

PhenoCam: An evolving, open-source tool to study the temporal and spatial variability of ecosystem-scale phenology

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Highlights:

- Over 60 y, the scope of phenological research published in AFM has evolved
- Agricultural applications were once dominant; climate change is now a recurring theme
- Review focuses on phenocam, or phenology camera, papers published in AFM
- Documents history and evolution of the PhenoCam Network, and lessons learned
- Opportunities for machine learning/computer vision to advance phenocam science

Abstract

Over the last twenty years, phenology—the study of seasonal life cycle events—has emerged as a key subfield of global change biology. Phenology provides an integrated measure of the organismal response to climate change and is a key driver of the functional responses of ecosystems to climate change. Since I established the PhenoCam Network in 2008, over 200 papers have been published using phenocam technology, and these papers have added to our understanding of phenology as both an indicator of climate variability and change and a key aspect of ecosystem function. This review examines: (1) the changing phenological research landscape, as represented by phenology-themed papers in *Agricultural and Forest Meteorology* (AFM), over the last 60 y; (2) the contributions of phenocams and the PhenoCam Network, as reported in the pages of AFM, to the study of phenology; and (3) the lessons I have learned from developing this grassroots effort, and how other researchers might benefit from the PhenoCam Network's successes and failures. Key conclusions to emerge from this review include: (1) the enormous, value-added power of research networks; (2) the importance of both interpersonal relationships and serendipity, in the metamorphosis of ideas into results; and (3) the potential for open, freely-available data to be transformative, in ways that cut across disciplinary, socioeconomic, and demographic barriers. Finally, the development of the PhenoCam Network has been a collaborative, multidisciplinary experiment in team science, and the commitment of my team members and the enthusiasm of my collaborators have been critical to the success of these efforts.

Keywords: Carbon cycle, ecohydrology, energy balance, FLUXNET, land-atmosphere interactions, seasonality.

1. Introduction

Phenology, the study of seasonal rhythms of plant and animal life cycle events, is a fascinating subfield of both biology and ecology that bridges across disciplinary axes from environmental biology to physiological ecology to biometeorology, and from natural history to climatology to biosphere-atmosphere interactions (Richardson et al., 2013a). Phenology is therefore inherently interdisciplinary; it is important not only for how individual organisms respond to their growth environment, but also as a regulator of how individuals interact on both intraspecific and interspecific levels, from reproduction to competition, and how organisms, by mediating fluxes of carbon, water, and energy, directly influence the climate system (Peñuelas et al., 2009; Schwartz, 2013). Furthermore, phenology has obvious relevance to many branches of resource management and conservation (Ettinger et al., 2022; Morisette et al., 2009; Richardson et al., 2017). Humans are also innately connected to the rhythm of the seasons and how signals of this rhythm are manifest—making phenology a key avenue of outreach to the general public.

While naturalists and agriculturists have kept records of germination, flowering, and other phenological events since at least the 18th century, the field of “phenology” as a distinct branch of natural history did not receive its name until the middle of the 19th century (Demarée and Rutishauser, 2009). Although sometimes confused with the Victorian pseudo-science of phrenology, phenology has in recent decades proven to be a sensitive indicator of biological responses to climate change. As such, the study of phenology has emerged as a key component of contemporary global change biology, as demonstrated by numerous publications in the highest-impact multidisciplinary journals in recent years (Meng et al., 2020; Wu et al., 2022; Yin et al., 2023; Zani et al., 2020). This change in perception has, to some degree, been the result of new approaches being brought to bear on decades-old questions such as “(1) how does

vegetation phenology vary in time and space?” and “(2) what are the key drivers of vegetation phenology?” In addition to molecular techniques (e.g., hormonal and omics studies on model organisms, e.g. *Populus* and *Arabidopsis*) that provide insight into processes at the cellular and sub-cellular level, other tools such as satellite remote sensing, eddy covariance, phenocams (see Box 1 and Figure 1), Bayesian statistics, and clever manipulative experiments, are providing new understanding of phenological patterns, and their relationship to environmental drivers and ecosystem function, across a wide range of scales. These bottom-up and top-down approaches are undoubtedly complementary, and together they can contribute to answering a two more questions, namely “(3) how will vegetation phenology respond to future climate change, in ecosystems around the world, and (4) what does this mean for how those ecosystems function?” In my mind, these questions have been driving the field of phenology for more than a dozen years and will continue to do so—until we have a predictive understanding of how ecosystems will respond to multiple nonlinear drivers, and how these drivers interact with each other and with climate change.

I was asked by the editors of *Agricultural and Forest Meteorology* (hereafter, AFM) to contribute a review paper to the 60th Anniversary special issue, highlighting recent “work on phenology and the lessons learned from the PhenoCam Network,” and including a “personal perspective on what has been accomplished and where the field is heading.” This is not a comprehensive review of the state of phenological research (instead, see Piao et al., 2019). Rather, it is selective, focused on papers that have appeared in AFM, and indeed I have tried to reference every AFM paper, through the summer of 2023, that has meaningfully referenced, in some way or other, phenocam data or imagery. Keeping in mind the “personal perspectives” directive, I have also endeavored to provide the “back story” behind the development of the

PhenoCam network, and some of the key papers in the phenocam literature—where the ideas originated, how they evolved, and who was involved (Baldocchi’s 2013 “history of eddy covariance” essay served as a model). I use text boxes to distinguish descriptive (Box 1: What is a phenocam?) or anecdotal (Box 2: The origins of the PhenoCam Network; Box 3. PhenoCam vs phenocam?) material from the main body of the manuscript. Some additional, more autobiographical, text (e.g. Supplementary Material, Box S1: My introduction to phenology), is contained in an online supplement.

This paper is organized around the following questions:

- 1) How has the focus of phenology-related papers published in AFM evolved over 60 years?;
- 2) How have papers published in AFM contributed to the development and evolution of phenocam science and phenology more generally?; and
- 3) Why has the PhenoCam Network been successful, and what lessons have we learned that might be of value to future collaborative, grassroots efforts in other fields?

2. The evolution of phenology research in Agricultural and Forest Meteorology

Phenology is an ideal area of study to be addressed by an inherently cross-disciplinary journal such as AFM. But, while “phenology” has for some time been listed in the journal’s “aims and scope”, as recently as 2007 the journal was publishing 10 or fewer papers per year on phenology, and from 1991 to 2000, the journal published, on average, less than 2 papers per year on phenology! With that caveat, I note that over the last 25 y as a whole, the number of AFM papers with “phenology” in the title, keywords, or abstract has surged, increasing at about 13%

per year (Figure 2), compared with 8% per year across all journals indexed in the *Web of Science*.

Over six decades, the emphasis of phenological papers appearing in the pages of AFM (and its predecessor, *Agricultural Meteorology*, which began publication in 1964), has shifted. From the 1960s through the 1970s, relatively few papers on phenology were published, and agricultural applications (Bridge, 1976; Carder and Hennig, 1966; da Mota, 1978; Jones and Laing, 1978; Neild, 1982; Neild et al., 1978; Williams et al., 1980) tended to dominate; even papers on the phenology of fungal parasites were presented in the context of agricultural management (De Weille, 1965). I found only two papers from this period that addressed the phenology of forest trees and their impact on the forest microenvironment (Hutchison and Matt, 1977, 1976). But, in an ahead-of-its-time paper, White (1979) tested a variety of temperature-accumulation models to characterize the timing of flowering by 53 different plant species—though the results were still framed in a management context. Related papers published in the early 1980s (Doraiswamy and Thompson, 1982; Kobayashi and Fuchigami, 1983; Lomas and Burd, 1983; Neild, 1982; Neild et al., 1983) point to the emergence of more quantitative and sophisticated approaches to phenological modeling. It is probably not a coincidence that this was around the same time that personal computers started to appear in research labs and academic offices, facilitating data analysis and modeling.

Phenological research has continued to evolve in recent decades (Table 1). Notably, by the 1990s, about 20% of phenology papers in AFM referred to climate change; over the last decade, that number has been about 75%. In AFM papers published 2013-2022, other themes commonly associated with phenology include modeling (65% of papers), trees or forests (60%), agriculture (35%), carbon and water fluxes (20%), and remote sensing (20%). Whereas much of

the early phenology work in AFM was conducted in North America, research from Europe, China, Japan, and Australia is now prominently featured. AFM now routinely publishes more than 50 phenology papers a year, and it is one of the preeminent journals in which early-career authors, in particular, aspire to publish their phenological research. In recent years, phenological research in AFM has shown quite clearly that this field is much more than an obscure subfield of natural history—instead, these papers represent some of the most vibrant and novel research published in the pages of this journal.

3. The evolution of phenocam science, as viewed through the AFM lens

Over the last dozen years, a small (7%) but increasing fraction of phenology papers in AFM have made use of “phenocam” technology—time-lapse digital cameras used to track the seasonality of vegetation activity and changes in vegetation structure (e.g., Box 1 and Figure 1; see also Richardson, 2019). In fact, as much of the phenocam literature has been published in AFM as in any other journal (Figure 3). The phenocam method, developed about 15 y ago (Richardson et al., 2007), has emerged as a direct link between on-the-ground phenological monitoring of individual organisms by an observer, and coarser-resolution satellite observations at the global scale. The quantitative data extracted from phenocam imagery are high-quality (or at least they can be—if appropriate precautions are taken with regard to camera make and model, camera settings, and set-up in the field), with minimal noise and a strong seasonal signal in most ecosystems (Richardson et al., 2018a; Seyednasrollah et al., 2019), even those with evergreen vegetation (Seyednasrollah et al., 2020). Thus, phenocams can provide objective, automated, phenological data at high temporal and spatial resolution—in many cases, in real-time. And, an advantage of phenocams over radiometric approaches (broad- or narrow-band radiometric

indices, including f_{APAR} [fraction of absorbed photosynthetically active radiation], NDVI [normalized difference vegetation index], PRI [photochemical reflectance index], etc.; Richardson et al., 2013) is that the phenocam images are a permanent visual record of what the camera was looking at, at a specific place and time. In this way, the long-term value of installing a phenocam at a research site can transcend phenology itself—over time, the accumulated imagery provides a unique history of the site, with a record of development and change over time: e.g., establishment, growth, and mortality; disturbance and recovery; responses to extreme events; changes in species composition; and, in cold sites, the timing and duration of snowpack.

I maintain a list of papers published independently by other researchers using data from the PhenoCam Network; as of July 2023, there were over 115 journal publications and 9 theses on that list, with over 30 publications in 2022 alone. But many other researchers have also set up phenocams at their own sites, and do not contribute the imagery to the PhenoCam Network (I distinguish PhenoCam from phenocam in Box 3)—so the “phenocam” literature is much broader than that of just “PhenoCam”. Based on a Web of Science search for “phenocam” in the title, abstract, or keywords, the number of phenocam-related publications each year is growing by about 30% annually since 2011 (Figure 2).

One of the objectives of this review is to examine how papers published in AFM have contributed to the development and evolution of phenocam science. I conducted a search from the journal’s home page to identify all AFM articles that included the word “phenocam”*. I quickly examined these to distinguish between the 50 articles that made use of phenocam imagery or data as part of the analysis and the 20 articles that only mentioned phenocam in passing in the Introduction or Discussion, or that cited a paper with phenocam in the title.

* <https://www.sciencedirect.com/search?cid=271723&pub=Agricultural%20and%20Forest%20Meteorology&q=phenocam>

Phenocam publications in AFM over the last decade can be loosely grouped into five categories, addressing: (1) methodological issues, including hardware and software advances; (2) interpretation of carbon and water fluxes measured by eddy covariance; (3) assessment of satellite remote sensing products; (4) development, calibration, or evaluation of phenological models; and (5) applications in other fields of environmental science beyond phenology *per se*. Below, I organize my review of the recent literature in AFM according to these categories.

3.1 Methodological issues

We started using the StarDot NetCam SC as the “preferred” camera for the PhenoCam Network in early 2008 (Figure 5). As noted in Box 1, this choice was more the result of good luck rather than exhaustively testing competing models to identify the best choice of camera. In the summer of 2010, Oliver Sonnentag and Koen Hufkens started work on a project at Harvard Forest to determine whether camera choice mattered. Sonnentag et al. (2012) compared about a dozen readily-available cameras, most with internet connectivity (i.e., IOT [internet of things] devices by StarDot, Axis, D-Link, and Vivotek) and some that were stand-alone models, including both consumer-grade point-and-shoot digital cameras and what have come to be known as “trail-cams.” Except for inexpensive webcams designed for indoor use, the other cameras were all found to yield similar patterns of autumn senescence, leading to the conclusion that “camera and image file format choice might be of secondary importance for phenological research.”

Sonnentag et al. (2012) made several other important contributions, mostly regarding questions about post-processing of the extracted data. For example, they showed that the green chromatic coordinate (Gcc) was generally better than the excess green (ExG) index at

suppressing hour-to-hour or day-to-day variation due to changes in lighting conditions, weather, clouds and aerosols, and illumination geometry. Secondly, based on work by coauthor Adam Young, Sonnentag et al. proposed alternative statistics for combining Gcc values from multiple images recorded over the course of a day to a daily value with the lowest day-to-day variability. Notably, the best statistic was often *not* the daily mean, median, or midday value of Gcc, but rather the 90th percentile value—“Gcc90”, and this approach has become widely adopted.

Although Sonnentag et al. (2012) resolved a number of key methodological issues, tools for region of interest (ROI) delineation, image processing, and phenological transition date extraction had not been standardized and remained cumbersome. A few years later Gianluca Filippa, Edoardo Cremonese, and Mirco Migliavacca led a team that developed the “Phenopix” R package, which was described in AFM by Filippa et al. (2016a). The Phenopix code, distributed through CRAN, simplified and made consistent all the data processing steps, while at the same time allowing flexibility for the user to choose their preferred curve-fitting and date extraction methods. A novel addition to this package was the introduction of a pixel-by-pixel analysis, which enabled characterization of the variability across the canopy or the crown of an individual tree.

In a 2014 paper developed from her undergraduate thesis at Harvard College, Anika Petach showed how the infrared sensitivity of the StarDot camera (Figures 5c, d) could be used to generate an NDVI-like index we called “camera NDVI” (Petach et al., 2014). Filippa et al. (2018) conducted a broader test of this idea using data from PhenoCam sites across a range of plant functional types (PFTs), in conjunction with *in situ* measurements of NDVI, and MODIS NDVI. Their analysis demonstrated that systematic differences in the seasonality of Gcc and camera NDVI tended to be PFT-specific—thus the two indices could be seen as complementary,

rather than redundant. Given the large number of in PhenoCams in deciduous broadleaf forests, a highly relevant take-home message was that “[Gcc] is more sensitive to changes in leaf color and [camera NDVI] is more sensitive to changes in leaf area.” The analysis by Filippa et al. (2018) nicely built on previous work by Keenan et al. (2014) showing that, for deciduous broadleaf forests, seasonal variation in Gcc could be predicted from the Gcc signature of the bare canopy, the changing Gcc signature of individual leaves, and the changing leaf area index, using a simple mixing model.

However, Brown et al. (2020) noted “previous work has demonstrated several features in time-series of [Gcc] are unrelated to canopy structure, limiting [its] utility to track specific biophysical properties such as leaf area index.” This motivated their study, which compared LAI estimated from below-canopy hemispherical photos with Gcc from an above-canopy phenocam (see also Toda and Richardson, 2018). Brown et al. (2020) observed seasonal hysteresis in the LAI-Gcc relationship, which resulted in differences between the two indices in the derived seasonal transition dates, and the conclusion that “phenological transition dates derived from [Gcc] cannot easily be linked to any one biophysical property.” To further investigate the interpretation of phenocam-derived transition dates, Nezval et al. (2020) compared ground observations of three deciduous tree species with transition dates extracted, using the Phenopix package, from the seasonal trajectory of Gcc. Surprisingly, and in contrast to some previous studies (e.g., Richardson et al., 2018), there were substantial and unresolved inconsistencies between the ground observations and the Gcc-derived dates, with observed budburst occurring 15 days before estimated green-up in one species, but 7 or more days *after* estimated green-up in two other species. The authors concluded that “classical ground-based observations by a phenologist are still crucial”. By comparison, ground observations of red oak budburst, leaf

coloration, and leaf fall at Harvard Forest *do* show a high correlation with Gcc-derived transition dates in both spring and autumn (Dunn et al., 2022), pointing to the relevance of phenocam-derived transition dates as indicators of biologically-relevant phenological transitions.

Alternative photographic methods for characterizing plant phenology have also been described in AFM in recent years. For example, Chianucci et al. (2021) demonstrated the potential for using inexpensive camera traps (“game cams”), mounted at ground level and looking upward through the canopy, to estimate fractional cover and leaf area index. Smith and Ramsay (2018) found that smartphones with hemispherical lens attachments could be used to reliably estimate the timing of canopy closure. And Koen Hufkens used repeat smartphone photography to track crop phenology and disturbance in India (Hufkens et al., 2019). Hufkens and coauthors argued this method could be used to “[support] crop modeling, extension, and insurance schemes to increase resilience to production risk and enhance food security in smallholder agricultural systems,” showing how phenocam-type approaches could help advance the welfare of human society.

An outstanding methodological challenge, yet to be addressed in the literature, is how to fully automate the processing of phenocam imagery. There is certainly an opportunity to leverage computer vision, deep learning, and image segmentation methods already used in other fields including medical imaging and diagnostics (Esteva et al., 2021; Hesamian et al., 2019). Automatic ROI detection, e.g., through segmentation, would also solve the ever-present problem of field-of-view shifts, and (to a lesser degree) low-quality imagery that is recorded under foggy or too-dark conditions, in that if there were images where relevant PFTs could not be identified, the image in question could simply be ignored. The application of deep learning methods to the PhenoCam Network image archive has been slow to develop, but there is huge potential here for

remarkable advances in how phenocam imagery is processed and the datasets curated. A large, annotated, training dataset derived from phenocam imagery could be invaluable for future deep-learning applications.

3.2 Interpretation of carbon and water fluxes

Because of the key role that phenology plays in regulating the seasonality of ecosystem-atmosphere carbon dioxide and water vapor fluxes, and the partitioning of the surface energy budget, many studies have used phenocam data and tower-measured fluxes from co-located sensors to link leaf phenology and canopy dynamics to the phenology of physiological processes such as photosynthesis and transpiration (D’Odorico et al., 2015)—sometimes referred to as “physiological phenology.” Phenocam data have also been used to estimate growing season length as a basic site attribute (Pappas et al., 2020; see also Reed et al., 2018 in the context of seasonal variation in energy balance closure). I am impressed by the breadth and creativity of studies that have integrated phenocam data and tower fluxes; this section is grouped around the following themes: (1) carbon dioxide fluxes and ecosystem productivity; (2) evapotranspiration and water fluxes; (3) land-atmosphere interactions; (4) management applications; and (5) extreme events and disturbance.

3.2.1 Carbon dioxide fluxes and ecosystem productivity

In a classic example of efforts to link phenology to forest productivity on interannual time scales, Oishi et al. (2018) used spring and fall transition dates derived from Gcc to provide context for deciduous forest carbon and water fluxes measured by eddy covariance. Intriguingly, growing season length was unrelated to interannual variation in annual NEE. And, although

warm temperatures tended to advance spring onset and increase seasonal carbon dioxide uptake, warm temperatures also tended to increase ecosystem respiration. Indeed, contrary to many studies concluding that future warming will potentially increase forest productivity through the extension of the growing season, Oishi and coauthors concluded that the “increasing frequency of high summer temperatures is expected to have a greater effect on respiration than growing season length, reducing forest carbon storage.”

Phenocam-supported studies of physiological phenology have not been limited to deciduous broadleaf forests; other examples include evergreen forests, grasslands, agricultural lands, and even wetlands. Bowling et al. (2018) investigated the controls on the seasonal variation in photosynthetic capacity of the high-elevation evergreen conifer forest at Niwot Ridge, Colorado—home to a PhenoCam since 2009. They reported that both G_{cc} ($r^2 = 0.92$) and the Green-Red Vegetation Index (GRVI, $r^2 = 0.76$) were strongly correlated with the light-saturated rate of canopy photosynthesis derived from eddy covariance measurements. Notably, there was evidence of modest phase differences between both indices and the seasonal course of photosynthesis, hinting at the physiological complexity of seasonal up- and down-regulation of photosynthesis, and the mechanics of photoprotection.

Although their analysis maintained a focus on the Australian mountain grassland site, Ninmo, Marchin et al. (2018) used PhenoCam data from sites around the world to synthesize patterns of growing season length in relation to elevation. Despite the modest annual carbon sink at Ninmo, the growing season was shown to be substantially longer than Northern Hemisphere sites at a similar elevation. But, the annual GPP (gross primary productivity, $\text{g C m}^{-2} \text{ y}^{-1}$) at Ninmo was unrelated to growing season length. Warm, dry conditions were found to advance grass senescence and limit productivity at the end of the growing season; Marchin et al. proposed

this was driven by a “VPD tipping point.” The unique combination of framing site-level results in the context of a global synthesis makes this a compelling paper.

Grazing lands cover much of the United States and more than half of the Earth’s land surface. They are important for agricultural production and for their carbon sequestration potential, among other ecosystem services. Fire plays a critical role in maintaining these systems. In a novel study of a native rangeland ecosystem in Florida, Bracho et al. (2021) observed good coherence between GPP estimated from eddy covariance measurements and PhenoCam Gcc. Gcc also provided a sensitive and high-resolution characterization of recovery dynamics following prescribed fire. Using conditional tree regression analysis to explore links between ecosystem function and biological/environmental drivers, Bracho et al. demonstrated that Gcc informed simulations of the seasonal dynamics of carbon dioxide fluxes. This kind of data-driven modeling is a promising alternative to the classic “process-oriented” approaches described below (Sec. 3.4), and I expect that applying machine learning algorithms to phenocam, flux, and meteorological datasets will be an exciting area of growth in the coming years.

A surprising number of studies linking PhenoCam data and co-located tower fluxes have focused on wetlands. For example, Dronova et al. (2021) found that Gcc seasonal trajectories were different across three restored wetland sites in California; the lower maximum Gcc at one site corresponded to earlier senescence and lower maximum carbon uptake and was proposed to be the result of plant stress from salinity. And, several important studies have emerged from the St. Jones Estuarine Research Reserve, a temperate tidal salt marsh, in Delaware. In one paper, Hill et al. (2021) examined the degree to which a wide range of spectral indices, derived from both phenocam imagery (7 indices), *in situ* spectral reflectance sensors (5 indices), and MODIS (5 indices) tracked NEE of carbon dioxide, measured by eddy covariance. Visible-wavelength

indices (e.g., Gcc) from phenocam yielded start- and end-of-season transition dates that best aligned with those calculated from NEE, while of all indices considered, Gcc had the highest linear correlation with daily NEE integrals ($r^2 = 0.93$). In another paper by Vazquez-Lule et al. (2021), phenocam and flux data were used together, in what the authors refer to as a “plant-phenological phase approach,” to investigate the relationships between salt marsh phenology and ecosystem-scale fluxes. Fluxes of both carbon dioxide and methane showed strong seasonality, with near-zero fluxes of both gases during the winter months, but net uptake of carbon dioxide and net release of methane during the summer months. However, the coupling of fluxes to plant phenology was weaker for methane than it was for carbon dioxide. While this result may not be entirely surprising, it is notable that this Vazquez-Lule and coauthors thought “beyond the [carbon dioxide] box”.

Gcc is, of course, not the only index that can be calculated from phenocam imagery (Richardson et al., 2013b). For example, in temperate deciduous forests with strong autumn coloration, the red chromatic coordinate (Rcc) is a reliable indicator of the timing and intensity of peak color (Richardson, 2019). But Rcc may have other applications as well. Using carbon dioxide fluxes and phenocam data from deciduous and evergreen forest sites, Liu et al. (2020) reported that local maxima and minima in Rcc could be used to identify the onset and cessation of photosynthetic uptake in spring and fall. Surprisingly, they found that while the seasonal dynamics of Rcc did not track those of canopy photosynthesis, transition dates derived from Rcc were a much better indicator of photosynthetic phenology than transition dates derived from Gcc. This was particularly true for evergreen forests. In contrast, a later study by Seyednasrollah et al. (2020) reported that, for evergreen sites that went through a winter-dormant stage, Gcc (and also GRVI, the Green-Red Vegetation Index) *was* a good indicator of photosynthetic phenology,

when the transition dates were calculated after phenocam images with snow on the canopy had been filtered out. For accomplishing the latter task, Jason Jewik developed a Python package that uses a trained deep learning algorithm to classify phenocam images (<https://github.com/jasonjewik/PhenoCamSnow>), showing the potential for new methods and algorithms to contribute to improving image processing workflows.

3.2.2 Evapotranspiration and water fluxes

A few papers have used PhenoCam imagery to investigate relationships between phenology and evapotranspiration, using either tower-measured latent heat flux (LE) or sapflow. For example, Luo et al. (2022) analyzed relationships between Gcc and canopy conductance in a Mediterranean evergreen broadleaf savanna. Seasonal variation in Gcc at the canopy level was driven by leaf flushing, maturation, and senescence, and newly-flushed leaves had spectral signatures that were distinct from those of mature and old leaves. Both canopy conductance and sap flux density were shown to be well-explained by a generalized additive model that included environmental factors as well as Gcc and cameraNDVI.

Nehemy et al. (2023) developed a method, based on high-frequency measurements of stem radius with automated dendrometers and the correlation of stem radius changes with sapwood temperature, to identify four key transitions that were shown to be closely associated with the phenology of transpiration. Intriguingly, across several evergreen boreal forest sites, the transition associated with the end of stem freeze-thaw cycles coincided with spring green-up transition dates derived from Gcc, as well as the onset of net carbon dioxide uptake, as estimated from eddy covariance measurements. This study nicely shows the potential for phenology to serve as an “integrative science” that cuts across fields and disciplines (Schwartz, 2013).

3.2.3 Land-atmosphere interactions

This section has mostly focused on how phenocam imagery has contributed to the interpretation of physiological phenology and/or seasonal-to-interannual variability in ecosystem-atmosphere carbon dioxide and water vapor fluxes. A recent paper by Adam Young and collaborators (Young et al., 2021) addresses the role of phenology as a regulator of aerodynamic resistance to heat transfer (R_{ah}) and implications for sensible heat flux (H). This synthesis leveraged 190 site-years of data from across more than 20 AmeriFlux sites with PhenoCams to show that seasonal changes in surface roughness are a key determinant of variation in aerodynamic resistance to heat transfer. Specifically, in deciduous broadleaf forests, grasslands, croplands, and shrublands, phenological green-up alters the surface roughness, which in turn has a large influence over seasonal patterns in sensible heat flux. This analysis offers new insight into the role of phenology in controlling feedbacks of the land surface to the atmosphere and climate system through partitioning of the surface energy budget, i.e., to sensible and latent heat flux.

In a similarly-themed study, Ziegler et al. (2023) examined how phenological transitions in a desert shrubland drove changes in the shear stress ratio: before green-up, wind-shear (friction) velocities at the soil surface were 20% of those above the canopy, whereas after green-up, wind-shear velocities at the soil surface were only 5% of those above the canopy. Phenological changes also drove seasonal variability in the aerodynamic roughness length, resulting from increased drag and surface sheltering. The study links these findings to rangeland management applications, specifically efforts to restore grazing lands and to reduce aeolian sediment transport.

3.2.4 Management applications

A number of papers described above, including those by Bracho et al. (2021), Hufkens et al. (2019), and Ziegler et al. (2023) have discussed potential management applications of phenocam-type data and imagery. With a more explicit emphasis on the management of an agricultural pasture, Zhou et al. (2017) used phenocam imagery to document the timing and impact of pasture management activities. They interpreted changes in Gcc in the context of those activities (burning, harvesting and baling, grazing) and the progression of phenological stages (green-up, summer flowering, fall flowering, senescence), and in relation to tower-measured carbon dioxide fluxes recorded at the site. Notably, the fine spatial and temporal resolution of the phenocam imagery offered insights that could not be obtained from satellite remote sensing—leading the authors to conclude that understanding the interactive effects of management practices and climatic conditions could be greatly advanced through the integration of phenocam and tower flux measurements. The large number of phenocams now deployed at sites in the USDA Agricultural Research Service’s LTAR (Long-Term Agroecosystem Research) Network (Browning et al., 2021) points to an opportunity for future cross-site analyses to quantitatively address the impact of management practices on land-atmosphere carbon dioxide fluxes.

3.2.5 Extreme events and disturbance

With climate change, warming temperatures and altered precipitation regimes, extreme weather events, particularly droughts and heat waves, are becoming increasingly frequent. Several studies have shown how phenocam data can contribute to monitoring the ecosystem impacts of extreme climate events and disturbance. For example, Cremonese et al. (2017)

investigated how the summer 2015 European heat wave affected the phenology and function of a mountain grassland in the Western Alps. Long-term data from the site indicated that in response to the heat wave, there was a 39% reduction in maximum Gcc, and senescence was advanced by a month, compared to previous years. There were parallel reductions in the light-saturated rate of photosynthetic uptake, estimated from concurrent eddy covariance carbon dioxide flux measurements. From the high-resolution PhenoCam data, it was also possible to see that forbs were more severely impacted by the heatwave than grasses. This paper highlights the potential for phenocam imagery to provide insights that may be undetectable with satellite remote sensing.

Phenocam imagery can also provide quantitative data on disturbance and recovery dynamics, particularly in remote locations where site visits may be intermittent even during the growing season. Established in 1996, the BERMS (Boreal Ecosystem Research and Monitoring Sites) Old Aspen tower in Saskatchewan, Canada, was one of the first long-term eddy covariance sites in the world. In 2016, a forest tent caterpillar infestation erupted during the leafing-out period, leading to virtually complete canopy defoliation. As demonstrated in the paper by Stephens et al. (2018), PhenoCam imagery, Gcc, and radiometric measurements enabled quantification of the timing and magnitude of this disturbance, and the subsequent forest recovery: remarkably, a second flush of foliage was produced and Gcc returned to near-normal summer values within 3 weeks. The defoliation reduced annual GPP to $800 \text{ g C m}^{-2} \text{ y}^{-1}$, compared with a 20-year mean of $1060 \pm 75 \text{ g C m}^{-2} \text{ y}^{-1}$. Additionally, the site was a substantial source of carbon dioxide to the atmosphere (annual NEE = $+130 \text{ g C m}^{-2} \text{ y}^{-1}$), compared with the 20 y mean annual NEE of $-120 \pm 55 \text{ g C m}^{-2} \text{ y}^{-1}$. Intriguingly, the tent caterpillar infestation had little effect on annual evapotranspiration. By quantifying the impact of canopy defoliation on site-level C balance, this paper gives a preview of the possible C-cycle consequences of

increases in the frequency of insect outbreaks in response to climate change. These impacts could be enormous, as a $1 \text{ g C m}^{-2} \text{ y}^{-1}$ flux from Canada's boreal forest equates to a total change in the boreal forest C balance of 2.7 Tg C y^{-1} .

In a similar vein, Matiu et al. (2017) integrated phenocam data and ecosystem carbon dioxide fluxes to investigate successional dynamics over six years following windthrow disturbance to a spruce forest in Germany. A clustering algorithm was used to separate the camera imagery into spruce, grass, and a grass-to-spruce transition zone, which began as grass but was overgrown by spruce at the end of the study. The increasing Gcc over time of the grass-to-spruce transition zone paralleled increasing trends in GPP, as estimated from the eddy covariance measurements. The authors' conclusion that digital imagery provides "a versatile tool that helps to understand successional and phenological processes after a disturbance" is further supported by the recent analysis by Spafford et al. (2023) of more than a dozen examples of disturbance events that have been observed by the PhenoCam Network. A notable feature of phenocam imagery is that it is possible to conduct retrospective "what happened?" analyses, even if other concurrent field surveys were not carried out, precisely because the images can be interpreted through visual inspection.

3.3 Assessment of satellite remote sensing products

Without a doubt, one of the areas in which the PhenoCam Network has made the greatest contribution to environmental and ecological science is the assessment of satellite remote sensing products from different platforms (Table 2). It is commonly recognized that the inherent differences between Gcc and NDVI, as well as the oblique view of PhenoCams and the nadir view of satellites, preclude true "validation," but the overall quality of the PhenoCam data has

479 proven to be invaluable for comparing spatial and interannual patterns and placing an upper
480 bound on the uncertainty in satellite products (Zhang et al., 2018). Furthermore, visual
481 interpretation of the PhenoCam imagery itself can provide environmental (e.g., presence/absence
482 of snow) and biological context for interpreting the seasonal changes that are manifest at the
483 pixel level. The AFM papers summarized below demonstrate that phenocam data—quantitative,
484 continuous, consistent, and spatially extensive—are extremely useful for these applications, and
485 an improvement over the hodgepodge of diverse data sets that have been used previously for
486 similar purposes (e.g., White et al., 2009).

487 Zhang et al. (2018) compared transition dates from more than 80 PhenoCam Network
488 sites against land surface phenology metrics derived from 500 m VIIRS imagery. Notably,
489 transition dates were “generally comparable for the vegetation greenup phase, but differed
490 considerably for the senescence phase.” Zhang et al. reported that agreement was weakest in
491 savanna sites where spatial heterogeneity is a persistent challenge. Agreement was good in
492 forested sites, and this can likely be at least partially attributed to the supposed greater
493 homogeneity of closed-canopy forests. However, sub-pixel heterogeneity of mixed-species
494 deciduous forests can still be substantial, as demonstrated by Klosterman et al. (2018), who
495 combined PhenoCam, Landsat and MODIS, and UAV (unmanned aerial vehicle) imagery to
496 investigate the scale-dependence of phenological patterns across scales from ≈ 10 m to ≈ 1 km.

497 Instead of evaluating transition dates, Brown et al. (2017) compared the overall seasonal
498 trajectory of PhenoCam Gcc with products derived from the MERIS (MEdium Resolution
499 Imaging Spectrometer; 300 m resolution) sensor on Envisat-1 (e.g., MGCI, MERIS Global
500 Vegetation Index; MTCI, MERIS Terrestrial Chlorophyll Index). Results from this analysis,
501 including poor agreement between phenocam data and MERIS at evergreen sites, suggested that

atmospheric, shadowing, and BRDF (bidirectional reflectance distribution function) effects led to “substantial variability within the growing season [in the indices derived from MERIS] that is unrelated to vegetation dynamics”—pointing to the need for “more rigorous atmospheric and BRDF correction schemes” for the satellite data. The authors speculated about the prospect of using near-surface observations, including phenocam imagery, to develop improved cloud screening algorithms; another obvious application of phenocam data is to test and improve satellite snow cover products, e.g., MODIS products MOD10A1 and MYD10A1 (Kosmala et al., 2018).

In addition to evaluating standard and established phenology products from different satellite platforms, PhenoCam data have been used to evaluate new indices that can be derived from existing satellite data. For example, Xie et al. (2022) introduced a hybrid “Background Free Phenology Index” (BFPI), which was calculated by integrating a remotely-sensed vegetation index with an environmentally-driven growing season index (GSI; after Jolly et al., 2005) model. In both spring and fall, derived transition dates from PhenoCam Gcc were in better agreement with transition dates from BFPI than they were with transition dates derived from classic vegetation indices such as NDVI or EVI.

The digital numbers (DN) that comprise a phenocam image are the product of viewing and illumination geometry, surface reflectance, and image exposure time; as such, DNs are not equivalent to reflectance values. Burke and Rundquist (2021) developed a method to standardize phenocam indices across sites, facilitating cross-site analyses, using a Gaussian Process machine-learning model and HLS (Harmonized Landsat-Sentinel) data. The approach scales the phenocam indices so they are aligned with HLS imagery, enabling improved comparison of the

seasonal trajectory and magnitude of vegetation indices derived from phenocam imagery. In the future, this approach could further increase the rigor of satellite data product evaluation efforts.

Zhang et al. (2018) noted the challenge of remote detection of savanna phenology, because of the heterogeneous mixture of trees/shrubs and grass. Where there are multiple plant functional types within a PhenoCam image, it is typical to delineate separate ROIs for each. Using cameraNDVI, Liu et al. (2017) demonstrated that in an oak/grass Mediterranean savanna, the phenology of the deciduous oak was distinctly different from the mixed grasses, with the oak having a much longer active season. Liu et al. then used fine-resolution aerial imaging to determine the fractional cover of oak and grass, at the landscape scale, across a grid representing satellite imagery at different resolutions, from Landsat at 30 m and MODIS/VIIRS at 500 m. Liu et al. applied a simple mixing model to upscale the PhenoCam time series of oak and grass endmembers, as a function of fractional cover, to this grid. In homogenous grassland, phenological transition dates were shown to be consistent regardless of spatial resolution, whereas in heterogeneous savanna this was not the case. This paper is important because of the framework it establishes for investigating and resolving the fine-scale heterogeneity that can be obscured in moderate-resolution satellite imagery.

3.4 Phenological modeling

In a 2013 review paper in AFM (Richardson et al., 2013a), I suggested a multi-tiered strategy for testing and evaluating phenology models, using ground observations, phenocam data, and satellite remote sensing at each of the different stages of model-data fusion (see Figure 1 in Williams et al., 2009). This approach has not been widely adopted, however, and phenological modeling papers in AFM that used phenocam data have taken a diverse range of

alternative approaches, ranging from efforts that leverage the rich seasonal trajectory that is provided by continuous Gcc data, to those that focus on modeling specific phenological transition dates.

Mirco Migliavacca and coauthors (2011) used phenocam data from an alpine grassland to estimate, using a variety of formulations of the GSI model by Jolly et al. (2005), the degree to which different environmental factors (snow, daylength, air temperature, and soil water content) were limiting to plant growth, and how these limiting factors changed over the course of the year. This paper also demonstrated that a light-use efficiency (LUE) model that incorporated a phenocam-derived canopy greenness metric could simulate the seasonal variation in GPP, estimated from eddy covariance measurements, with good fidelity—providing a convenient and elegant means for scaling up fluxes in time and space.

Members of the Berkeley Biomet Lab have been long-term PhenoCam collaborators, and have repeatedly come up with creative ways to use digital camera data in conjunction with tower-measured fluxes to improve process understanding. For example, the “Cow Cam Index” described by Baldocchi et al. (2012) used object-oriented image analysis to identify methane-producing bovines in the camera field of view. A similar technique was later used in work by Laubach et al. (2023). Recent Berkeley work has focused on wetland greenhouse gas fluxes. For example, Sarah Knox used a light-use-efficiency model, parameterized using tower-measured carbon dioxide fluxes and PhenoCam Gcc, to estimate the productivity of temperate freshwater marshes (Knox et al., 2017). An important finding was that model performance degraded as site complexity increased, suggesting the need to explicitly incorporate metrics related to spatial heterogeneity in the model. In this way, the study expands on the previous LUE modeling work by Migliavacca et al. (2011).

Wang et al. (2020) used the Excess Green (ExG) vegetation index, derived from phenocam imagery, in conjunction with satellite-derived EVI (enhanced vegetation index) to estimate daily fAPAR, which was then used again in a LUE model with temperature and water availability scalars to estimate daily GPP for semi-arid grassland in central Northeast China. While the parameterized model worked quite well, Wang et al. noted that improvements to LUE modeling could take advantage of either a two-layer (sun-lit and shaded leaves) representation of the canopy or information on direct-beam and diffuse solar radiation.

Grassland responses to soil moisture availability are commonly modeled as a linear function, but Yang et al. (2023) introduced a simple, one-parameter, non-linear function that would allow the response to soil moisture to be concave down, linear, or concave up. This parameterization was implemented in the grassland model initially developed by Choler et al. (2010) and later revised and calibrated using PhenoCam data by Hufkens et al. (2016). Yang and collaborators used phenocam imagery from several grassland experiments near Sydney, Australia, to constrain model parameters; allowing for nonlinear responses to soil moisture reduced model errors by 7%.

Migliavacca et al. (2011) highlighted the enormous value of continuous phenological monitoring, as provided through vegetation indices such as Gcc, compared with traditional ground-based observational approaches, which focus on specific phenological events. They suggested that continuous monitoring would be particularly valuable in ecosystems with high intra-annual variability in phenological dynamics. The follow-on work by Knox et al. (2017), Wang et al. (2020), and Yang et al. (2023) provides strong confirmation of this assertion. However, for some applications, a model that predicts the start or end of the active season may

be more useful. Two AFM papers, by Meng et al. (2021) and Post et al. (2022), have tackled this kind of event-based modeling.

Lin Meng and Jiafu Mao recognized that phenocam data could be used to improve phenology schemes in a global earth system model, where onset and offset triggers are needed. In Meng et al. (2021) they used data from the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment in northern Minnesota to parameterize the seasonal-deciduous phenology scheme in the land model of the US Department of Energy's (DOE) Energy Exascale Earth System Model (ELM of E3SM). At SPRUCE, 10 open-topped enclosures are used to apply warming treatments up to +9°C above ambient, as well as elevated carbon dioxide to half of the plots. Phenocams installed in each SPRUCE enclosure have been monitoring the experiment since 2015. The combination of experimental warming superimposed on natural variation in weather occurring over the first three years of the experiment provided strong constraints on phenology model parameters. Notably, changes to the ELM phenology scheme had cascading effects on carbon and water fluxes—as noted by Meng et al., “highlight[ing] the importance of phenological processes in affecting complex terrestrial-climate interactions.”

Alison Post used the extensive repository of PhenoCam data for grasslands (43 sites, 195 site-years), across a range of climate zones to test 53 phenological models to predict spring onset (Post et al., 2022). New model structures were presented, which included either precipitation or soil moisture, in conjunction with classic degree-day approaches. The best model, which required sufficient accumulated precipitation to be followed by warm temperatures for spring onset to be triggered, performed quite well, with a single set of parameters, across sites from temperate to arid grasslands. But, model predictions were also substantially improved when parameters were optimized for different climate zones. Post’s careful consideration of tradeoffs

between generalizability vs. performance shows how the “best” model may depend on the specific application. Forward model runs, using IPCC climate projections, found that in colder, temperature-limited grasslands, spring onset is likely to advance in response to climate change. In precipitation-limited sites, spring onset is highly variable but does not show a clear trend in either direction when results from multiple regional and global climate models are considered together. This paper nicely builds on past work modeling deciduous tree phenology (Chuine et al., 1998; Melaas et al., 2016a), and leverages the open-source PhenoR modeling package (Hufkens et al., 2017), to bring the state-of-the-art in grassland modeling up to a level approaching that of deciduous forests.

There are still many avenues open to new and exciting advances in phenological modeling. Migliavacca et al. (2012) noted the important distinction between different sources of phenological modeling uncertainty—model structure, model parameterization, and model drivers. Testing different model structures and parameterizing these structures using ground observations remains an important area of research; this kind of work has its roots in some of the phenology modeling papers published in AFM in the early 1980s. At a very basic level, we still do not have good models to predict phenological transition dates for numerous plant functional types, or different ecosystem types. These models remain urgently needed (to be calibrated, validated, and adopted) for incorporation into earth system models so that these models can accurately represent vegetation seasonality and feedbacks of vegetation to the climate system (Richardson et al., 2012). A challenge remains that many ecosystem types remain poorly represented in databases of phenological observations—for large swaths of the Earth’s surface, “more data are needed” remains a valid assessment of the state of availability of phenological data for model calibration and validation.

The “process-oriented” phenological models described here are based on a highly prescribed relationship between drivers and responses—this means that they inherently encapsulate some prior knowledge or understanding of these relationships. At the same time, this also means they are limited in their flexibility. I am curious to see how machine-learning techniques will change the field of phenological modeling, and how these techniques may be applied to phenocam data. Machine learning methods can accommodate diverse data streams and, at the same time, adaptively “learn” the underlying relationships—which need not be smooth or linear. Training and validation will, however, remain a challenge—models must have a demonstrated ability to generalize well in time and space, and not be over-fit to a small set of location-specific training data.

3.5 Other applications in environmental science

In a study on the use of long-term, continuous, and high-frequency thermal imaging to understand canopy temperature dynamics over diurnal to seasonal time scales, Aubrecht et al. (2016) used Gcc data from a collocated phenocam to demarcate the growing season, providing information about whether the thermal camera “sees” a green canopy or bare branches, and context for interpretation of canopy-to-air temperature differences (see also Taborski et al., 2022).

One area where phenocam data and imagery are being creatively analyzed and interpreted is for studies of snow cover dynamics. I distinguish these applications from other AFM studies that have deployed time-lapse cameras for the express purpose of snow monitoring, e.g., Ge et al. (2022). For example, Julitta et al. (2014) used imagery from the same Alpine grassland site initially described by Migliavacca et al. (2011), and by subdividing the ROI using a fine-scale

grid, they quantified spatial variation in snowmelt dates. They then examined how the timing of snowmelt related to vegetation greenup dates. A surprising result was that earlier snowmelt was associated with later greenup, and this was found to be explained by microtopography and species composition of hollows vs. hummocks. In contrast to these results, Zheng et al. (2022) used data from MODIS, AmeriFlux, and PhenoCam to investigate relationships between snowmelt and a range of phenological metrics across Alaska. They found that earlier snowmelt tends to drive earlier spring onset because earlier snowmelt leads to warmer, wetter soils. Zheng's results are important because across virtually all of the study domain there has been a trend towards earlier snowmelt over the last two decades.

Phenocam images have also been used to determine when there is snow on an evergreen forest canopy so that data from other sensors (e.g., solar-induced fluorescence, Yang et al., 2022; thermal imaging, Bowling et al., 2018) can be filtered accordingly. And, in a study of wintertime water and energy fluxes by MacDonald et al. (2018), phenocam imagery from Larry Flanagan's Lethbridge, Alberta, flux site was used in lieu of regular snow surveys to qualitatively describe snow cover. Thus, potential applications of phenocam imagery extend far beyond merely characterizing phenological events such as the start and end of the growing season.

4. Lessons learned over the first 15 y of PhenoCam Network

From one camera at Bartlett Experimental Forest (2005; Figure 5a), and then 12 sites across the northeastern United States and adjacent Canada (2009; Supplementary Material, Figure S2), the PhenoCam Network has grown to be a continental-scale phenological observatory, with more than 500 active "Type I" cameras across North America configured and deployed according to a common protocol (Figure 6). There are now Type I PhenoCam Network

sites on every continent except Antarctica. In the middle of a typical day, over 2500 images are uploaded to our FTP server every hour, or an average of one image every 1.5 s. The vast image archive (Figure 4a) spans a wide range of plant functional types, and while deciduous broadleaf forests are still the most common, even arctic tundra, wetlands, and deciduous needleleaf forests have decent representation (Figure 4b). These data have enabled experimental and observational studies, at site-level to continental scales, with all manner of applications. Undoubtedly there are applications of these data that have not been envisioned—and may not be defined for many years. But because the underlying imagery provides a permanent visual record, the value of the archive will only increase over time as more sites are included, and each time series becomes longer. At this point, I would like to reflect on what I think are some of the key factors that have made this kind of growth possible.

1) *Timing*. The IPCC's AR4 noted that "phenology... is perhaps the simplest process in which to track changes in the ecology of species in response to climate change" (IPCC, 2007). By chance, the development of the PhenoCam Network was perfectly timed to ride the surge of interest in phenology that would build over the coming decade. The fact that interest in ecosystem-scale fluxes of carbon and water also boomed during the same period—as witnessed by the concurrent rapid growth of AmeriFlux—did not hurt. The relevance of phenology to contemporary global change ecology, as well as ecosystem ecology and management, ensured site collaborators could see the value in PhenoCam data and imagery.

2) *Low barriers to entry*. By adopting a single model of camera, providing a standardized deployment protocol and a simple script to facilitate configuration, and offering archiving and processing to network collaborators, as well as troubleshooting support, we made it easy for new collaborators to join the network. While the camera was not inexpensive, it was affordable,

707 compared to other instruments PIs were mounting on towers. For example, a phenocam generally
708 costs a little more than a temperature/relative humidity sensor, but much less than a net
709 radiometer.

710 3) *Technology*. Over the last 15 y, massive improvements in solar power, WiFi and cellular
711 telemetry (Supplementary Material, Table S2), data storage and high-performance computing
712 (HPC) and data processing, and remote access software have all enabled the expansion of the
713 PhenoCam network. Many site PIs and their technicians have also become more adept at
714 working with this kind of technology, although as noted below, this kind of technical training for
715 ecologists is still relatively rare.

716 4) *Accessibility and relevance for outreach*. Imagery from phenocams, particularly from the
717 StarDot NetCam (Figure 5), can be visually stunning—and it is concrete and tangible, in that it
718 provides a visually interpretable record of how a site looked at a certain point in time. In this
719 way, it has numerous advantages over other near-surface remote sensing approaches, because
720 even elementary school children can understand the concept of “virtual travel in space and time”
721 that is enabled by browsing the PhenoCam Network gallery on our website
722 (<https://phenocam.nau.edu/webcam/gallery/>). This has led to exciting opportunities for outreach
723 and education in K-12 classrooms.

724 5) *Real-time data delivery*. Daily images from the original Bartlett and Howland cameras
725 were mirrored to my University of New Hampshire web page as early as 2006. By 2010, the
726 PhenoCam Network web page was displaying images within minutes of being recorded. Users
727 could also browse the full image archive (drilling down by site, year, month, and day). By about
728 2012, we were processing the camera imagery each night, and plotting Gcc time series for each
729 site, updated through the previous day’s images. Our ability to deliver images and data products

with low latency allowed almost real-time monitoring of site conditions and also ended up enabling cutting-edge ecological forecasting efforts (Thomas et al., 2023).

6) *Open data policy*. Early AmeriFlux “Fair Use” data policies, were, for me, an inspiration—sharing, rather than protecting, data was an ideal I aspired to. My PhenoCam team realized, too, that more research questions could be investigated with PhenoCam Network data than we could ever attempt to answer on our own. So, from the beginning, the imagery has all been open-access and publicly available, and for at least a half-dozen years we have enabled “provisional” processed data to be directly downloaded from our web page. We have also released and documented curated data sets (Richardson et al., 2018a; Seyednasrollah et al., 2019) under lenient CC-BY licenses that allow re-use, re-mixing, and re-distribution. These policies have democratized data access, enabling the use of PhenoCam Network data by individuals and teams around the world in theses, dissertations, presentations, and peer-reviewed publications.

7) *A sense of place*. One thing that has surprised me is how site collaborators regularly engage with their phenocams—they like being able to check on their field sites in near-real time. This is particularly valuable when research sites are a long drive, or a plane flight, from the home institution. This engagement also means that ensuring continuity is a priority for the site collaborators—a win-win, as this improves the quality of data we can derive.

8) *Funding (at the right time)*. While all scientists have “side projects” that they conduct, out of curiosity and without any funding, it is impossible to sustain an effort such as the PhenoCam Network without funding to pay the salaries of the grad students, postdocs, and technicians who are keeping the effort afloat. We were fortunate to obtain funding when we needed it most. This funding allowed us to expand the network, develop and maintain our cyber-infrastructure, and document and publicly release curated data sets.

9) *Serendipity and citizenship*. One of the graduate-level classes I lead is a seminar on “Ecoinformatics”—or ecological informatics. When invited speakers present their work, a student always does the speaker introduction and then engages in a short Q&A session that includes an opportunity for the speaker to provide insights into their career path and the events and decisions that led them to where they are now. Two themes have emerged over and over again. First, serendipity—many careers have been built around fortuitous and unexpected discoveries, and PhenoCam is no exception; I never would have imagined that our initial “webcam” efforts at Bartlett Experimental Forest would lead to the development of an automated, continental-scale, phenological observatory. Second, being a nice person and a good citizen can go a long way: with PhenoCam, I have been fortunate to have had a dedicated and hard-working team, and a fantastic and ever-growing group of site collaborators. Dennis Baldocchi has noted that the success of FLUXNET, the global network of eddy covariance sites, was “due to people from many different cultures willing to work together and share data for a common goal and product that is more than the sum of the individuals.”[†] Similarly, with PhenoCam, synergies from teamwork, collaboration, and shared goals have led to the Network evolving into something that is much more than the 70 million images that comprise our current data archive (Figure 4A).

I think it is also worthwhile to acknowledge several ongoing and emerging challenges that the PhenoCam Network faces. These include:

1) *Technical knowledge*. Facility with R and Python, and expertise in high-performance computing, computer science basics, scripting, and data wrangling are important skills for PhenoCam Network data consumers to have; fortunately, this is now common in many graduate

[†] <https://nature.berkeley.edu/biometlab/pdf/Fluxnet%20Research%20Innovation%202012.pdf>

training programs. But, most ecosystem scientists have little training in computer networks and network protocols (IPv4, FTP, WiFi 802.11, POE 802.3, Telnet, SSH, etc.), which is often helpful for both setting up and troubleshooting inevitable camera issues (and other instruments, many of which are network-enabled). In this day and age, graduate-level training in the basics of computer networks is as important as basic electronics was for previous generations of scientists.

2) *Dated workflow*. Our current workflow is effective but more labor-intensive than it might be, requiring human intervention at too many steps in our processing and data curation workflow, such as defining ROI masks, identifying field of view shifts, and even visually inspecting each Gcc time series. I hope that deep learning and other advances in computing technology can help us simplify our workflow in the future.

3) *Obsolescence*. The StarDot NetCam SC we have used since 2008 has provided hundreds of sites with crisp and vibrantly-colored imagery. This camera has also been extremely robust and durable; the camera I installed on the Harvard Forest EMS tower on April 3, 2008, is still running and has recorded over 180,000 images in the last 15 years. In the spring of 2023, we learned that because of supply chain issues, this model of camera would not be available in the future. Going back to Sonnentag et al. (2012b), it is clear that other cameras can do the job equally well—but finding the right camera, with customizable settings and exceptional reliability, is non-trivial.

Overall, it is clear that in spite of these challenges, the PhenoCam Network has come a long way over the last 15 y. I hope to be able to contribute an update when the AFM 75th Anniversary special issue is in preparation.

5. Conclusions

The field of phenological research has changed enormously over the 60 y history of AFM. The pace of change has accelerated greatly in just the last two decades as climate change research has exploded, and phenology has become a key area of research within the field of global change ecology. The development of the PhenoCam Network over the last 15 y has contributed greatly to our understanding of the controls on phenology and relationships between phenology and ecosystem processes related to carbon and water. Much of the important phenocam literature has been published in AFM, and in this review I have identified 5 key themes of this research and highlighted the AFM papers that have contributed to new understanding. I have also identified key areas where I think we can expect to see exciting new advancements in phenocam-driven research. Given the size of the PhenoCam Network data archive, and the standardized data formats that we have adopted (facilitating ingestion of data from multiple sites), there is huge potential for leveraging cutting-edge deep learning and machine learning approaches for both improved data processing but also modeling, upscaling, and extrapolation. Finally, I think one reason the PhenoCam Network has been so successful is that human connections have resulted in an organic, grassroots network that is rooted in shared values of trust, respect, and collaboration. For me, it has been both remarkable and humbling to see how these efforts have led to a collaborative, continental-scale phenological observatory network that is so much more than the sum of the images and data products in our data archive—and has enabled the amazing and diverse scientific research that I have reviewed here.

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Table 1. Summary of keyword trends in AFM phenology papers, by total paper counts (left) and proportions (right), by decade. The “trend” column indicates whether the proportion increased (↑), decreased (↓), or stayed approximately the same (→) between the first and the second decade (first symbol), or between the second and third decade (second symbol). Since many phenology papers likely included more than one of the selected keywords, columns do not add to 100%.

Title, abstract, or keywords contains <i>phenology</i> and...	Count by Publication decade			Proportion by Publication decade			Trend
	1993-2002	2003-2012	2013-2022	1993-2002	2003-2012	2013-2022	
<i>climate change</i>	4	63	341	21%	58%	75%	↑↑
<i>model</i>	15	71	293	79%	65%	65%	↓→
<i>tree or forest</i>	9	69	272	47%	63%	60%	↑→
<i>agriculture</i>	8	22	154	42%	20%	34%	↓↑
<i>flux</i>	5	48	95	26%	44%	21%	↑↓
<i>remote sensing</i>	2	15	93	11%	14%	20%	→↑
Total papers	19	109	454				

Table 2. Phenological data products from a range of satellite platforms have been evaluated using PhenoCam data.

Satellite Platform	References	Notes
GOES	Wheeler and Dietze (2021)	GOES-16 and -17 are geostationary platforms with the radiometric ability to measure NDVI at daily resolution.
Harmonized Landsat-Sentinel (HLS)	Bolton et al. (2020)	Phenology products derived from HLS data at moderate-to-high spatial resolution (30 m) and high temporal resolution (1-4 d repeat)
Landsat	Melaas et al. (2016b)	PhenoCam Network data used in conjunction with ground observations and transition dates derived from carbon dioxide fluxes measured at long-term AmeriFlux sites to evaluate transition dates
MERIS	Brown et al. (2017)	See Sec. 3.3
MODIS	Hufkens et al. (2012) Klosterman et al. (2014) Richardson et al. (2018)	Hufkens et al. used data from just four PhenoCam Network sites; Richardson et al. used roughly 600 site-years of data from 128 camera sites in V1 of the PhenoCam Dataset. As satellite products become longer, and new products at higher resolution come online, there are new opportunities for product evaluation and benchmarking.
PlanetScope and HLS	Moon et al. (2021)	PlanetScope data enable characterization of phenological variability that occurs at spatial scales smaller than an HLS pixel. Strong coherence of Planet and PhenoCam time series.
SPOT-VGT and PROBA-V	Bórnez et al. (2020)	Used a range of different transition date extraction methods applied to PhenoCam and FLUXNET time series.
VIIRS	Zhang et al. (2018)	See Sec. 3.3

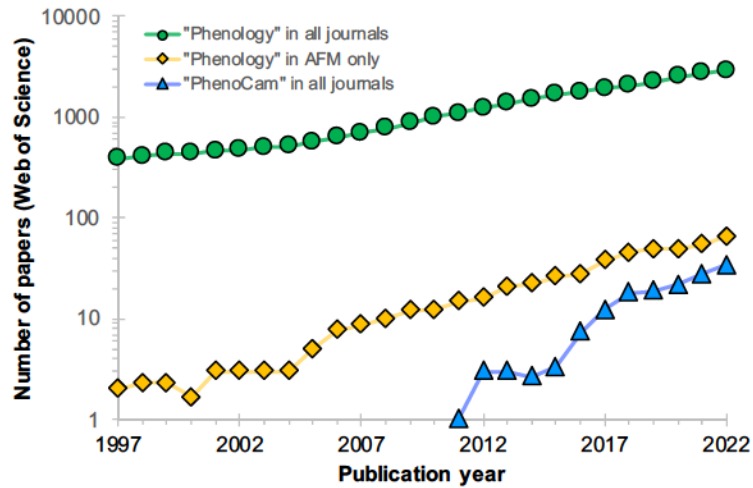
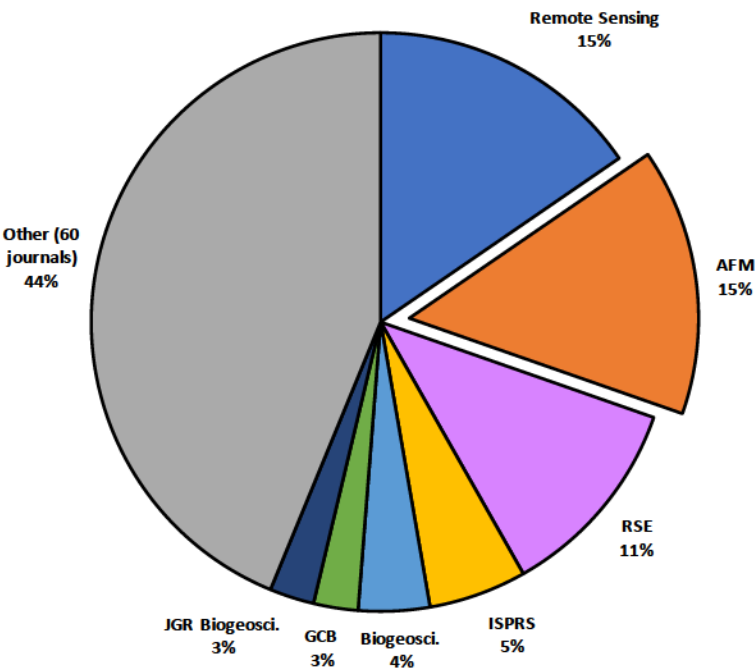


Figure 2. Publication trends since 1997 for phenology-themed papers. Based on a Web of Science search (June 10, 2023), I identified the number of papers published by year containing the word “phenology” in the title, abstract, or keywords. Results are shown since 1997. Green symbols show paper counts for all journals (increasing at 8.3% annually), yellow symbols show paper counts for *Agricultural and Forest Meteorology* only (increasing at 13.1% per year). Blue symbols show papers published (all journals) containing the word “phenocam” in the title, abstract or keywords (increasing at 30.1% per year). Note logarithmic scale of the y-axis. For clarity, data have been smoothed with a 3-y moving average.



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Figure 3. Of roughly 200 papers published containing the word “phenocam” in the title, abstract, or keywords, 15% have been published in *Agricultural and Forest Meteorology* (AFM). However, the overall diversity of publication outlets is also quite remarkable; note that the “Other” category includes 60 different journals, which have each published an average of 1.5 phenocam-related papers. Abbreviations: RSE, *Remote Sensing of Environment*; ISPRS, *ISPRS Journal of Photogrammetry and Remote Sensing*; Biogeosci., *Biogeosciences*; GCB, *Global Change Biology*; JGR Biogeosci., *Journal of Geophysical Research—Biogeosciences*.

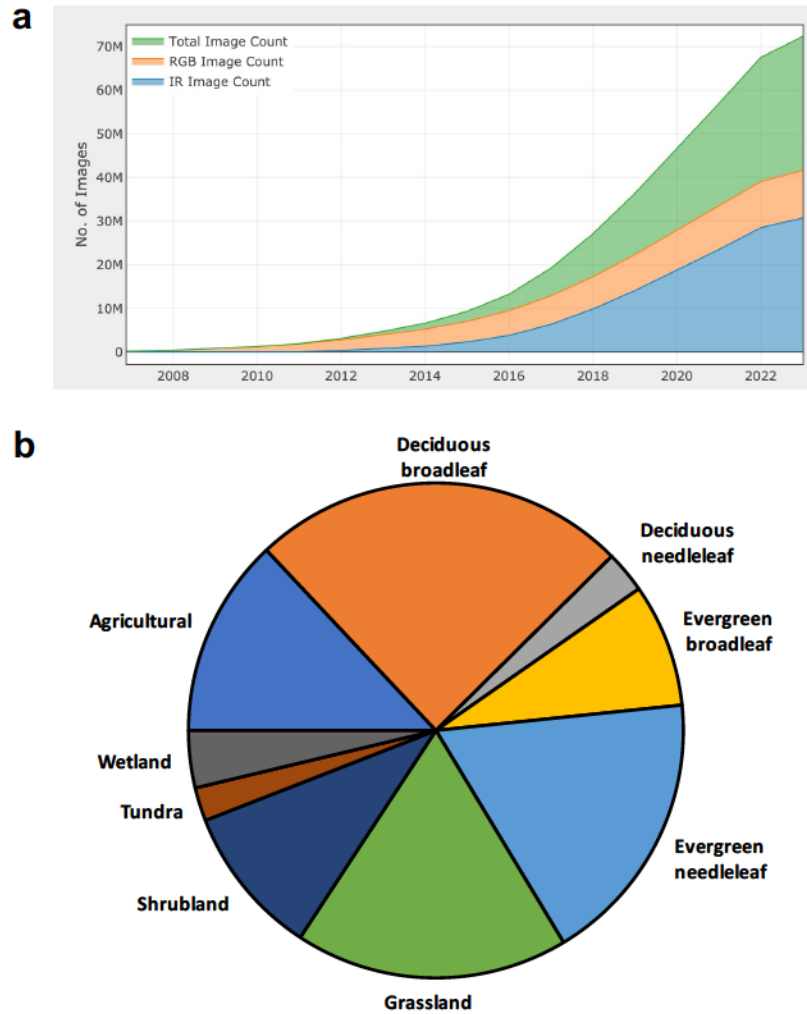


Figure 4. (a) Cumulative number of images in the PhenoCam network archive, 2007-2023. The current total of ≈ 70 million images includes 40 million visible-wavelength (RGB) images, and 30 million monochrome RGB+NIR images. Figure is a screen grab of the automatically updated plot at: <https://phenocam.nau.edu/webcam/archive/yearly/> (accessed 15 June 2023). (b) Breakdown of 4600+ site-years of phenocam imagery, by vegetation type (derived from <https://phenocam.nau.edu/webcam/roi/search/>, 16 June 2023).

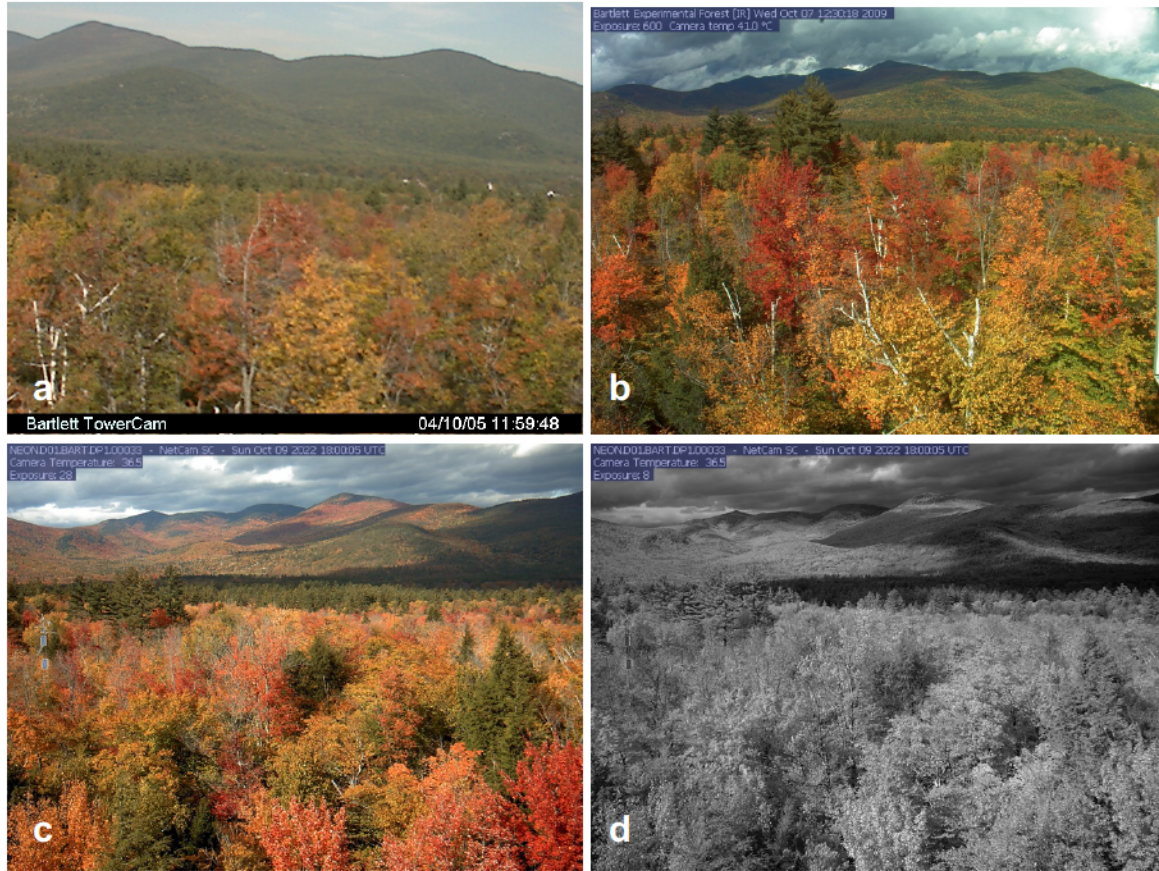


Figure 5. PhenoCam imagery, over the years, from Bartlett Experimental Forest, NH: (a) the first image recorded from a camera on the Bartlett AmeriFlux tower (Axis 211 camera, installed October 4, 2005); (b) Improvements in resolution and color reproduction (StarDot NetCam SC, installed April 8, 2008); (c and d) Visible- (left) and visible+near-infrared imagery (from which “camera NDVI” can be calculated; Petach et al., 2014) from the National Ecological Observatory Network tower phenocam (StarDot NetCam SC IR, installed December 13, 2016). The Bartlett AmeriFlux tower is visible on the left edge of the frame.

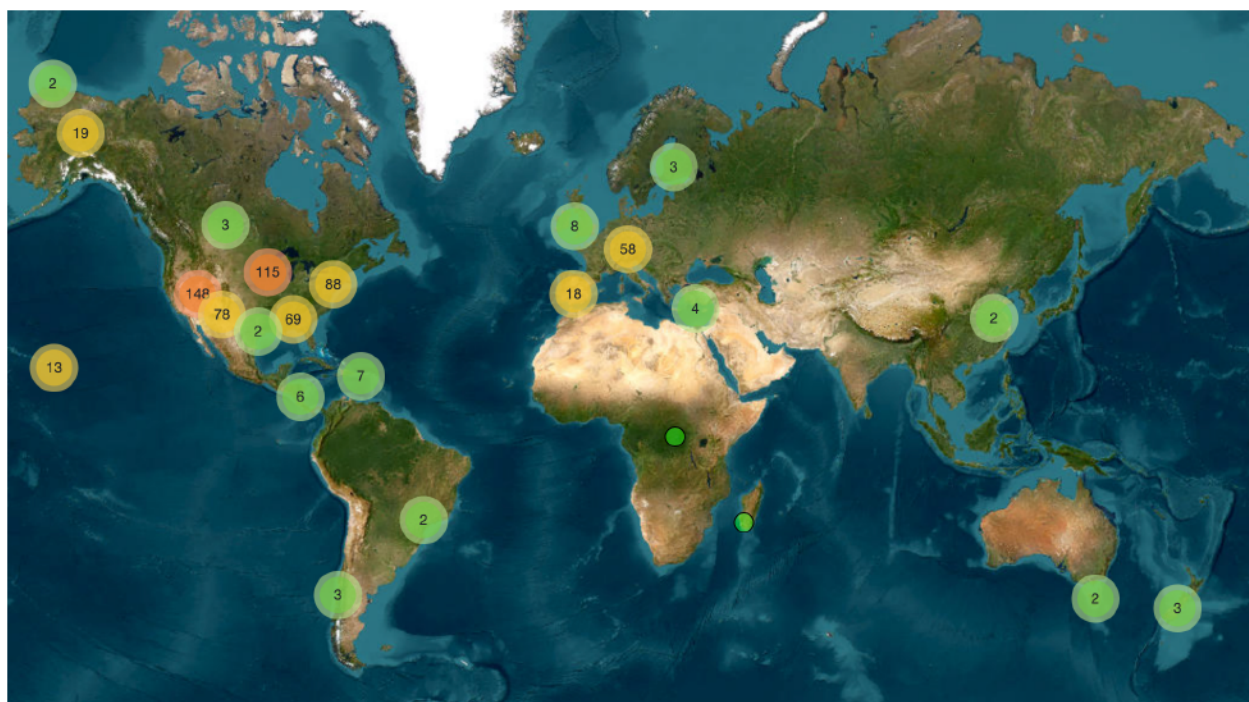


Figure 6. Global distribution of PhenoCam sites, spring 2023. Although most cameras are located in the conterminous United States, the network now includes sites on every continent. The 646 cameras shown are currently designated as “active” sites, and all follow the standard PhenoCam deployment protocol (StarDot NetCam SC, configured using the PhenoCam Installation Tool). Retrieved 24 September 2023, from <https://phenocam.nau.edu/webcam/network/map/?type=I&active=true>. Symbol color highlights the number of cameras (<10, green, ≥10 but <100, yellow; ≥100, red).

Box 1. What is a phenocam?

A phenocam, or phenology camera, is a digital camera used to record time-lapse pictures of plant canopies or communities so that the seasonal rhythms—the phenology—of that vegetation can be characterized using color-based image analysis. Images may be recorded at varying frequencies, from once daily to as often as every 15 minutes. The higher-frequency imaging is not strictly necessary from a phenological perspective, as few phenological events occur over such a short time interval. However, it does typically lead to higher-quality data and a lower signal:noise ratio because there is a greater likelihood of images being captured under ideal lighting conditions.

Most phenocams are mounted on towers, masts, tripods, or field station roofs, with an oblique view across the vegetation of interest. Typically, some sky is included in the field of view. Examples of installations in different vegetation types, from forests to shrublands to grasslands, are shown in Figure 1. Options for local storage or long-distance telemetry of phenocam imagery are summarized in Supplementary Material, Table S2.

Digital cameras use the red-green-blue (RGB) additive color model to represent colors as perceived by the human eye. Basically, this means that digital images are comprised of three “layers”, with each layer corresponding to one of the three color channels. For each color channel, there is a two-dimensional array of pixels that represent the image in that color. The resulting color and brightness of a given pixel is then characterized by the intensity of the pixel in each color layer, which is stored as a digital number (DN) triplet: R_{DN} , G_{DN} , B_{DN} . Notably, the imaging sensor in most digital cameras is sensitive to near-infrared wavelengths, and some phenocams leverage this capability to capture information about this fourth spectral band. For example, the StarDot NetCam SC, which has in the past been the standard camera adopted by the PhenoCam network, has a sliding infrared cut filter that enables back-to-back visible-wavelength and visible+near-infrared imagery to be recorded (see Section 3.1).

There are several steps involved in processing phenocam imagery and extracting quantitative data. First, a mask defining the vegetation of interest must be defined, e.g., “deciduous broadleaf trees.” This mask is often referred to as the ROI, or region of interest. Note that if the field of view of the camera shifts over time, the ROI mask must usually be updated. Second, images are read in by the processing code, and statistics of the RGB DN values, across the ROI mask, are extracted and summarized. In this way, phenocam images are treated analogously to satellite remote sensing images, with each of the RGB channels corresponding to a distinct spectral band. The PhenoCam Network conducts this processing automatically each night, and updated imagery, plots, and data summaries are publicly available through the PhenoCam web page in near-real time.

Just as vegetation indices, such as the well-known Normalized Difference Vegetation Index (NDVI) are calculated from satellite remote sensing, a similar approach has often been adopted with phenocam imagery. By far the most common index applied to phenocam imagery is the Green Chromatic Coordinate, or Gcc. Gcc is a measure of the intensity of the green channel relative to the total intensity of the red, green, and blue channels:

$$G_{cc} = \frac{G_{DN}}{R_{DN} + G_{DN} + B_{DN}}$$

Whereas NDVI leverages the contrast between low reflectance by foliage in red wavelengths, and high reflectance by foliage in near-infrared wavelengths, Gcc is more an index of relative “greenness”. Gcc has proven to be a reliable vegetation index for many phenocam studies because annual cycles of foliage development and senescence are often marked by increasing and decreasing greenness, respectively. Sample time series of Gcc in different ecosystem types are illustrated in Figure 1d.

Box 2. The origins of the PhenoCam Network

In the first year of my postdoc at the University of New Hampshire (UNH), my advisor, David Hollinger (USDA Forest Service; PI of the Howland Forest AmeriFlux site, and former lead of the AmeriFlux network) was keen to set up a new tower in a 60-80 y old deciduous stand at Bartlett Experimental Forest, NH. Scott Ollinger, at UNH, and Marie-Louise Smith, USDA FS, were also involved; the idea was that the tower would contribute to UNH-USDA FS efforts in support of the North American Carbon Program (<https://www.nacarbon.org/nacp/>), with the specific objectives of “provid[ing] a scientific basis to implement carbon accounting on regional and continental scales” and “measur[ing] the carbon balance of North America.” Hollinger and I are now in our 20th year of running that site (US-Bar), and the opportunity to be part of that effort has, without a doubt, had an enormous influence on my professional career. The key papers from that site have all been published in AFM (Jenkins et al., 2007; Lee et al., 2018; Ouimette et al., 2018).

In the fall of 2005, someone on our team suggested we put a “webcam” (as they were then known) on our Bartlett tower. “Security monitoring” was how we presented it to Forest Service purchasing department, but our real motivation was to have nice pictures that we could use to illustrate talks and posters, and (if we were lucky) to identify major phenological events, such as when leaves came out and fell off, which we thought would be useful for interpreting our flux measurements. This was not a particularly novel idea; in a prescient paper published that same year, Dennis Baldocchi had written “we encourage colleagues to install video cameras at all FLUXNET sites and record the state of the canopy each day” (Baldocchi et al., 2005). Shin Nagai, and others in Japan, had by this time also already started the Phenological Eyes Network (PEN) (Nagai et al., 2018, 2010; Nasahara and Nagai, 2015), while in Switzerland, Werner Eugster and his student Hella Ahrends were doing similar work at the Lägeren FLUXNET/ CarboEuropeIP site (Ahrends et al., 2008). And, Erik Graham’s visionary efforts with the University of California’s James Reserve “MossCam,” deployed in 2003, had already showed how digital camera imagery could be used to estimate photosynthetic activity of the bryophyte, *Tortula princeps* (Graham et al., 2006).

Largely unaware of these parallel efforts, we installed an Axis 211 (Axis Communications, Lund, Sweden) security camera on our tower on October 4, 2005 (Figure 4a). Our site ran on solar power (which was in short supply during most of the winter, and even during cloudy periods in summer) and from the top of the tower we had a shaky wireless connection back to the Forest Service headquarters about 1 km to the north. We turned on our camera and WiFi link only for a few hours around noon, and we had software running on an old Windows 95 PC at the headquarters that would grab several images from the camera each day, and then send them via FTP to my account on the UNH server. The image resolution, image quality, and color reproduction all left something to be desired; my inability to get a level horizon didn’t make the imagery any more compelling. But, this was the start of what would grow into PhenoCam.

We logged imagery through the fall of 2005 and into the spring and early summer of 2006. At that point, I was working with one of Ollinger’s PhD students, Julian Jenkins, who was a whiz with image processing and MATLAB coding, and who also understood what phenology was about (Jenkins et al., 2002). One day that spring, we talked about the imagery we had accumulated so far, and he agreed to see if he could extract anything useful or relevant from it. Jenkins quickly figured out how to characterize the red, green, and blue color channel intensities (digital numbers) for a rectangular canopy-level region-of-interest in the center of our images, and calculated time series of two indices that had been previously used in the precision agriculture literature (Woebbecke et al., 1995), *excess green* (ExG) and *green chromatic coordinate* (Gcc).

In retrospect, it seems so simple—of course it should have “worked,” if our camera was faithfully recording information about the colors in the scene it was observing. Still, for me, at least, it was a major “a-ha!” moment, when Jenkins showed me the time series with such a clear and well-defined “spring green-up,” at daily temporal resolution. These data nicely illustrated, at the site level, Mark Schwartz’s “green wave” (Schwartz, 1998). I soon realized then that there was the potential for this to be much greater than a single site.

During the summer of 2006, in 5 days, from an off-grid cabin on a lake 3 h north of Toronto, I wrote the first draft of the paper we would submit to and publish in *Oecologia* (Richardson et al., 2007). This paper showed the strong green-up signals in both “greenness” indices, and the general synchronicity of “webcam”-derived greenness indices and tower-based estimates of net and gross ecosystem uptake of carbon dioxide. Our camera gave us high-resolution data on the state of the canopy, which could then be related to ecosystem function. The advantage of the camera imagery, over radiometric indices like broadband NDVI, fAPAR, or albedo (e.g., Jenkins et al., 2007), was that the images could be visually inspected to see what was actually going on! I concluded the paper by observing that “[g]iven the widespread popularity of webcams, and the fact that they are already ubiquitous in our landscape ... our results suggest that images from such cameras could offer a novel opportunity to provide data that would complement the efforts of the [USA-National Phenology Network] NPN, at relatively low cost. This could easily be integrated into hands-on science education programs for primary and secondary school students ... which would provide chances for public outreach by the earth systems science community.” This vision ended up driving my career for the next 15+ y.

A camera at Hollinger’s Howland Forest AmeriFlux site, where the canopy was dominated by the conifers red spruce and balsam fir, followed in late 2006, and while seasonal variation in the evergreen signal in canopy greenness was more subtle, it was still there—and it proved to be a good indicator of photosynthetic activity in ENF forest types (Richardson et al. 2009, Seyednasrollah et al. 2022).

At the end of 2006, Hollinger and I began to work on a response to a “Request for Information” from the nascent National Ecological Observatory Network (NEON), in which we argued for the relevance of phenological monitoring to the “Grand Challenges” that NEON was designed to address. Our response was submitted in early 2007, and using our initial results from Bartlett as a case study, we argued that digital camera imagery could provide automated, high-frequency data on phenology at relatively low cost, and a “decadal-scale record of canopy phenology, coupled with concurrent carbon dioxide flux and meteorological data, would permit quantification of phenological and [carbon]-cycle responses to climate change across a range of ecosystem types.” This idea was enthusiastically embraced by NEON, but the first NEON cameras would not come online for almost a decade, in early 2016.

Around the same time as our *Oecologia* paper was published, in the spring of 2007, I applied to the Northeastern States Research Cooperative (NSRC; <https://nsrcforest.org>) for a small grant to establish a “Northeast Webcam Phenology Network”. I lined up collaborators at established research sites across New England and adjacent Canada; early adopters included a number of AmeriFlux and FLUXNET-Canada site PIs, including Steve Wofsy and Bill Munger (US-Ha1), Harry McCaughey (Ca-Gro), Hank Margolis (Ca-Qfo), HaPe Schmid (US-MMS), and Christoph Vogel and Peter Curtis (US-UMB).

By 2009, Bobby (“Rob”) Braswell, another UNH researcher, was an unfunded but enthusiastic team member. Braswell’s presentation at the European Geosciences Union meeting in the Spring of 2009 (also coauthored by Mark Friedl, from Boston University, who would go on to be a long-term collaborator), was, I believe, the first public announcement of the existence of an actual “PhenoCam Network” (Supplementary Material, Figure S2). At that time, we had 12 “core sites,” all of which were equipped with the StarDot NetCam SC (Figure 5b), but we were also archiving imagery from a number of USDA Forest Service and National Park Service cameras (all different makes and models), which had been installed for air quality monitoring. For many of these cameras we were able to obtain imagery back to the year 2000, and the long-term records from sites like the Mammoth Cave National Park site were instrumental in many of our early analyses (e.g., Hufkens et al., 2012). Greater emphasis on standardization and protocols would come in the following years, but in the first years, we worked with what was available.

Our early success was followed by stumbles. I wanted to obtain funding to take PhenoCam from a regional network to a continental-scale phenological observatory, as I had argued for in the

2007 *Oecologia* paper. It turned out to be harder than I expected. Although we had proof-of-concept across different ecosystems, and we could demonstrate that we had the initial cyberinfrastructure to serve up real-time imagery, proposals to a variety of federal agencies were unsuccessful. Finally, in 2011, a proposal I had led and submitted to the new NSF program in “Macrosystems Biology” (MSB) was successful—and thanks to the enthusiastic support of Program Officer Liz Blood, my career trajectory was forever changed.

In our MSB proposal, we said we would expand PhenoCam to a continental-scale “phenological observatory,” and we would tackle three main research questions:

1. *How do photoperiod, temperature, and precipitation govern phenological transitions in different plant functional types at local, regional and continental scales?*
2. *How will vegetation phenology respond to rising temperatures and changing precipitation regimes, and what are the associated uncertainties?*
3. *What are the forecasted impacts on ecosystem services related to carbon and water, at regional and continental scales, of these phenological shifts?*

These were big questions, and even a dozen years later I feel we have only begun to scratch the surface of answering any of them; the questions remain as relevant now as they were in 2011.

New collaborators brought into this MSB project included many AmeriFlux and FLUXNET-Canada site PIs, from diverse ecosystems across North America, including Russ Monson, Bev Law, Andy Black, Larry Flanagan, Alan Barr, Dennis Baldocchi, Shashi Verma, and Altaf Arain. Their enthusiastic support was key to the future success of our evolving PhenoCam Network. Around this time, Braswell took a job in the private sector, and Tom Milliman, a research scientist at UNH, took over as our data manager—a position he would hold for the next dozen years. I would like to thank all of my early collaborators for their faith and commitment; the quality of imagery, and data continuity, that resulted from their efforts. The opportunities my students and postdocs had to interact directly with these world-class scientists provided critical networking opportunities. It was a win-win situation, and it set the stage for our future success.

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Box 3. PhenoCam vs. phenocam?

The short MATLAB script that Julian Jenkins wrote in 2006 to process our Bartlett imagery had been fatefully named *phenocam.m*. When in 2008 Rob Braswell developed the first web page for our unnamed “webcam network,” he adopted the PhenoCam name for the landing page and URL, and the PhenoCam Network was born. Julian deserves credit for coming up with the name, and Rob for the branding. Over time, “phenocam” has come to be used generically (like Kleenex, Velcro and Lego; see Gordon, 2019) in reference to any digital camera used to monitor plants and plant phenology. For me, this is an affirmation of the value of what we have developed and created. For clarity, in this paper I use “PhenoCam” (with capitalization, inspired by the capitalization of AmeriFlux) to refer specifically to the PhenoCam Network, while I use “phenocam” (all lower-case) to denote more generic applications.

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1453 **Supplementary Material:**

1454 **PhenoCam: An evolving, open-source tool to study the temporal and spatial variability of**
1455 **ecosystem-scale phenology**

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Supplementary Material, Box S1. My introduction to phenology

I was a graduate student at the Yale School of Forestry & Environmental Studies (renamed the Yale School of the Environment in 2020) in the late 1990s and early 2000s. I completed my MF (Master of Forestry) degree at Yale in 1998 and had been encouraged during my second year of that program to apply for the PhD program. The encouragement came from two of my mentors, Graeme Berlyn, a tree physiologist, and Xuhui Lee, a micrometeorologist.

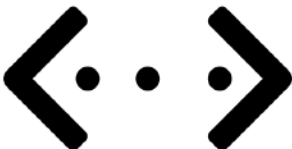
There was a long and fascinating history of biometeorology research at Yale, and a correspondingly long history of Yale involvement in AFM. Notably, Bill Reifsnyder, Lee's predecessor as a professor of forest meteorology and biometeorology (1955-1990), had been a founding editor of the journal (initially titled *Agricultural Meteorology*) and served as editor-in-chief from 1984-1995. Kya Tha Paw U, a student of Reifsnyder's, and professor at UC Davis, served as editor-in-chief of AFM from 1998-2008, and Lee would later serve as editor-in-chief of AFM from 2008-2019.

Lee's class on Biometeorology, which I had taken as a second-year MF student, was one of the reasons I stayed on to do a PhD. I was fascinated to learn of emerging methods, such as "eddy correlation," as it was then commonly called. At the time I had almost no concept of how eddy covariance would ultimately come to revolutionize our understanding of land-atmosphere interactions, carbon cycling, or evapotranspiration, thanks to the work of pioneers like Steve Wofsy, Mike Goulden, Shashi Verma, Dennis Baldocchi, Bev Law, and David Hollinger.

For my dissertation research, I ended up investigating the structure and function of conifer foliage along the elevational and canopy light gradients. One of my projects involved quantifying the microclimatology of my study sites, and how those varied along the elevational gradient, from deciduous to conifer forest, and across treeline to tundra, and across different mountain ranges of the northeastern USA (Richardson et al., 2004; this was my first paper in AFM). I assembled my environmental monitoring stations for this project in Lee's lab, which had previously been Reifsnyder's lab.

Offhandedly, in one of our meetings, Lee suggested I put a quantum sensor not just *above* the canopy but also *below* the canopy—so I could look at how much photosynthetically active radiation was transmitted by the canopy, and how this changed with the seasons, i.e., with *phenology*. "Then you could do some modeling," he added. "Great idea!" I thought. But, I quickly came to realize that Murphy's Law, which basically states that "if anything can go wrong, it will," might have priority over Hopkins' (1920) "Bioclimatic Law," which describes phenological patterns in relation to latitude and elevation: at my high-elevation site, the cable running from my CR10 data logger to a quantum sensor below the deciduous dwarf birch canopy was chewed by a malicious rodent after a few months, whereas the quantum sensor in the mid-elevation evergreen spruce-fir forest kept running for a few years. I had no useful data on phenology in the high-elevation site, and in the mid-elevation site, changes in solar zenith angle—not changes in leaf area—dominated the signal. Still, these unsuccessful efforts were a learning experience, and I had also been introduced to phenology.

Supplementary Material, Table S2. Options for local storage or long-distance telemetry of phenocam imagery. Technological advancements over the last 15 y have not only opened up new options for remote connectivity, but they have also greatly reduced the costs of both hardware and data transfer fees. Verifying system uptime on a daily basis is ideal, but this is not always possible.

Icon	Description
	Most stand-alone cameras (e.g., trail cams or game cams) record images to an SD card, which can store a year or more of 30-minute images. Field technicians swap cards, download images, and conduct image processing in an <i>ad hoc</i> , rather than automated, manner. A limitation of this approach is that it is impossible to remotely verify system uptime.
	At field sites without Internet connectivity, images can be stored on a local computer connected to the same network as the camera. In most cases, the computer will be running an FTP (file transfer protocol) server that accepts incoming connections from the camera, but in other cases, software or scripts running on the computer will pull images from the camera. Images are then manually uploaded to an external FTP server, e.g., PhenoCam, for automated processing, or processed locally in an <i>ad hoc</i> manner. As with storing images on an SD card, a limitation of this approach is that it is impossible to remotely verify system uptime.
	At many sites, a local network is connected to an Internet node (e.g. at the field station or site headquarters) via a wired Ethernet connection. Images are then sent to an external FTP server in real-time for viewing, archiving, and automated processing.
	Alternatively, other sites use a wireless connection between devices (e.g., PhenoCam) and the Internet. Some phenocams are WiFi-enabled, but even for those that are not, the phenocam can be connected via Ethernet to a WiFi client or repeater, which then connects to a nearby WiFi access point (50-100 m, maximum). In other cases, the camera might be just one of several devices connected to a long-range, point-to-point wireless bridge, which then connects to a distant (up to 20 km) wireless bridge, which is then connected to the Internet. The latter solution is common at field sites where Internet connectivity is desired across a large area (1-1000 km ² , or more). Either solution allows images to be sent to an external FTP server in real-time for viewing, archiving, and automated processing.

	Wherever cellular phone service is reliably available, cell modems offer an alternative route to Internet connectivity without the infrastructure requirements of a point-to-point long-distance wireless network. Over the last decade, cell modems have become much more widely used as both the hardware and the data transfer fees have become less expensive. When a cell modem is used, the PhenoCam obtains an outgoing Internet connection through the cell modem, and images are generally sent to an external FTP server in real-time for archiving and automated processing. But, cellular network connectivity may be poor in some rural and wilderness areas in which ecological research is often conducted.
	Satellite communications offer virtually global connectivity for cameras and other scientific monitoring equipment, but at a cost that is much higher than for cellular M2M (machine-to-machine) data connections. At sites where topography, remoteness, or other factors may preclude wireless or cellular connections, satellite may be the only option. At these sites, one way to minimize data charges is to store sunrise-to-sunset phenocam images locally, but to send a mid-day image out via the satellite connection. In this way, system uptime can be verified on a daily basis.

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Supplementary Material, Figure S3. The 12 “core sites” in the PhenoCam network, spring 2009, as presented in a talk at the European Geosciences Union meeting in Vienna by Rob Braswell. We focused the initial network on forested research sites in northeastern US and adjacent Canada; sites spanned 10° latitude and 10°C mean annual temperature, and a range of forest types from oak-hickory in the southernmost sites, to northern hardwoods (maple-beech-birch), to boreal mixedwood (birch-poplar-fir), and boreal conifer (spruce-fir) in the north. Seven of 12 sites were already measuring surface-atmosphere carbon dioxide and water vapor fluxes with eddy covariance, and a number of sites had ongoing observer records of phenology (e.g., Richardson and O’Keefe, 2009).

