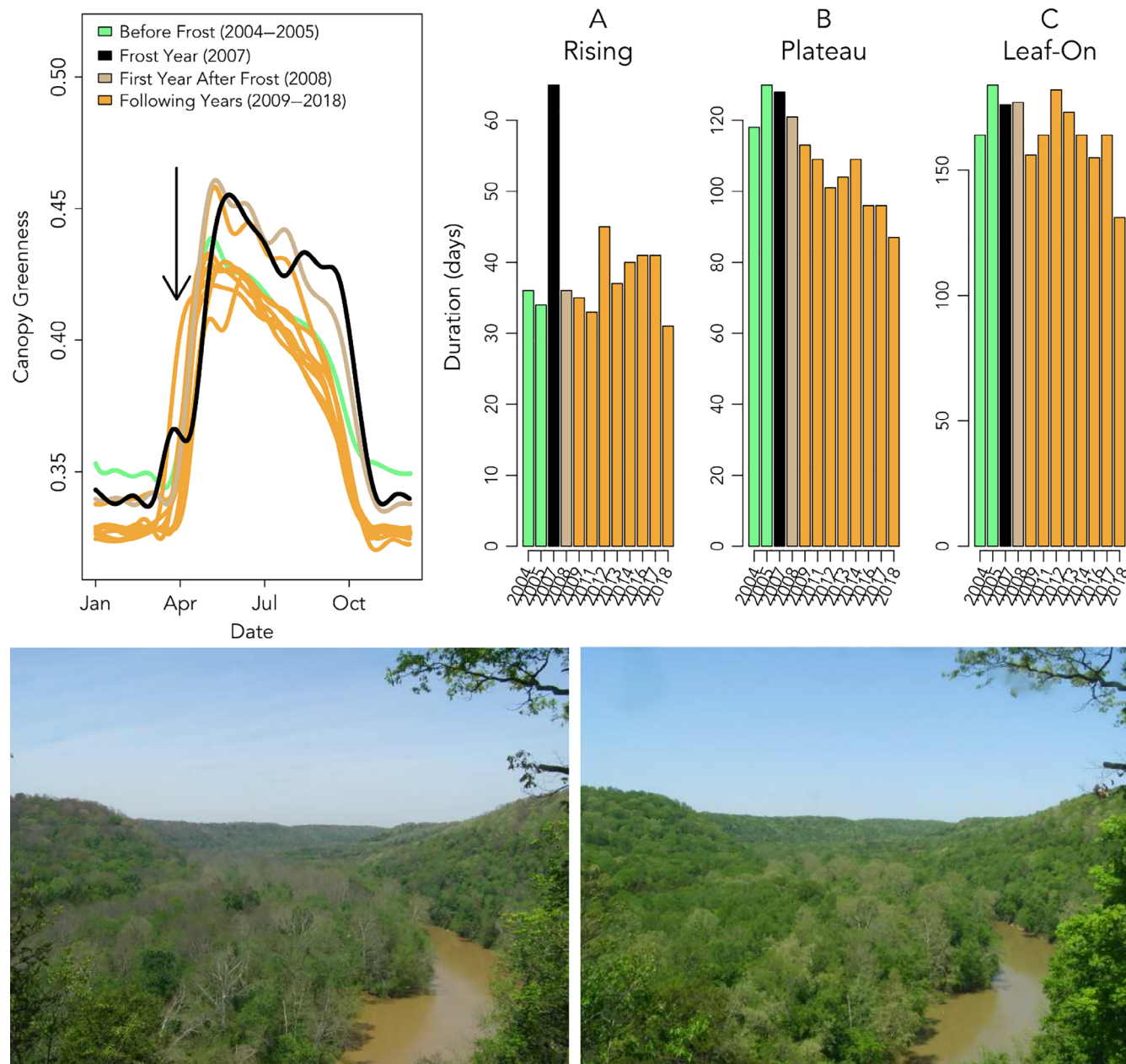


FIGURE 8 Greenness signals from before and after a frost event on April 8, 2007, which led to leaf damage captured by the “mammothcave” phenocam. Several years were excluded from analysis for this phenocam due to field-of-view shifts or data gaps occurring during the growing season. The time of year during which the frost damage occurred in 2007 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from immediately after and one year after the frost event are shown on the bottom.

period to a seasonal greenness peak, which was late and reduced relative to reference growing seasons. The greenness rising period in 2019 was 39 days longer (118%) than the 33-day average of reference years. The plateau period was 59 days shorter (42%) in 2019 than that of the 141-day average from reference years. The leaf-on period was also shortened in 2019 though to a lesser extent of 23 days (13%) relative to the 179-day average from reference years.

This suggests that the herbivory of the winter moth prompted sufficient damage to impact seasonal leaf development in both the 2018 and 2019 growing seasons.

Drought conditions led to an enhanced gypsy moth (*Lymantria dispar*) outbreak in 2015 in Massachusetts and widespread defoliation over subsequent growing seasons across more than 4000 km² of the eastern United States (Pasquarella et al., 2018). Defoliation by the

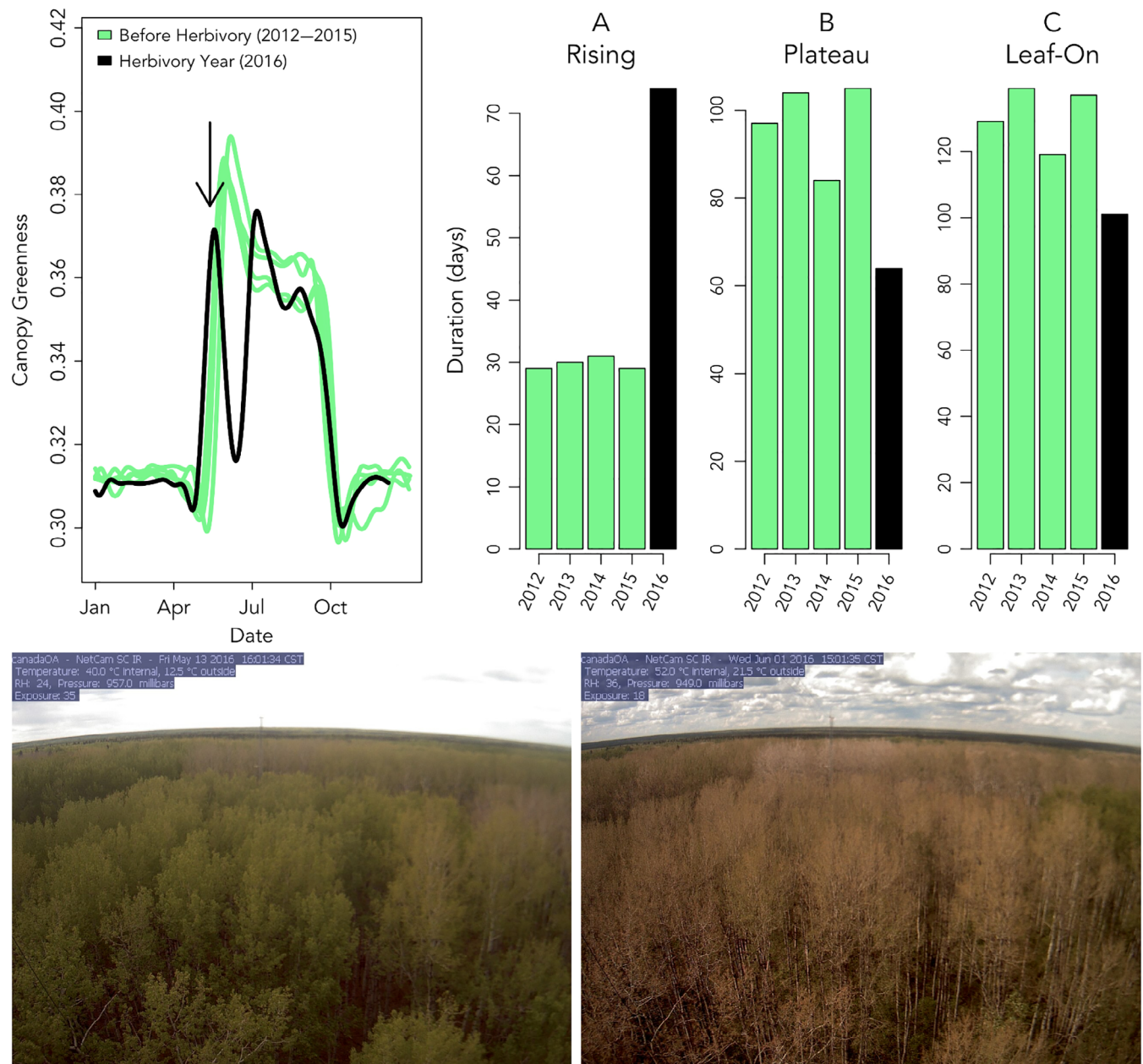


FIGURE 9 Greenness signals from before and after insect defoliation by the forest tent caterpillar captured by the “canadaOA” phenocam (Stephens et al., 2018), with an onset date of May 13, 2016. The timing of the onset of defoliation in 2016 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from before and after the defoliation are shown on the bottom.

gypsy moth was captured by the “worcester” phenocam on the Worcester State University campus in Worcester, Massachusetts, with an estimated onset date of June 10, 2018. The gradual post-peak decline in the greenness signal usually observed in June exhibited a steep decline before stabilizing and rising to a local maximum over a 26-day period in late July (Figure 11). The reduced greenness peak prompted by this herbivory led to an apparent rising period that was shortened by 7 days (21%) in 2018

relative to the 34-day average from reference years without disturbance from 2014 to 2017 and 2019 to 2021. This detected reduction prior to the onset of defoliation was likely due to the herbivory reducing the peak greenness value and thus the time between 10% and 90% amplitude in the rising portion of the greenness curve, even though the herbivory occurred following the greenness peak. Surprisingly, the plateau period was not distinct in comparison to reference growing seasons, as the early timing

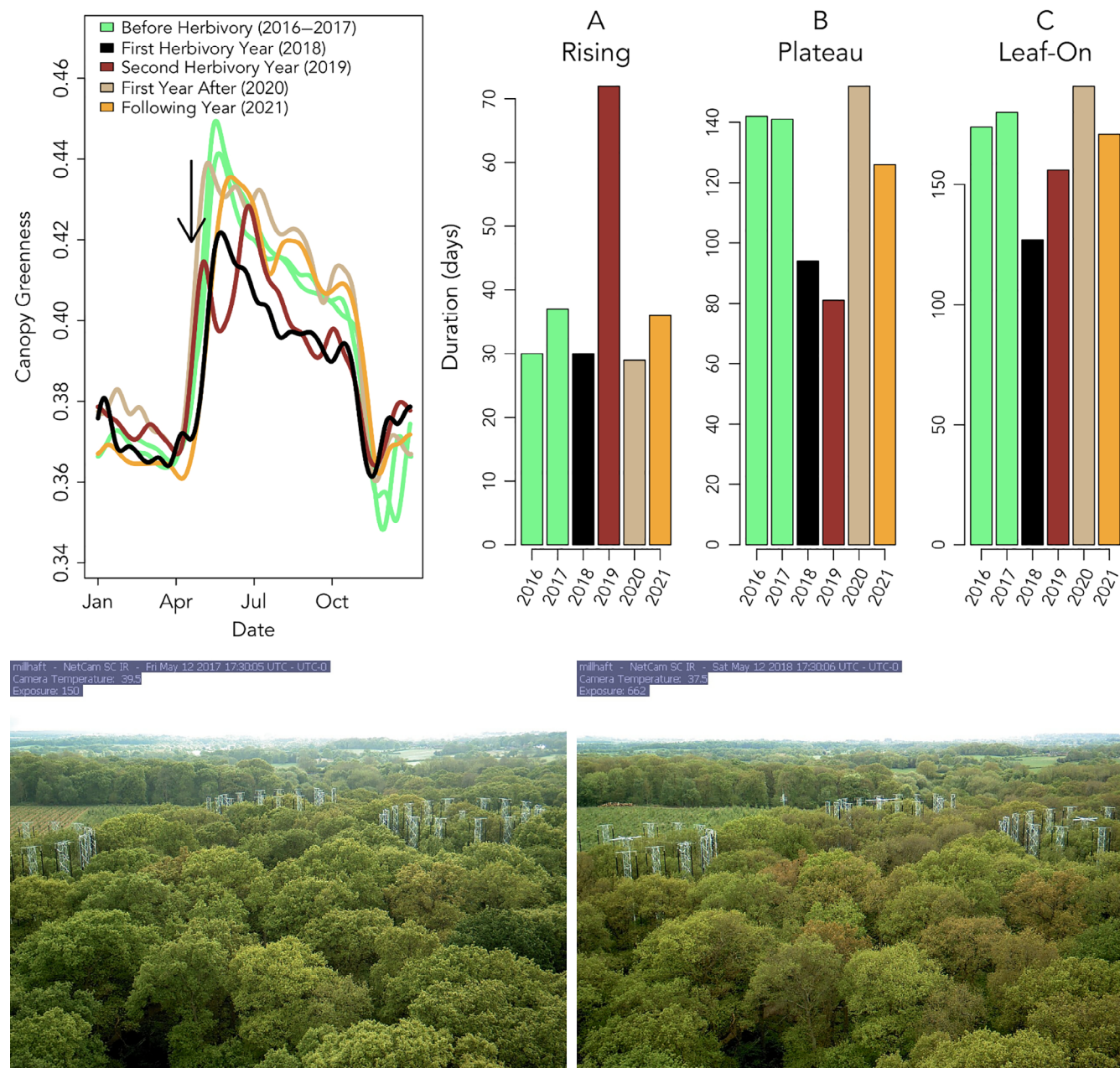


FIGURE 10 Greenness signals from before and after insect defoliation by the European winter moth captured by the “millhaft” phenocam, with estimated onset dates in April 2018 and 2019. The timing of the estimated onset of defoliation in 2018 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from one year before and immediately following the defoliation are shown on the bottom.

of 95% amplitude in the falling portion of the curve was followed by an early timing of 50% amplitude in the falling portion of the curve, which was two weeks earlier than the average of reference years. The leaf-on period was reduced by 13 days (8%) in comparison to the 159-day average from reference growing seasons. This suggests that herbivory by the gypsy moth led to sufficient damage to impact seasonal leaf developmental periods in the 2018 growing season.

Disturbance: Winter ice storm

An ice storm on December 11 and 12, 2008 damaged canopy vegetation in the Harvard Forest, including vegetation captured the by “harvard” phenocam. Minimal influence in the greenness time series was evident, but there was a substantial reduction in leaf area index (LAI) from ground data by 22% following this storm in the 2009 growing season relative to 2008 (Keenan et al., 2014).

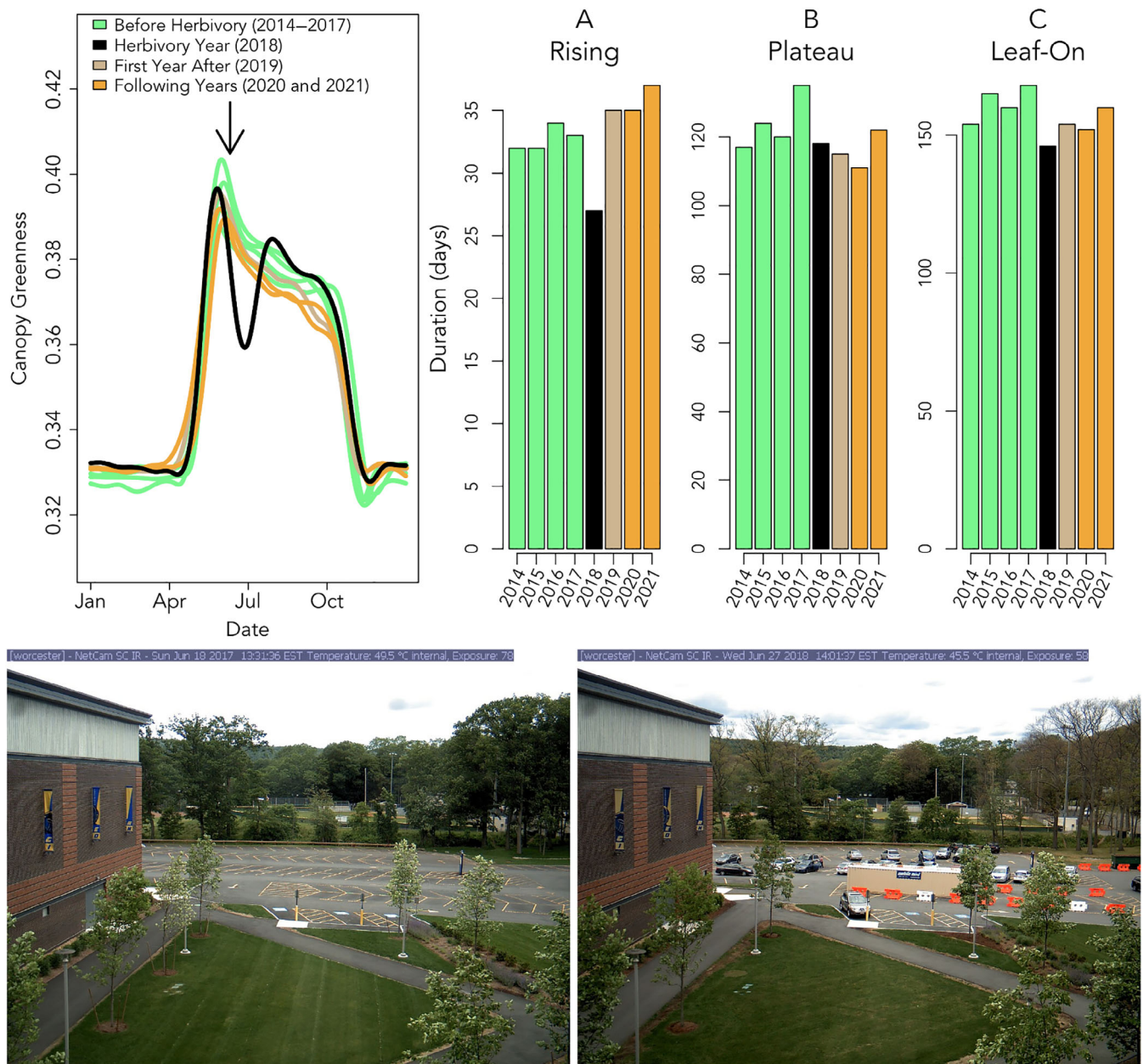


FIGURE 11 Greenness signals from before and after insect defoliation by the gypsy moth captured by the “worcester” phenocam, with an estimated onset date of June 10, 2018. The timing of the estimated onset of defoliation in 2018 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from one year before and immediately following the defoliation are shown on the bottom (note the vegetation in the top center to top right portion of the image following defoliation).

Mid-summer LAI values showed a gradual recovery to near-pre-ice storm levels by 2012, and seasonal maximum greenness values continually increased following 2009, while our length metrics did not follow any such trend (Figure 12). The length of the rising period in 2009 was six days longer than that observed in either 2008 or 2010, though only four days longer (12%) than the 31-day average from all other years. The length of the plateau and leaf-on periods in 2009 were intermediate relative to other

years. Despite this ice storm impacting local LAI values, our approach did not yield detection of anomalous leaf developmental periods.

Stress: Drought mortality

Four successive years of drought in the Kings Canyon National Park, California, led to unprecedented forest

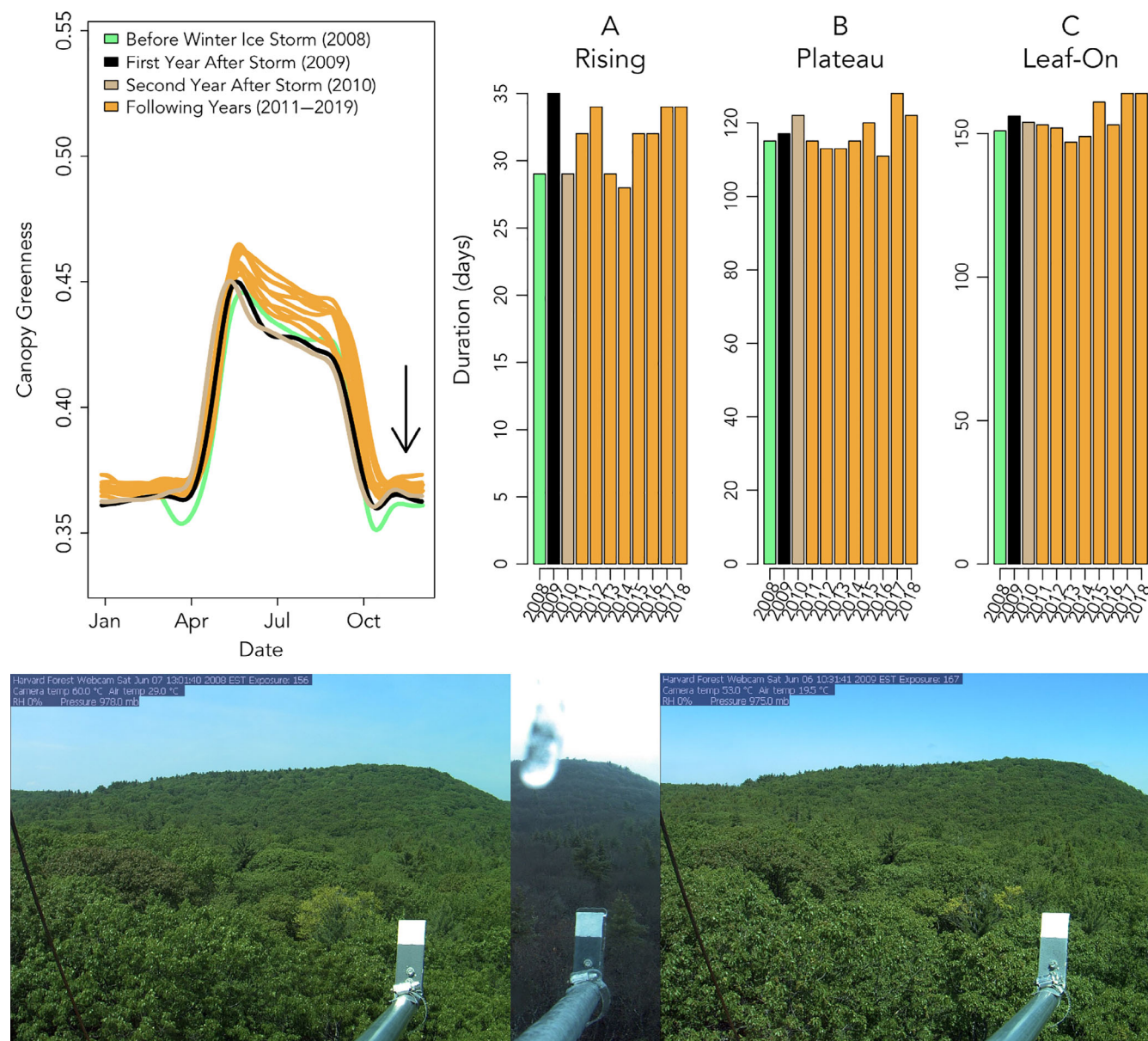


FIGURE 12 Greenness signals from before and after an ice storm in December of 2008 captured by the “harvard” phenocam. The timing of the ice storm in 2008 is denoted with an arrow. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from before, during, and after the ice storm are shown on the bottom (note the gaps in the canopy following the storm).

dieback with mortality becoming evident in the summer of 2015 captured by the “sequoia” phenocam (Richardson, Hufkens, Milliman, & Frolking, 2018; Stephenson et al., 2018). This led to a continuous decline in the maximum greenness signal observed during the growing season, with a considerable 60% reduction in the 2015 spline-smoothed greenness curve amplitude relative to 2012 (Figure 13). Each of the rising, plateau, and leaf-on periods were reduced in 2015 by 25 (43%), 35 (58%), and 55 (42%) days, respectively relative to 58, 61, and 132-day averages from the previous three years. This suggests that this drought

led to sufficient damage to impact seasonal leaf developmental periods in the 2015 growing season.

Indicator potential for disturbance or stress detection

To better assess the aptitude of leaf developmental periods extracted from the greenness curve as indicators, we examined how these deviations compare to interannual fluctuations observed in the absence of

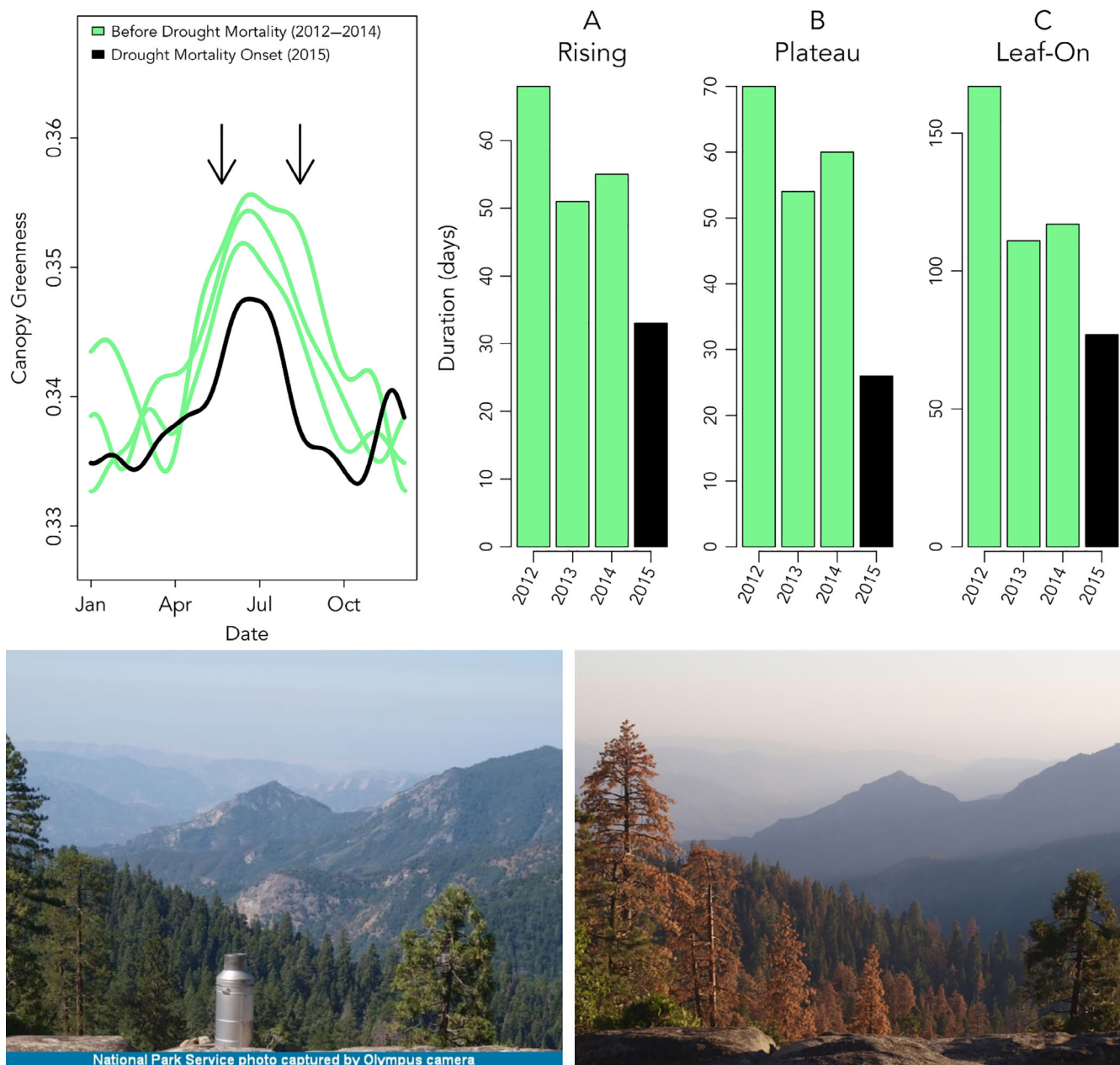


FIGURE 13 Greenness signals during successive years of drought captured by the “sequoia” phenocam (Stephenson et al., 2018), with drought-induced foliage dieback becoming evident in 2015. Arrows provide a reference for comparing successive years of greenness signals over the June–August growing season period. Greenness time series are shown for spline-smoothed 3-day 50th percentile green chromatic coordinate values on the top left. The duration of the A (rising), B (plateau), and C (leaf-on) periods are shown on the top right. Phenocam images from before (August 2011) and after (July 2016) the onset of drought mortality are shown on the bottom.

disturbance or stress across the PhenoCam Network. Probability density functions of the ratio of each period in a given year to the reference average for other years are shown in Figure 14 for all broadleaf and needleleaf sites from the PhenoCam Network without known cases of disturbance or stress. Together these probability density functions demonstrate that these periods are generally stable under normal conditions and fluctuate in response to disturbance or stress. As the rising period was shorter than other periods, cases of disturbance or stress,

which influenced the rising period, led to greater relative deviations from the average, though the probability density function was also more extensive (A in Figure 14). Typical interannual variability for the ratio of the rising period in a given year to the average of alternate years in the absence of disturbance or stress corresponds to an interquartile range of 1 ± 0.06 times the average (25th–75th percentile). Several of the rising period ratios observed in the context of stress or disturbance were more extreme than all nondisturbance rising period average ratios from the

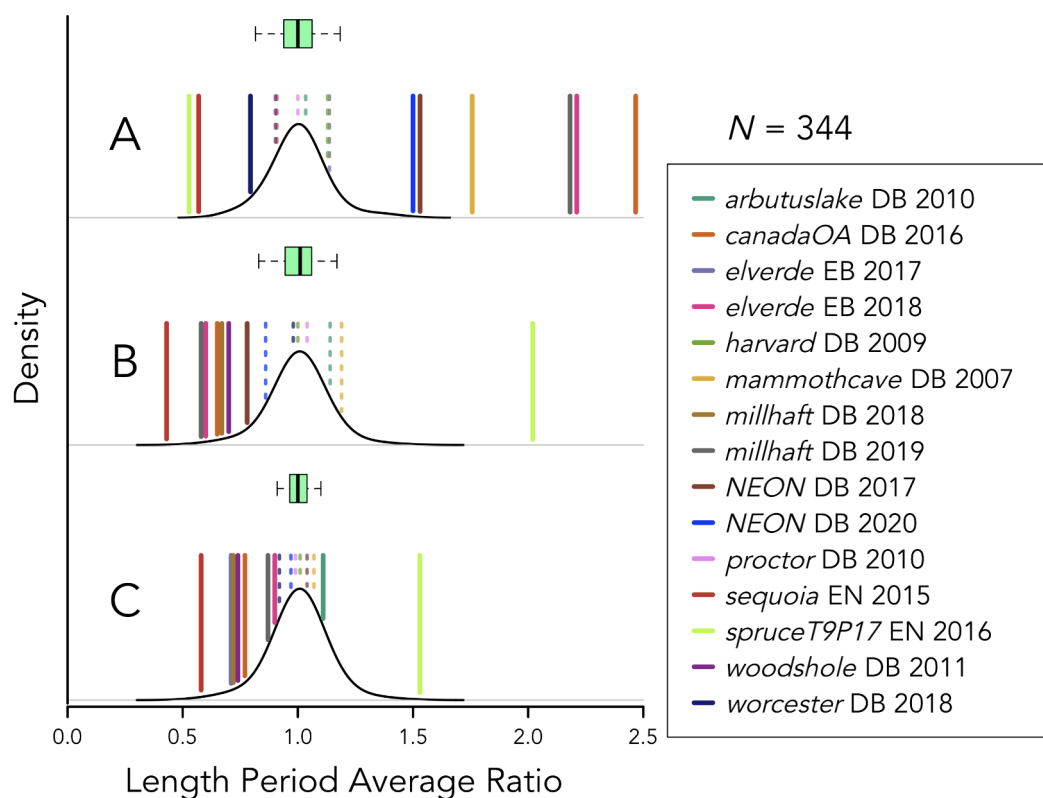


FIGURE 14 Probability density functions of the ratio of the length of a period during a given year compared with the average for all other years from PhenoCam sites hosting broadleaf and needleleaf plant functional type vegetation without known cases of disturbance or stress for a total of 344 site-years. Box plots denote the median and ± 1.5 times the interquartile range for the average ratio of each period. Solid vertical lines denote examples of known cases of disturbance or stress affecting one or more of these periods. Dashed vertical lines denote examples of disturbance or stress that had mild effects on one or more of these periods. The A (rising) period is shown on the top, the B (plateau) period is shown in the middle, and the C (leaf-on) period is shown on the bottom. The phenocam names for each case of disturbance or stress along with the dominant plant functional type (DB, deciduous broadleaf; EN, evergreen needleleaf) is shown in the legend. “NEON” stands for the *NEON.D07.GRSM.DP1.00033* phenocam.

PhenoCam Network. These extreme cases included the 2007 rising period ratio of 1.76 observed by the *mammothcave* phenocam, the 2016 rising period ratio of 2.47 observed by the *canadaOA* phenocam, the 2016 rising period ratio of 0.52 observed by the *spruceT9P17* phenocam, the 2017 and 2020 rising period ratios of 1.53 and 1.5 observed by the *NEON.D07.GRSM.DP1.00033* phenocam, the 2018 rising period ratio of 2.14 observed by the *elverde* phenocam, and the 2019 rising period ratio of 2.18 observed by the *millhaft* phenocam. A spring rising period of 0.57 times that of the average for other years, such as observed with the *sequoia* phenocam in 2015, is equivalent to a probability of less than 1% more extreme values. In contrast, the rising period observed by the *worcester* phenocam in 2018, which corresponded to a ratio of 0.79 times the average of reference years, was associated with a probability of approximately 4% more extreme values in nondisturbance rising period average ratios from the PhenoCam Network.

The duration of the plateau period was generally reduced in the context of disturbance or stress, with the exception of the warming treatment and frost event observed by the *spruceT9P17* phenocam (B in Figure 14). The degree of deviation relative to the reference average for the plateau period was less pronounced in terms of probability than that of the spring rising period, though greater than that of the leaf-on period. Similar to that observed for the rising period average ratio, typical interannual variability for the ratio of the plateau period in a given year to the average of reference years without disturbance or stress corresponds to an interquartile range of 1 ± 0.06 times the average (25th–75th percentile). Two of the plateau period ratios observed in the context of stress or disturbance were more extreme than all nondisturbance plateau period average ratios from the PhenoCam Network. These included the extended plateau period observed by the *spruceT9P17* phenocam in 2016, which was 1.75 times the average, as well as the reduced plateau period observed by the *sequoia*

phenocam in 2015, which was just 0.43 times the average from previous years. Several of the plateau period ratios observed in the context of disturbance or stress were associated with a probability of less than 1% in detecting more extreme values in the absence of disturbance or stress. These included the plateau period ratio of 0.71 times the average observed by the *woodshole* phenocam in 2011, the plateau period ratios of 0.67 and 0.58 observed by the *millhaft* phenocam in 2018 and 2019, the plateau period ratios both equal to 0.6 observed by the *elverde* phenocam in 2017 and 2018, as well as the plateau period ratio of 0.65 observed by the *canadaOA* phenocam in 2016. In contrast, the plateau period ratio of 0.78 observed by the *NEON.D07.GRSM.DP1.00033* phenocam in 2017 corresponded to a greater probability of 3% more extreme cases.

The length of the leaf-on period was found to respond less acutely to disturbance or stress relative to the other periods (C in Figure 14). This may be due to reductions in the rising and plateau periods due to disturbance or stress being compensated to some degree by a delayed or extended senescence process (Zohner et al., 2019). The leaf-on period also had reduced interannual variability in the absence of stress or disturbance compared with the rising and plateau periods. The ratio of the leaf-on period in a given year to the average of reference years without disturbance or stress corresponds to an interquartile range of 1 ± 0.04 times the average (25th–75th percentile). Four of the leaf-on period ratios observed in the context of stress or disturbance were more extreme than all nondisturbance leaf-on period average ratios from the PhenoCam Network. The most distinct deviation in the leaf-on period was observed by the *spruceT9P17* phenocam in 2016, with a ratio of 1.53 times the average of reference years. Other leaf-on period average ratios, which were unprecedented in the absence of stress or disturbance across the PhenoCam Network, included the leaf-on period ratio of 0.58 observed by the *sequoia* phenocam in 2015, the leaf-on period ratio of 0.71 observed by the *elverde* phenocam in 2017, and the leaf-on period ratio of 0.72 observed in 2018 by the *millhaft* phenocam. Similarly, the leaf-on periods observed in 2011 by the *woodshole* phenocam and in 2016 by the *canadaOA* phenocam were 0.74 and 0.77 times the average of other years, each corresponding to a probability of less than 1% more extreme cases. The leaf-on period observed in 2019 by the *millhaft* phenocam was 0.87 times the average of reference years, corresponding to a probability of about 3% more extreme values. A less distinct leaf-on period of 0.9 times the average was observed by the *elverde* phenocam in 2018, which corresponded to a probability of about 7% more extreme values. The only two extended leaf-on periods were observed in 2010 by the *arbutuslake*

phenocam and 2016 by the *spruceT9P17* phenocam. The *arbutuslake* phenocam leaf-on period in 2010 was 1.11 times that of the average from other years, corresponding to a probability of approximately 6% more extreme cases, while the leaf-on period was observed by the *spruceT9P17* phenocam in 2016 as mentioned above was 1.53 times the average of reference years.

A confusion matrix conveying the prevalence of true damage detection due to disturbance or stress shifting one or more of the rising, plateau, and leaf-on periods beyond an indicator threshold is shown in Figure 15. We designated threshold indicator ratios based upon the probability density functions presented in Figure 14 to optimize the signal-to-noise ratio in detecting anomalous periods while avoiding the false classification of periods as anomalous. These threshold ratios therefore differ from the interquartile ranges presented above to limit the misclassification of slightly unusual periods as a result of disturbance or stress. If disturbance or stress, which led to leaf functional decline, shifted one or more of these periods beyond our indicator thresholds, it was counted as a true detection. If, on the other hand, leaf functional decline was known to have occurred though none of the periods were shifted beyond the threshold, this was considered a false nondetection of damage. Likewise, if no disturbance or stress was known to have occurred, we assumed there was no leaf functional decline or damage. If under these circumstances one or more of these periods was beyond our indicator thresholds, we considered this a false detection. Under the same circumstances, if these periods

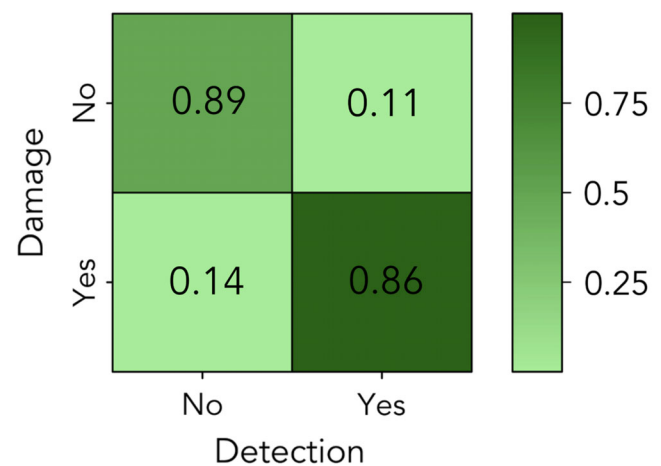


FIGURE 15 Confusion matrix for the combined detection of anomalous rising, plateau, or leaf-on periods associated with leaf damage due to either disturbance or stress versus normal conditions. The x-axis labels correspond to the predicted classification or detection while the y-axis labels correspond to the true classification. True predictions are along the diagonal. The proportion of each classification is shown as a number and color in each matrix cell, with higher proportions corresponding to a darker green hue.

were not beyond our indicator thresholds, we considered these cases to be examples of true nondetection. This matrix also includes the incidences of false detections, true nondetections, and false nondetections, based upon the probability density functions above. A designated indicator ratio of the spring rising period being beyond 1 ± 0.2 times the average correctly detected nine cases of disturbance or stress as anomalous rising periods. This indicator ratio corresponds to a combined probability of approximately 9% being false positives. Several of the 29 nondisturbance site-years, which were associated with rising periods beyond 1 ± 0.2 times the average, were observed at SPRUCE experimental sites, which may have shown these fluctuations in response to experimental treatments as well as the spring frost event in 2016. For the plateau period, an indicator ratio of the period being 1 ± 0.2 times the average from other years would correctly detect the nine cases of disturbance or stress influencing the plateau period observed from the PhenoCam Network, with a probability of approximately 9% being false positives. Several of the 26 nondisturbance site-years, which were associated with plateau periods beyond 1 ± 0.2 times the average, were also observed at SPRUCE experimental sites. Lastly, an indicator ratio of the leaf-on period being beyond 1 ± 0.1 times the average from other years would capture the nine cases of disturbance or stress influencing the leaf-on period observed from the PhenoCam Network, with a probability of approximately 15% being false positives. A minor adjustment of this indicator ratio by just 0.01 would omit the case of disturbance observed through the *arbutuslake* phenocam, necessitating the relatively high false detection error rate. As with the other indicator periods, several of the 32 nondisturbance site-years, which were associated with leaf-on periods beyond 1 ± 0.1 times the average, were observed at SPRUCE experimental sites. Disturbance cases observed by the *harvard* and *proctor* phenocams were not detected as anomalous rising, plateau, or leaf-on periods through our approach, amounting to the 14% false-negative error rate across indicator periods. Twelve of fourteen cases were correctly detected, amounting to an 86% true detection rate. Together the combined application of anomalous rising, plateau, or leaf-on periods as an indicator of probable disturbance or stress effects amounts to an 11% average probability of false positives, and an 89% probability of true classifications of nondamage.

DISCUSSION

Here we provide a novel and comprehensive exploration of the potential of phenocams to capture declines in leaf function associated with various forms of disturbance and stress. With analysis of phenocam records, we

detected disturbance and stress-driven declines, which occurred in the early, middle, and late growing seasons for both deciduous and evergreen vegetation. The disturbance and stress agents we examined included hurricanes, windstorms, frost, herbivory, and drought. This highlights the applicability of phenocams for monitoring ecologically relevant phenomena beyond leaf phenology.

The approach of classifying disturbance-related impaired leaf function based upon vegetation indices time series has been previously applied with satellite-based observations and found to perform well following ground validation (Bascietto et al., 2018; Löw & Koukal, 2020). The application of phenocams we present here allows for the sensitive detection of leaf functional decline at a fine spatial scale, with the potential for developing species-specific insights (Berra & Gaulton, 2021; Hufkens, Friedl, Sonnentag, et al., 2012). Previous studies have shown leaf damage or defoliation resulting from disturbance or stress during the optimal growing season period can disrupt forest ecosystem processes (Bonan & Shugart, 1989; Stephens et al., 2018). As ecological integrity is determined by the cohesion of ecosystem processes, monitoring leaf function through phenocams provides valuable insights for the purposes of ecological integrity monitoring. The scale of observation afforded by phenocams is equivalent to that of manual ground-based observations, though with the potential for quantitative monitoring with enhanced perception beyond the capabilities of human eyesight. The imagery records produced by phenocams provide a means to precisely detect and review the evolution of disturbance or stress effects both through computational processing and from visual inspection of images. This allows for precise characterization of the timeline of such effects and an enhanced insight into probable cause. Additionally, phenocams enable the exploration of how fine-scale ecological and microclimate contexts influence susceptibility to disturbance or stress (Field et al., 2020; Lukasová et al., 2020). A previous study employing more than 40 years of observations classified premature fall discoloration as when the date occurred within the lower 5% of a normal distribution, which was 2–3 months earlier than typical (Bigler & Vitasse, 2021). The methods we proposed here are capable of autonomously identifying such acute deviations, as well as some more moderate deviations, which may be associated with stress or disturbance. Given the streamlined PhenoCam Network processing chain of image collection, storage, and processing, the detection of anomalous leaf developmental periods associated with potential disturbance or stress presented here could be delivered in real time for conservation managers. The methods we propose here would similarly be promising for the recently established Acadian Phenocam Network in eastern Canada, which spans three provinces and five National Parks. Figure 16

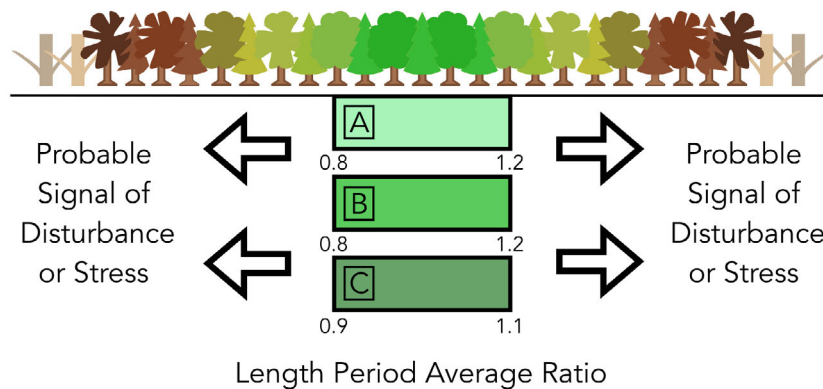


FIGURE 16 Conceptual representation of the probabilistic relationship between leaf function and deviation in the length of the A, B, or C periods each year relative to the average of other years. Period A is the greenness rising portion of the curve between the onset of leaf growth and the seasonal peak in greenness calculated as the time between the 10% and 90% amplitude, period B is the greenness plateau following the seasonal peak in greenness calculated as the time between 95% and 50% amplitude in the falling portion of the greenness curve, and period C is the entire leaf-on period calculated as the time between 50% amplitude in the rising portion and 50% amplitude in the falling portion of the greenness curve. The numbers at the bottom edge of each row denote the threshold indicative of probable disturbance or stress effects rather than interannual variability. An A rising period of beyond 1 ± 0.2 times the average, a B plateau period of beyond 1 ± 0.2 times the average, and a C leaf-on period of beyond 1 ± 0.1 times the average correspond to probable disturbance or stress.

provides a conceptual framework for the designation of our indicator periods.

These metrics allow for the quantification of impacts in terms of the deviation in the duration of leaf developmental periods, though further investigation is needed to distinguish between fluctuations consistent with immediate defoliation versus prolonged declines in leaf function. While our duration metrics fluctuated more in response to disturbance or stress than due to inherent variation for some sites, caution is warranted in assigning indicator scores from these periods due to the relatively few phenocam time series available to monitor such effects. Additionally, recovery transitions may continue to occur more than a growing season following disturbance or stress, altering the utility of apparent reference growing seasons for our duration metrics. A strategic approach for classifying future observations would be to use our duration metrics as a means of assigning priority for further investigation. With each growing season, the reference average and interannual variability for these periods can be automatically refined as periods are iteratively recalculated, or manually refined by conservation managers familiar with site characteristics. Additionally, some disturbances did not result in a deviation of leaf developmental periods outside that of the range from years without disturbance, such as for the phenocams *proctor* and *harvard*. These latter cases may be due to disturbance events having a mild influence on phenocam-derived greenness curves due to saturation in the greenness metric (Keenan et al., 2014; Yang et al., 2014), or due to our length metrics not encompassing the portions of the curve

that were most affected by these events. In some cases, such as for the *arbutuslake* phenocam, the detected deviation in indicator periods was mild, which may have been due in part to the monitored region of interest including a variety of species that were affected to different degrees by the frost event. Additionally, we also explored the use of original unsmoothed spring greenness time series for the *proctor* and *arbutuslake* phenocams and found that this still did not result in pronounced anomalous periods for the 2010 frost year. This indicates that the additional research is needed to develop a more sensitive indicator for detection of frost damage. Further investigation is warranted to optimize the indicator potential of periods calculated from a greater variety of amplitude thresholds, especially between the beginning of senescence and the onset of dormancy to better understand the impact of disturbance or stress on the senescence process. A promising avenue for future research is to examine change over time in leaf maturation and senescence rates, as this would allow for the detection of gradual changes in leaf phenological states over time. A stable representation of the integrated area under the growing season greenness curve may provide an alternative approach to detecting deleterious disturbance or stress effects. We conducted a preliminary analysis that yielded an anomalous integrated area for the 2010 spring frost growing season for the *proctor* phenocam, though variable areas for some of the other sites in the absence of disturbance or stress. Another promising avenue for future research is the development of a resiliency indicator through the quantification of leaf damage severity in terms of the rate of change in greenness

following disturbance or stress, as well as the rate of subsequent recovery, which may contribute to ongoing works within the ecological community (Scheffer et al., 2009; Smith et al., 2022). In addition, the interaction between disturbance or stress effects and the status of vegetation prior to disturbance or stress could be investigated with the use of phenocam data. For example, disturbance in the form of severe insect defoliation is often a consequence of drought or other preexisting stress factors, and there may be preemptive signals preceding such disturbance events, which may provide actionable insights to conservation managers (Anderegg et al., 2015; McLennan & Zorn, 2005).

Using the length of time between different amplitude percentages of the greenness curve as ecological indicator metrics rather than the timing of a given phenophase extracted from the greenness curve is potentially advantageous in reducing the influence of uncertainty due to extraction approaches (Toomey et al., 2015). A previous phenocam study found that greenness amplitude thresholds were suitable proxies for various stages of leaf development (Zhang et al., 2020). Additionally, this approach provided a clear signal for the drought mortality onset observed through the *sequoia* phenocam, which is focused on evergreen needleleaf vegetation, which typically has a lower seasonal amplitude and potentially greater uncertainty in curve-derived phenology relative to deciduous broadleaf vegetation across both phenocam- and satellite-based observation platforms (Ling et al., 2022; Seyednasrollah et al., 2021). However, this approach is also susceptible to reduction in the greenness curve amplitude due to disturbance influencing the time between amplitude percentages in unexpected ways, and potentially eclipsing disturbance or stress signals. Rigorous quality control in the form of omitting records with instability in target ROIs and extensive observational gaps during the leaf-on period is necessary to avoid false attribution of anomalous periods to disturbance or stress effects. Another promising avenue for future research would be to examine the influence of site ecological memory on the stability of these indicator periods. One benefit of the approach of automated leaf phenology monitoring with phenocams is the option to reprocess archived imagery data using new and improved techniques. In addition, the establishment of long-term monitoring programs with phenocams in a variety of environmental contexts for species can provide enhanced insight into typical ranges of periods between leaf phenology stages for a given species.

Toomey et al. (2015) and Matiu et al. (2017) both found correspondence between phenocam-derived greenness and gross primary production over time, indicating that greenness can be used as a dynamic ecosystem function indicator beyond the timing of leaf phenology.

We also explored the timing of leaf phenology itself as an ecological integrity indicator, though found that variation due to other factors was of a similar magnitude or in some cases greater than variation due to disturbance or stress, and that this approach neglects the role of developed frost hardiness, which may not vary consistently with phenology between species (see Zohner et al., 2020). Extreme weather like Hurricane Dorian (>10,000 ha of forest damage), which led to widespread forest damage on the order of >500 ha, may affect Nova Scotia, the province in which 22 of the 33 Acadian Phenocam Network cameras are managed, as frequently as once every seven years (MacLean et al., 2022; Taylor et al., 2020). Insect outbreaks such as that of *Choristoneura fumiferana*, the spruce budworm, which lead to widespread damage of predominant native tree species, may also occur in Nova Scotia once every 30–40 years (Smith et al., 2010). Additionally, two of the Acadian Phenocam Network phenocams are focused on eastern hemlock (*Tsuga canadensis*) within the Kejimikujik National Park, amidst an ongoing invasion of the hemlock wooly adelgid (*Adelges tsugae*), which began in 2017 and has already led to hemlock mortality. The hemlock wooly adelgid is an invasive pest known to rapidly defoliate entire stands with wide-reaching ecological impacts, as the eastern hemlock is a foundational species providing specialized habitat for both terrestrial and aquatic species (Brantley et al., 2015; Emilson & Stastny, 2019). Therefore, monitoring protocols such as those we explored here are promising in allowing for the sensitive individual-scale detection of both gradual and abrupt decline in leaf function and ecological integrity due to global change throughout both the Acadian Phenocam Network and PhenoCam Network, and beyond. The insights gathered from monitoring leaf developmental periods can also help to understand the changing frequencies of cases of leaf damage due to disturbance or stress in the context of global change, and the implications of these cumulative effects for ecosystem functioning and the carbon cycle (Curtis & Gough, 2018; Dubé et al., 2013). While our investigation was focused on disturbance and stress, another important consideration is community-level phenological synchrony in the context of global change. Further work is required to understand what level of change may jeopardize the continued synchrony of ecological interactions, and how to correctly attribute variation in phenology over time (Renner & Zohner, 2018).

This study provides a novel means to systematically quantify the severity of disturbance or stress effects on leaf function with ground-based imagery provided by phenocams, which is increasingly valuable in the context of ongoing global change. The duration of leaf developmental periods explored here can provide a framework

for assessment of the vegetation functional component of ecological integrity and insight toward characterization of ecological tipping points consistent with critical adverse effects on ecosystem ecology. The application of the duration of periods from phenocam-derived greenness patterns as an ecological integrity indicator may be more complex than other traditional indicators in that it requires a nuanced consideration of a variety of factors, such as signal quality, species, and environment. Despite this complexity, the use of phenocams for ecological integrity monitoring provides several distinct advantages including automation, cost-efficiency, fine-scale sensitivity, and quantitative monitoring, with the potential for reduced complexity as new monitoring insights are developed. Other traditional methods for the monitoring of disturbance or stress effects such as aerial or field surveys require considerable time and financial resources for conservation managers. Phenocams also provide potential for ancillary research objectives with image time series including the dynamics of ice, snow, flowering, and other ecologically important phenomena in the scene (Jacobs et al., 2009). Understanding which species are robust, resilient, or susceptible to global change through the monitoring protocol we proposed here will provide insight for effective conservation and management activities (Chamberlain et al., 2019). This would allow for informed decisions regarding ecological forestry practices in the context of global change, which species to plant for remediation following disturbance events, and which species may require additional focus for protection from disturbance agents (MacLean et al., 2022; Price et al., 2013; Taylor et al., 2020).

CONCLUSION

Leaf phenology serves as a direct and integrative indicator of the biological effects of climate change. Near-continuous observations from phenocams allow for the quantitative monitoring of seasonal leaf development. Ecological integrity, or the intactness of ecosystem processes, such as water and carbon cycling, is a crucial assessment tool for conservation efforts. Phenocams are a promising ecological integrity monitoring tool, as they can be efficiently applied and produce high-resolution quantitative data of leaf function and potential disruptions due to disturbance or stress. Here we examined phenocam observations of vegetative responses to disturbance and stress with 14 site-year examples from the PhenoCam Network, including disturbances in the form of hurricanes, windstorms, spring frost, insect defoliation, and a winter ice storm, as well as stress due to drought. Reductions or extensions of at least $\pm 20\%$ in the rising

section in the seasonal greenness curve, $\pm 20\%$ in the plateau section following the greenness peak, and $\pm 10\%$ for the entire leaf-on period were indicative of a response to a major disturbance or stress. The duration of these periods each year in comparison to the average for other years with these thresholds resulted in average true detection rates of 86% and false-positive detection rates of 11% when sampling from probability density functions of 344 broadleaf and needleleaf PhenoCam site-years. True-negative detection rates were 89% on average, while average false-negative detection rates were 14%. Together these rates indicate that the duration of the rising, plateau, and leaf-on periods serve as sensitive indicators of disturbance and stress, and that these periods may provide novel insights into species-specific recovery processes. Despite the complexity of phenocam-derived leaf developmental periods as ecological integrity indicators, their application is strategic in providing a wealth of information with cost-effective operation. Phenocams present a promising means to assess which forest ecosystems are robust, resilient, or susceptible to global change, which will facilitate informed conservation practices.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sets utilized for this research are as follows: PhenoCam V2.0 data set (<https://doi.org/10.3334/ORNLDAAAC/1674>; Seyednasrollah, Young, Hufkens, Milliman, Friedl, Frolking, Richardson, Abraha, et al., 2019), and a pre-release of the PhenoCam V3.0 data set (https://phenocam.nau.edu/phenocam_explorer_prerelease/; Hufkens et al., 2018; Richardson, Hufkens, Milliman, Aubrecht, Chen, et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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