Popular summary:

Phenology focuses on the timing of biological events such as flower opening or bird migration. This paper discusses some of the challenges in predicting and assessing phenological responses. The paper also reviews some of the advances being made in phenological research, including 1) satellite phenology products, 2) ground-based instrumentation, and 3) cyber-infrastructure. Finally, the paper described how these advances are helping diverse research and application areas, including the assessment of climate change on phenology as well as how phenological research can help land management decisions.

Learning the rhythm of the seasons in the face of global change: phenological research in the 21st Century

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Abstract

Phenology is the study of recurring life-cycle events, of which classic examples include flowering by plants as well as animal migration. Phenological responses are increasingly relevant for addressing applied environmental issues. Yet, challenges remain with respect to spanning scales of observation, integrating observations across taxa, and modeling phenological sequences to enable ecological forecasts in light of future climate change. Recent advances that are helping to address these challenges include refined landscape-scale phenology estimates from satellite data, advanced instrument-based approaches for field measurements, and new cyber-infrastructure for archiving and distribution of products. These advances are aiding in diverse areas including modeling land-surface exchange, evaluating climate-phenology relationships, and aiding land management decisions.

In a nutshell

- Phenology focuses on the timing of biological events such as flower opening or bird migration.
- Predicting and assessing phenological responses can be challenging due to issues associated with spatial scale, differences across taxa, and forecasting in time.
- Satellite products, ground-based instrumentation, and cyber-infrastructure are all advancing phenological research.
- These advances are helping diverse research and application areas including assessing impacts of climate change and aiding land management decisions.

Panel 1. Author contribution for this article

JTM, ADR, AKK, JIF, EG, and JA co-conceived and co-developed the idea for the manuscript. All authors helped edit each draft. JTM refined the content and scope, led sections 1 and 5, provided figure 2, compiled all drafts, prepared the final version of the manuscript, and facilitated the gathering of contributions. ADR co-led section 4.1, contributed to section 3, provided figure 3, and led the development of figure 1. AKK co-led section 4.2. JIF led section 4.3. EG co-led section 3. JA co-led section 4.1 and 4.2. BEW co-led section 3. DDB co-refined the intellectual content and scope and helped connect the various contributions. GMH co-developed sections 2 and 3 and made significant contributions to figure 1. JMH and LL co-developed section 2.

1. Introduction

> "In June as many as a dozen species may burst their buds on a single day. No man can heed all of these anniversaries; no man can ignore all of them."
>
> Aldo Leopold, *A Sand County Almanac*

The Leopold quote above only partially captures the profound complexity and ubiquity of seasonal biological events. Yet it is the ever-present and ever-changing cyclical nature of all living things, and their interactions with each other and the abiotic environment, that make phenology such a complex, intricate, and challenging field. Fortunately, this growing field is starting to address this complexity, and new advances are helping the ecological community address some key research and practical issues.

Phenology is the study of recurring life-cycle events that are initiated and driven by environmental factors. Examples of such events in plants, which are the primary focus of this article, include the onset of growth and photosynthesis in the spring and the senescence and abscission of deciduous vegetation in the fall. Since there is an interaction between plants' life-cycle events and temperature and precipitation (Menzel et al. 2005; Kathuroju et al. 2007), phenological studies integrate climate-biosphere relationships and can be used to document and evaluate the effects of climate change at both the individual species and aggregate levels (Schwartz et al. 2006; Cleland et al. 2007). Furthermore, observing and documenting changes in the phenologies of various species support efforts to reconstruct past climates and make predictions about biological responses to future climate scenarios (Chuine et al. 2004; Cook et al. 2005). Multiple and intricate links between plant phenology and variations in weather (short-term, days to weeks) and climate (long term, years to centuries) can also feed back to the atmosphere and climate system, as well as influence ecological interactions at multiple scales (individual to community to ecosystem) and trophic (producers to consumers) levels (Figure 1).

In this paper we first present some of the challenges for research in the field of phenology. We continue by describing some recent advances in phenological research. Finally. we describe how the knowledge gained from these advances can address some challenges and advance our understanding of phenological events and their connection to climate and management issues.

2. Cross-cutting challenges for phenological research

Phenological responses are increasingly relevant for addressing applied environmental issues, yet some key challenges require additional attention if phenological responses are to be used to effectively link climate drivers and land management:

1. Reconciling scales of observation
2. Integrating observations across taxa; and
3. Modeling phenological sequences to enable forecasting.

These challenges are considered cross-cutting issues because they can relate to research on any of the phenological topics shown in Figure 1. The first two issues have received some attention in the literature while the third is expected to be an active area of future research.

Phenological observations cover a wide **range of scales** (Table 1), and hence challenges remain in relating observations from the scale of an individual leaf up to observations that span landscapes. Monitoring of plants and animals has traditionally been conducted at the ground level (Schwartz, 2003). Records of plant phenology have varying extents and spans but are generally restricted to particular species at discrete locations (Caprio, 1966). In the last 25 years, monitoring of the vegetated land surface by space-borne sensors has introduced multiple new scales of observation, which now extend from ecosystems to regions and continents (Reed et al., 1994; Zhang et al., 2003). Land surface phenology can provide a synoptic view of vegetation dynamics (Moulin et al., 1997; de Beurs and Henebry, 2004). Recent work on bioclimatic models track meteorological drivers to simulate regional scale phenological responses to climatic variations (de Beurs and Henebry 2005; Jolly et al. 2005; Schwartz et al., 2006; Zhang et al., 2007). Increasing spatial extent often implies consideration of more than one species. For both remote and proximate sensors, comprehending how discrete life events of multiple species will impact various measurements remains an active area of research (Chuine et al., 2000; Schwartz et al., 2002; Graham et al., 2006; Richardson et al., 2007).

Integrating observations across taxa requires a cooperative and cross-disciplinary effort to synthesize extant phenological data from diverse sources; such synthesis across taxa poses an analogous challenge to the previously discussed issues of spatial scale. These must be brought together under a common conceptual framework of plant, insect, and animal phenologies from terrestrial and aquatic environments across diverse biomes (Schwartz, 2003; Cleland et al., 2007, Parmesan, 2007). Phenological studies are now tackling some of the more complex and challenging issues associated with systems of mixed dominance of woody and herbaceous plants (e.g., Harris et al. 2003), which pose particular challenges in tracking the cause of phenological response, most notably after major disturbance events (Rich et al. 2008).

Forecasting of phenological sequences is currently a key challenge if observations are to be used to improve land management. Recent advances hold the promise of providing much needed feedback to numerical weather prediction and biogeochemical models (White and Nemani 2006; Kathuroju et al., 2007). Further efforts are needed to establish sufficient understanding of phenological processes, based on present and past data, to allow extrapolation into the future.

3. Recent advances in phenological research

There has been steady and continued improvements in satellite sensors and related data processing algorithms, imaging tools used as *in-situ* sensors, and expanded connectivity through the Internet. These have created three major advances that can contribute to improved applications in phenology, especially with respect to the cross-cutting challenges presented above:

1. Refined landscape-scale phenology estimates from satellite data

2. Novel, affordable and convenient instrument-based approaches to field measurements and
3. Cyber-infrastructure to coordinate archiving and distribution of data products.

Land surface phenology is defined as the seasonal pattern of variation in the properties of vegetated land surfaces on the regional or global scale and is typically characterized using satellite remote sensing products (Friedl, et al., 2006). While the observed patterns are related to biological phenomena, land surface phenology is distinct from traditional definitions of vegetation phenology, which refer to specific life cycle events such as budbreak, flowering, or leaf senescence and are based on *in-situ* observations of individual plants or species. Land surface phenology provides aggregate information at moderate (250-m) to coarse (25-km) spatial resolution; which relates to the timing of vegetation growth, senescence, and dormancy and associated surface phenomena at seasonal and inter-annual scales (Friedl, et al., 2006). An example land surface phenology product, length of the 2005 growing season, is shown in Figure 2; where broad gradients related to latitude, elevation, and vegetation type can be discerned.

Currently, data from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) are being used to produce a global phenology product at 1km spatial resolution (Zhang et al. 2003). New efforts are underway to use MODIS data to produce a 250m-spatial resolution phenology product for North America (Figure 2, MODIS for NACP, the North American Carbon Program: no date). Moving from 1km to 250m represents a 16-fold increase in resolution. This will help show more local patterns related to microclimate, species composition, disturbance and land use. Also, research is being directed to consider phenology across a range of scales (Fisher and Mustard, 2007). Finally, public-domain software is now available to extract phenology metrics from satellite time-series data (Jönsson and Eklundh, 2004), thus allowing researchers to more easily conduct their own specific land surface phenology analysis.

Modeling efforts to characterize land surface phenology have generally relied on simple functions of meteorological drivers such as accumulated growing degree-days (de Beurs and Henebry, 2005), minimum temperature, photoperiod, vapor pressure deficit (Jolly et al. 2005), and minimum relative humidity (Brown and de Beurs, accepted). Forecasting land surface phenology with these approaches has been explored (White and Nemani 2006) but models are not yet adequate for long-term prognostication.

Advanced field monitoring devices that can provide phenological information are becoming less expensive, easier to use, and smaller in size, even as they have expanded in capacity. With newly-developed radiometric sensors and digital imagers, phenological monitoring can now move from a labor-intensive pursuit to a state approaching automation. These methods have been described as "near" remote sensing (Richardson et al., 2007). Indeed, imaging with digital cameras (capable of detecting red, green, blue, and, in some cases, near-infrared, channels) is now commonplace and examples of their use in agriculture and ecology is growing (Goddijn and White 2006). Timing and duration of flowering has been measured with imagers (Adamsen et al., 2000). Large-scale networks of battery-operated wireless imagers have now become technologically feasible for use in tight areas that are hard to observe without disturbing the environment being monitored (Rahimi et al. 2006). For example, Ko et al. (2007) used imaging hardware placed in avian nest boxes to automatically detect bird presence and count eggs over the nesting cycle. Automated discovery of phenological events using imagery has recently been successful through a combination of low-level, robust image analysis with more complex machine learning algorithms. Examples include automatically identifying and counting individual flowers from images captured in a 5000 m^2 field with a pan-tilt-zoom camera and calculating of leaf areas of Rhododendron in a temperate forest using a camera on a mobile platform (Figure 3, Graham, unpublished data).

Recent studies have combined automatic imaging, simple color analysis, and sophisticated CO_2 measurements to quantify carbon cycles at a range of scales (from patches of moss, Graham et al. 2006, to large stands of deciduous trees, Richardson et al. 2007). Figure 4 shows images from a networked digital webcam at the Bartlett AmeriFlux site in the White Mountain National Forest of New Hampshire. The color channel information extracted from these images is used to quantitatively track seasonal changes in phenology of the maple-beech-birch canopy, and these have been related to tower-based measurements of surface-atmosphere exchanges (via eddy covariance methods, Richardson et al., 2007). The image sequence shows early spring, prior to leaf out; late spring, when the canopy is nearly fully developed; and early autumn, at the peak of fall color.

Features such as remote pan, tilt, and zoom of fixed-position cameras, as well as motion detection and automatic image acquisition and web posting, offer opportunities for researchers not only to obtain scientifically valuable data but also to engage the public through outreach and educational activities. The list of potential applications will undoubtedly grow as sensor technologies become even more applicable, accessible, and affordable.

Cyber-infrastructure plays a critical role in the collection, management, and dissemination of information in modern research efforts, particularly as these efforts involve: multiple research entities, data collected across a range of spatial and temporal scales, and study complex systems (Atkins et al., 2003). With the recent development of a United States National Phenology Network (USA-NPN, no date: Betancourt et al. 2007), the cyber-infrastructure challenge of coordinating numerous data streams, collected across a range of spatial and temporal scales, becomes paramount. This network must be able to take data from at least three different types of providers: (1) research and monitoring networks (e.g. Ameriflux, the USA National Science Foundation's Long Term Ecological Research sites, Monarch Watch, Hummingbird Monitoring Network, the Global Learning and Observations to Benefit the Environment Program, etc.), (2) professionals in agricultural and land management activities, and (3) citizen scientists from a wide variety of backgrounds and interests. Indeed, a flagship USA-NPN effort, "Project Budburst" (2007), is highly successful in using the Internet and a consistent set of protocols to create a large network of citizen scientists interested in contributing to a phenological database. Studies of citizen science networks (Cooper et al. 2007) outline such issues as integration of citizen science data with other sources, concerns about quality of data, and incentives for researchers. Nevertheless, data from citizen sources as well as other research and monitoring networks must feed into a broad set of end users, including researchers, land managers, and policy decision makers. A key cyber-infrastructure challenge for the USA-NPN, as well as the broader phenology community, is how these multi-scale observations can be integrated into a cohesive data framework that will provide access to a broad and dense network of raw observations of defined quality, as well as synthesized higher-order products derived from these observations.

A number of recent cyber-infrastructure developments will help the phenological community achieve these goals. There are now common tools for managing ecological data and metadata (Michner, 2006). In addition, the work in astronomy to develop virtual observatories is beginning to migrate into earth science and there is much progress being made in combining data from multiple places into virtual observatories (McGuinness et al., in press). As a result, there is growing pressure from sponsoring agencies on the various earth observing networks to work together to enhance data sharing to meet societal needs (e.g. Adang, 2006).

4. Research and practical implications

How do these recent advances address the cross-cutting challenges listed above to address key environmental challenges of concern? Here, we provide examples in the areas of climate research and land management.

4.1 Interactions between changing phenologies and climate change

In the context of global climate change the "phenology – climate connection" presents a challenge to ecologists and climatologists alike. The challenge of scale is particularly critical here since phenological observations are typically done at the plant level, while climate-change research has focused on much larger scales. It is crucial for the ecological community to better quantify phenological responses to climatic drivers. Likewise, it is crucial for the climate community to better quantify the influence of phenology on climate (e.g., through surface-atmosphere exchanges). Ample evidence exists that 20th century climate change has altered phenologies (Schwartz et al, 2006;). And land surface phenology can be coupled with assimilated meteorological information to explore relationships across large areas (Zhang et al., 2007). Given the increasing rate of climate change projected in the 21st century, there is a pressing need to establish the spatial and temporal phenological response to climate change. Improving our understanding, across all taxa and scales, of intra- and inter-species phenological sensitivity to climate change will help ecologists identify vulnerable ecosystems and potential ecological asynchronies (e.g., Williams et al., 2007).

Questions remain unanswered as to how the multivariate influence of meteorological conditions (e.g., temperature, precipitation, solar radiation) drives phenology. In addressing these questions, it is important to disaggregate phenological response to climate change from that associated with climate variability. For example, it is critical to understand the influence of extreme events (e.g., heat waves, hard freezes, drought) and dominant modes of climate variability (e.g., El Niño-Southern Oscillation, Northern

Annular Mode) on phenological events, as well as the "memory" of flora and fauna to antecedent conditions.

While the causal link between climate and phenology is conceptually straightforward, less appreciated is the potential influence of phenology on climate (Alessandri et al., 2007). Changes in the surface energy balance, induced by phenology, act to modify local surface temperatures, humidity, and regional circulation regimes. Given the potentially important role of phenology on local climate through physical feedback processes, it is essential to include phenological changes as part of the land-surface atmosphere interaction in the next generation of regional climate models. Similarly, accounting for phenology in hydrologic models may further improve the representation of coupling between the land-surface and atmosphere to improve local and regional analysis.

Feedbacks between vegetation and the lower atmosphere occur across a range of timescales, from minutes (e.g., transpiration) to centuries (e.g., species distribution, Pielke et al., 1998; see also Figure 1). Seasonal changes in the phenology of deciduous canopies, especially spring green-up and autumn senescence, can alter both physical (surface energy balance and surface roughness) and biogeochemical (nutrient uptake and release; photosynthesis and carbon sequestration) properties of the land surface. Together these have consequences for the structure of the planetary boundary layer, ambient surface temperature and humidity, cloud physics and precipitation patterns, soil thermal properties, and levels of atmospheric CO_2 (e.g., Schwartz 1992).

In order to best resolve the intricate details that govern both present day and future climate processes, climate models must account for bidirectional feedbacks between the biosphere and the atmosphere (Pitman 2003). This requires the implementation of coupled dynamic global vegetation – climate models (Kucharik et al., 2006). Phenology schemes currently implemented in state-of-the-art land surface schemes; e.g. Integrated Biosphere Simulator (IBIS), Simple Biosphere Model, version 2 (SiB2), Community Land Model (CLM), are inadequate to resolve the complexities of surface-atmosphere exchanges associated with phenology. Either phenology is prescribed or driven in the models. When prescribed, phenology is not responsive to environmental drivers. When driven by the model, phenology predictions tend to be biased because the models use a limited number of plant functional types and overly simple representations of ecosystem processes (Kucharik et al., 2006).

The advances in phenological research can improve our understanding of the climate-phenology connection. Improvement and standardization of land surface phenology products can facilitate the climate modeling community's use of such data. Coincident field monitoring of both phenological and meteorological observations will help inform the coupling between the two. Finally, advances in sensors and cyber-infrastructure can ensure that a full suite of both phenological *and* climatic measurements can be collected in an integrated and consistent fashion across a wide range of sites. These measurements, together with improved land surface phenology products and assimilated meteorological data are the required components to improve our understanding of the phenology-climate change connection and sensitivities at local to regional scales.

4.2 Land use and management

Many ecosystem processes, from which we derive economic benefit, depend on climatic patterns and follow seasonal cycles (Figure 1). The ability to predict both seasonal and inter-annual variation in the phenology of a range of ecosystems has significant management implications for grazing, forestry and agriculture, pest management, disease vectors and allergens, energy consumption, water availability and conservation, and tourism and hunting, amongst others applications. In each of these disciplines, improved understanding and forecasting of phenologies may be able to improve management techniques and, in some cases, also reduce the risk of undesirable outcomes (e.g., disease outbreaks, crop failure, or forest fires). For example, grass protein content falls rapidly through early summer as the grasses mature and senesce. By timing grazing to phenology, forage quality can be maintained longer prior to senescence (Ganskopp et al., 2007) and managers can selectively graze to optimize returns and sustainability. In terms of public health, better phenological forecasting would be relevant for improved prophylactic treatment of asthma and allergies. Early work, correlating climate with pollen production (e.g. Subiza et al., 1992) found that near-term pollen abundances could be predicted with reasonable accuracy. Finally, Chuine and Belmonte (2004) used species-specific temperature-driven phenological models to predict pollen abundance for 13 highly allergenic species in France and Spain with moderate success. This is bound to be an active area of future research.

For land management, the predominant challenge is related to prediction. Managers need to know how today's management decisions will impact tomorrow's ecosystem processes. But issues of scale and taxa are also relevant. For most land management scenarios, the management unit includes many individual plants or animals. Thus individual observations must be scaled up to the management unit. Also, interactions between ecosystem processes implies that management of one domain will effect others. So, understanding phenological response across taxa can be important.

New work in land surface phenology (Fisher and Mustard, 2007, MODIS for NACP (no date) provides satellite-derived phenology data at a higher spatial resolution. While land managers are likely to be more familiar with measurements collected at a local scale (individual plant or animal), when these measurements are coupled with higher-resolution landscape phenology data there may be new insights on how local activities relate to the larger management area. Also, a better link between climate and phenology can help connect existing climate forecasts to phenological forecasts. By having predictions of both future climate and future phenology, land managers will have added insight about the ecosystem services relevant to them.

5. Conclusion

As long as there are living organisms on our planet, we can expect to see seasonal patterns in life cycle events. Understanding these events define the scope of phenological research. The better we understand these cycles, the better we will understand the world around us. This understanding can help us adapt to climate change and better manage our natural resources.

Remote sensing of land surface phenology will continue to be refined and coupled with more traditional ground observations. Retrospective studies will extend phenology records further back in time. Field sensors will become more affordable and accessible, thereby allowing a full suite of measurements to be collected across globally distributed science, management, and citizen scientist networks. Cyber-infrastructure will enable these data to be synthesized and utilized by increasingly advanced spatial-temporal analysis and modeling activities, perhaps in a manner analogous to the way in which real-time meteorological observations are fed into numerical models to provide continually updated weather forecasts for distribution to a wide range of end users.

Promoting an awareness of the synergy and connectedness of these activities will help the research and management communities make the most of the new information. The USA-NPN will promote such awareness (Betancourt et al., 2007). The USA-NPN has been established to help coordinate phenological research in the United States and connect that research with the international community. Given the advances and issues presented here, it is certainly a timely idea now blooming with possibilities.

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Spatial Scale	Data Sources	Examples	Metrics	Advantages	Limitations
Plot (< 10 km^2)	Observational networks; historical documents; non-conventional records; controlled experiments	European Phenology Network (EPN), century long; Kyoto cherry blossom records, millennium long (Schwartz, 2003); Arboretum fixed date photographing (Miller-Rushing et al., 2006).	Mainly dates (in day of year) of critical life cycle events; BBCH scale* for economical plants in Germany.	In-situ accuracy; long time span; regional extent. (Varying with different datasets)	Discrete point data separated from local ecological context; limited geographic extent.
Landscape (Visually distinct patches of vegetated land; 10 - 10^2 km^2)	Intensive research sites	Ameriflux flux tower sites (Kuchark et al., 2006).	Customized continuous life cycle protocol with fine details	Improved in-situ accuracy with pixel sized landscape representative-ness.	Labor intensive; short temporal coverage (2006-present).
Regional ($10^2 – 10^5$ km^2)	Bioclimatic Modeling;	Spring Indices (SI), based on cloned species (Schwartz et al., 2006).	SI First Leaf and SI First Bloom	Standardized response, regional coverage	Limited to temperate land regions with weather data coverage; model inadequacy.
Continental to Global ($>10^5$ km2)	Spaceborne Sensors; Data Assimilation Systems	Vegetation indices from AVHRR (since 1982, Moulin et al., 1997); MODIS (since 2000, Zhang et al., 2003).	Start of season (SOS), end of season (EOS), and growing season length; peak VI position in thermal time	Integrated land surface signals; regional to global coverage.	Sensitive to method; multiple sources of noise: clouds, sensor calibration and artifacts; trade-off between spatial and temporal resolutions.

*Biologische **B**undesanstalt, Bundessortenamt and **CH**emical industry (Meier,2001)

Table 1: Phenological Monitoring Across Scales

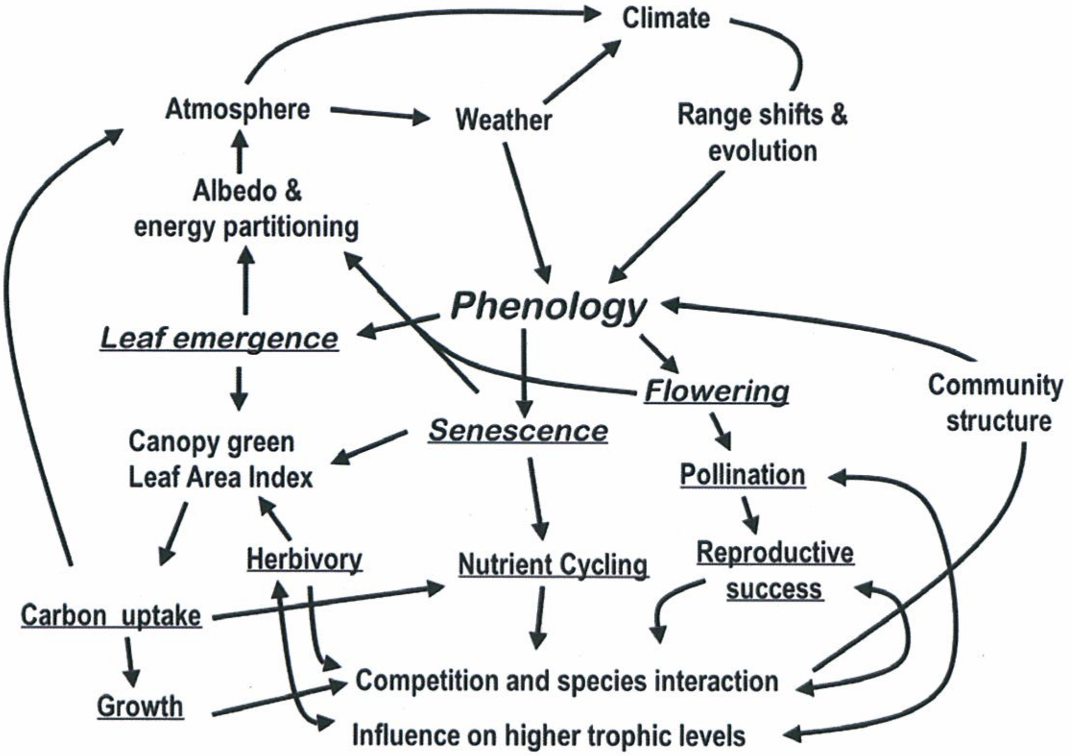

Figure 1: Conceptual model showing some of the ways in which plant phenology in temperate climates is intricately linked to variation in weather (short-term, days to weeks) and climate (long term, years to centuries), feeds back to the atmosphere and climate system, and influences ecological interactions at multiple scales (individual to community to ecosystem) and trophic (producers to consumers) levels. Underline denotes ecosystem services from which management or economic benefits are derived.

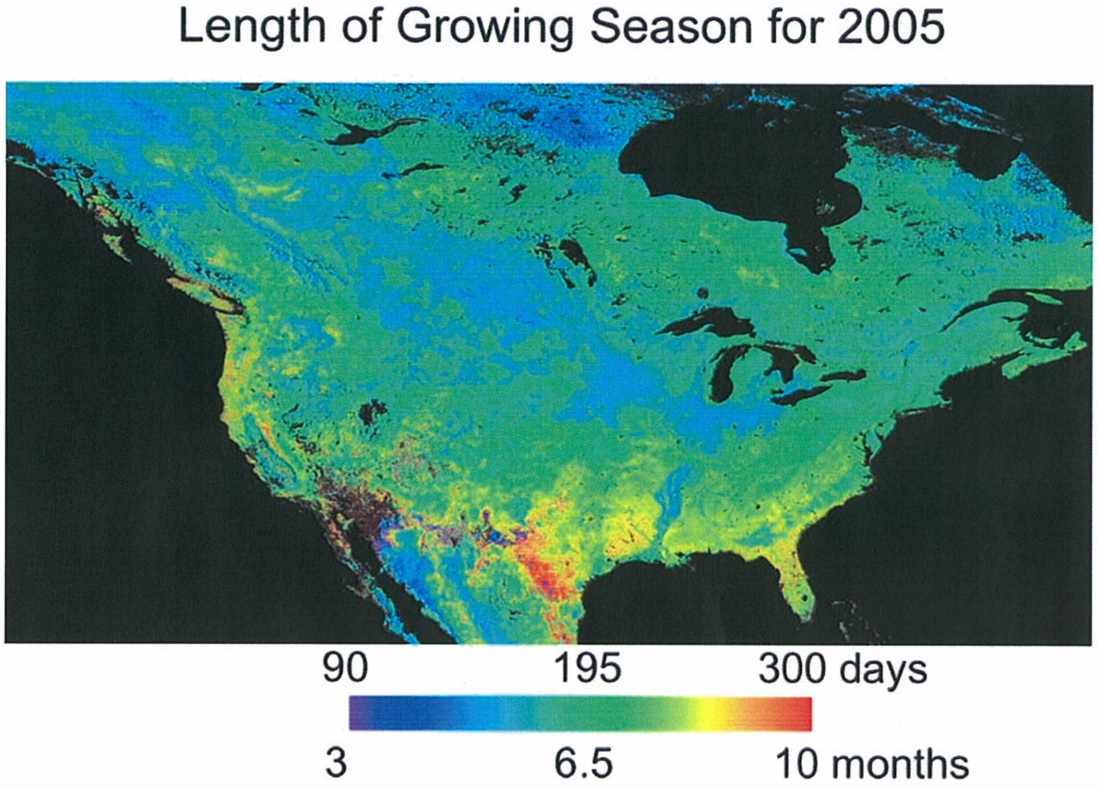

Figure 2: Example phenology product derived from 250m time series data from NASA's Moderate Resolution Imagine Spectroradiometer (MODIS for NACP, no date).

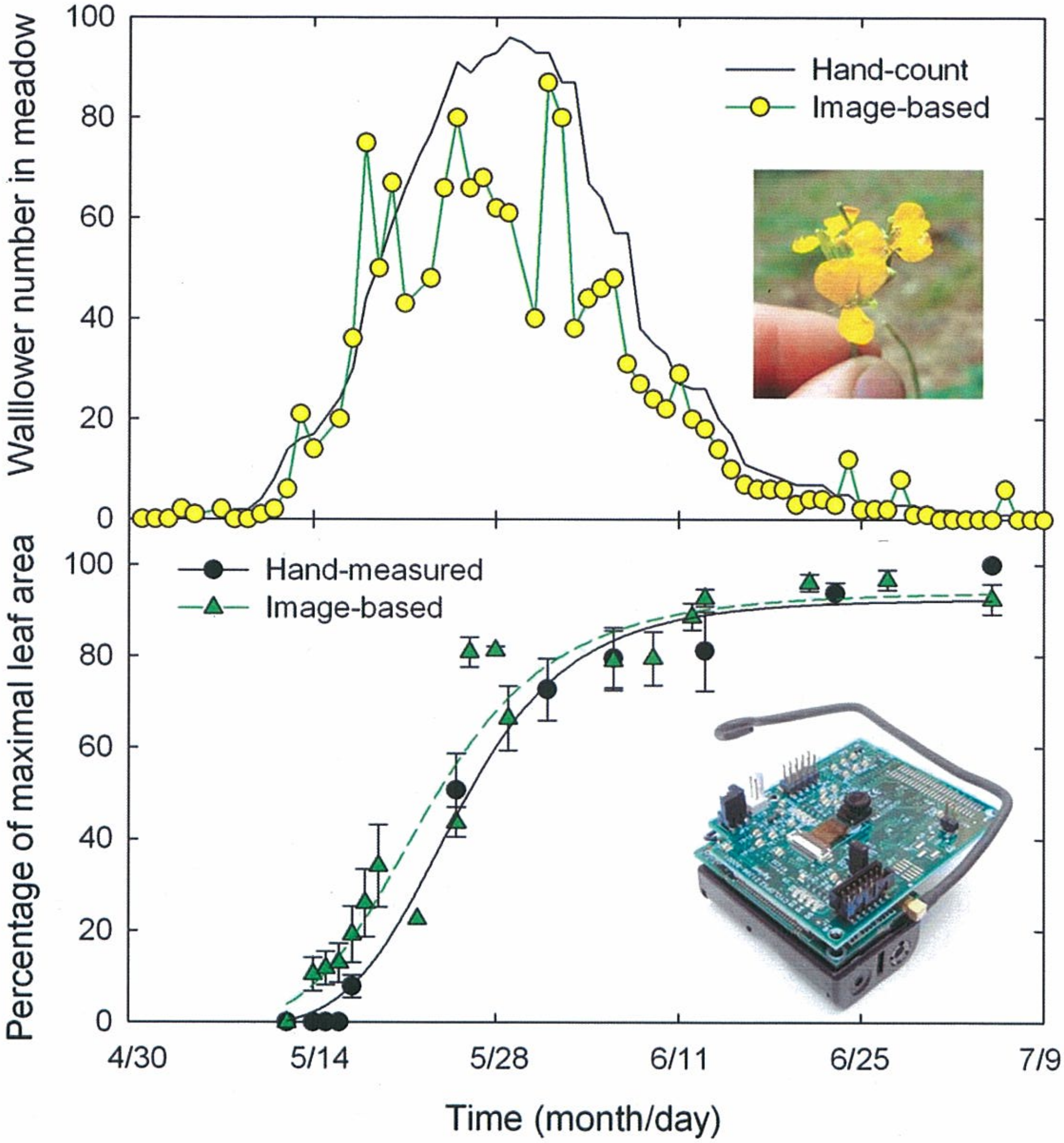

Figure 3: Example of automatically identifying and counting individual flowers from images captured in a 5000 m^2 field with a pan-tilt-zoom camera (top panel) and calculating of leaf areas of Rhododendron in a temperate forest using a camera on a mobile platform (bottom panel). Inset is an example of a small, wireless, battery-powered camera that can be networked for automated image retrieval (http://research.cens.ucla.edu/).

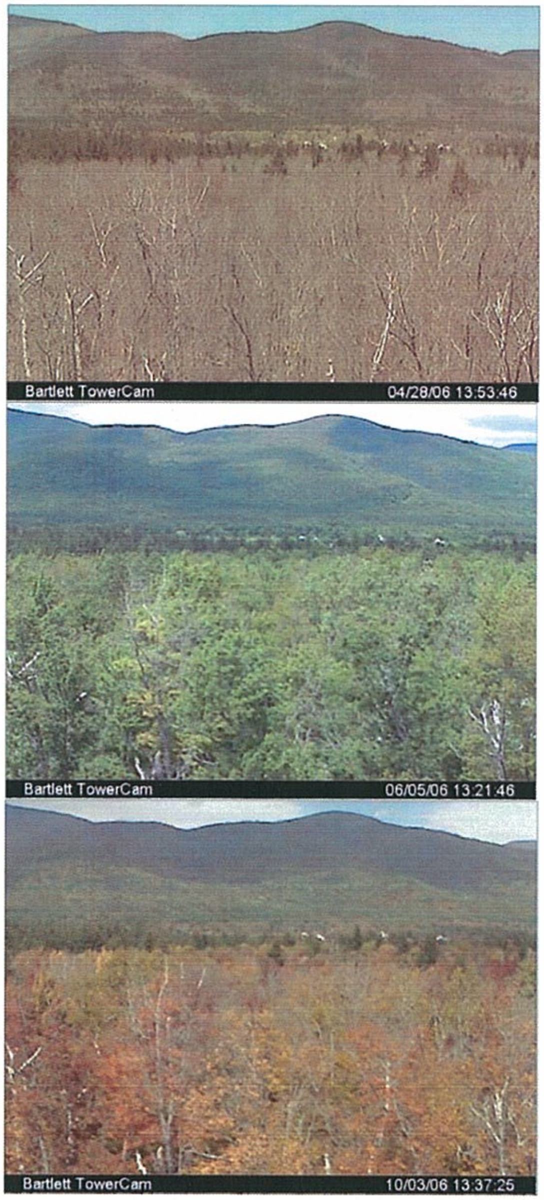

Figure 4: Webcam images from a field site in the White Mountain National Forest: a: early spring, b: late spring, and c: early autumn.