Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century

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Phenology is the study of recurring life-cycle events, classic examples being the flowering of plants and 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 questions include refined landscape-scale phenology estimates from satellite data, advanced, instrument-based approaches for field measurements, and new cyberinfrastructure for archiving and distribution of products. These breakthroughs are improving our understanding in diverse areas, including modeling land-surface exchange, evaluating climate–phenology relationships, and making land-management decisions.

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Aldo Leopold once wrote,"*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.*" (Leopold 1949). This quote 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 and intricate field. Fortunately, current research is beginning to address this complexity, and new advances are helping the ecological community to tackle key research questions 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, and influence ecological interactions at different scales (individual to community to ecosystem) and trophic levels (producers to consumers; Figure 1).

In a nutshell:

- Phenology examines the timing of biological events, such as flower blooming or bird migration
- Predicting and assessing phenological responses can be difficult, due to issues associated with spatial scale, differences across taxa, and forecasting in time
- Satellite products, ground-based instrumentation, and cyberinfrastructure are all advancing phenological research
- These breakthroughs are proving useful in various research and application areas, including assessment of the impacts of climate change and land-management decision making

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Cross-cutting challenges for phenological research

Phenological responses are increasingly relevant for addressing applied environmental issues, yet some key questions 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 are considered to be cross-cutting issues because they can relate to research on any of the phenological

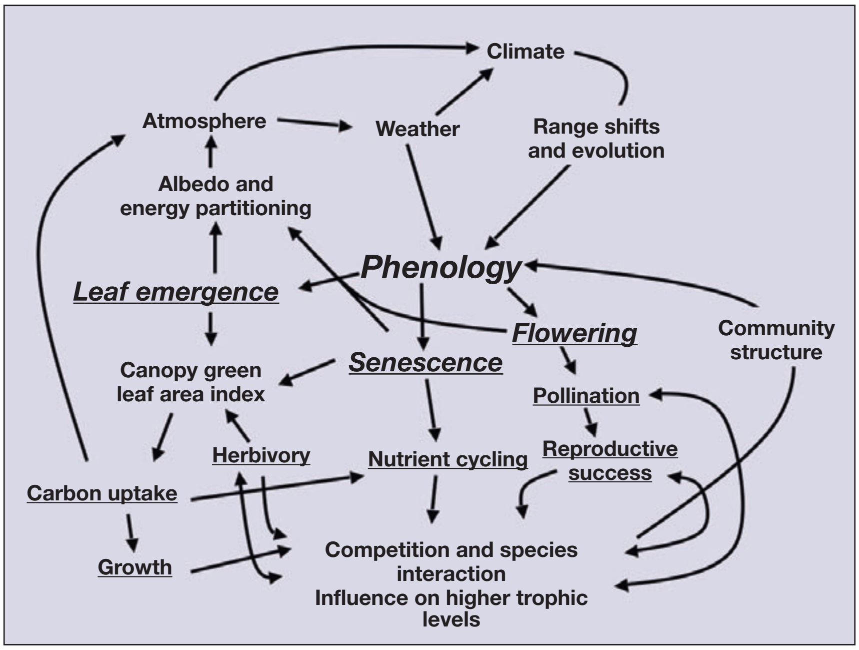

Figure 1. *Conceptual model showing some of the ways in which plant phenology in temperate climates is intricately linked to variation in weather (short term, days to weeks) and climate (long term, years to centuries), feeds back to the atmosphere and climate system, and influences ecological interactions 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.*

topics shown in Figure 1. The first two issues have received some attention in the literature, while the third is expected to be an area of active research in the future.

Addressing a wide range of scales

Phenological observations cover a wide range of scales (Table 1), making it difficult to link observations from an individual leaf to the landscape scale. Monitoring of plants and animals has traditionally been conducted at ground level (Schwartz 2003) and, although records of plant phenology cover varying extents and spans, they are generally restricted to particular species at discrete locations (Caprio 1966). However, in the past 25 years, monitoring of the vegetated land surface by space-borne sensors has introduced 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 tracks 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 and, for both remote and proximate sensors, understanding how discrete life events among different 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

Integration of observations across taxa requires a cooperative and cross-disciplinary effort to synthesize extant phenological data from various sources; this kind of 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 and animal phenologies from terrestrial and aquatic environments across different biomes (Schwartz 2003; Cleland *et al.* 2007; Parmesan 2007). Phenological studies are now tackling some of the more complex issues associated with systems involving mixed dominance of woody and herbaceous plants (eg Harris *et al.* 2003), where it is particularly difficult to track the cause of phenological responses, most notably after major disturbance events (Rich *et al.* 2008).

Forecasting

Forecasting of phenological sequences is 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.

Recent advances in phenological research

There have been steady and continued improvements in satellite sensors, related data-processing algorithms, and imaging tools used as in-situ sensors, and expanded connectivity through the internet. These advances can contribute to improved applications in phenology, especially with respect to the cross-cutting challenges discussed above: (1) refined landscape-scale phenology estimates from satellite data; (2) novel, affordable, and convenient instrument-based approaches to field measurements; and (3) cyberinfrastructure to coordinate archiving and distribution of data products.

Land-surface phenology

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 tradi-

Table 1. Phenological monitoring across scales

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 (Kucharik *et al.* 2006)	Customized continuous life-cycle protocol with fine details	Improved in-situ accuracy with pixel-sized landscape representativeness	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 responses, regional coverage	Limited to temperate land regions with weather data coverage; model inadequacy
Continental to global (>10^5 km^2)	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

*BBCH: Biologische Bundesanstalt, Bundessortenamt and CHemical industry (Meier 2001). **AVHRR: Advanced Very High Resolution Radiometer.

tional 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, dormancy, and associated surface phenomena at seasonal and inter-annual scales (Friedl *et al.* 2006). An example of a 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 seen.

Currently, data from NASA's moderate-resolution imaging spectroradiometer (MODIS) are being used to produce a global phenology product at a spatial resolution of 1 km (Zhang *et al.* 2003). New efforts are underway to use MODIS data to produce a 250-m spatial resolution phenology product for North America (MODIS nd; Figure 2). Moving from 1 km to 250 m represents a 16-fold increase in resolution; this will help to reveal more local patterns related to microclimate, species composition, disturbance, and land use. Research is also addressing phenology across a range of scales (Fisher and Mustard 2007), and public-domain software is now available to extract phenology metrics from satellite time-series data (eg Jönsson and Eklundh 2004). This allows researchers to more easily conduct their own specific land-surface phenology analyses.

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), or minimum relative humidity (Brown and de Beurs 2008). Forecasting of land-surface phenology using these approaches has been explored (White and Nemani 2006; Fisher *et al.* 2006), but the models are not yet adequate for long-term prediction, and they indicate potentially complicated relations with climate.

Advanced field monitoring devices

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 has evolved from a labor-intensive pursuit toward 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 have been measured with imagers (Adamsen *et al.* 2000). Use of large-scale networks of battery-operated wireless imagers has now become technologically feasible for areas that are difficult to observe

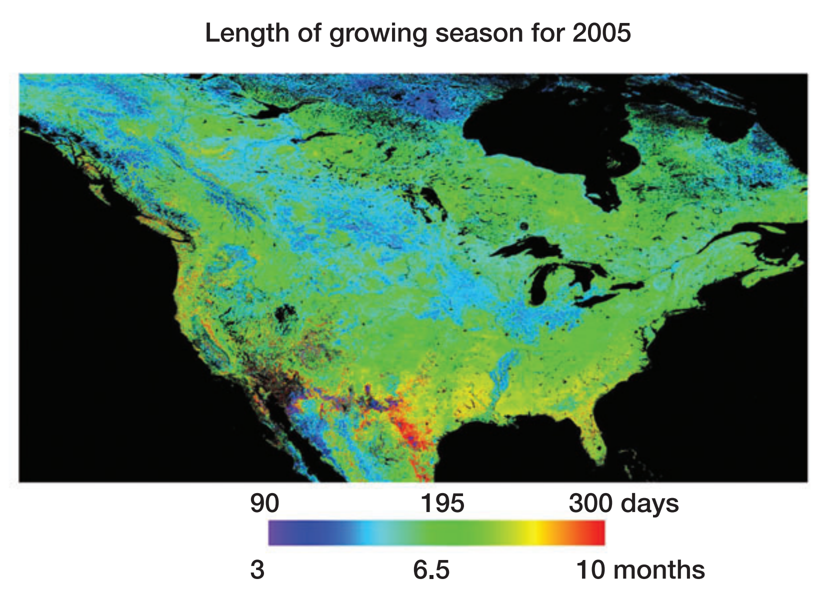

Figure 2. *Example of phenology product derived from 250-m time series data from NASA's moderate resolution imaging spectroradiometer (MODIS nd).*

without disturbance to the environment being monitored (Hamilton *et al.* 2007). 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 leaf area of rhododendron in a temperate forest, using a camera on a mobile platform (EAG unpublished; Figure 3).

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.

Cyberinfrastructure

Cyberinfrastructure plays a critical role in the collection, management, and dissemination of information about modern research efforts, particularly as these efforts involve a variety of different research entities, data collected across a range of spatial and temporal scales, and complex systems (Atkins *et al.* 2003). With the recent development of a United States National Phenology Network (USA–NPN nd; Betancourt *et al.* 2007), the challenge of coordinating numerous data streams, collected across a range of spatial and temporal scales, becomes paramount. This network must be capable of accepting data from at least three different types of providers: (1) research and monitoring networks (eg AmeriFlux, the US National Science Foundation's Long Term Ecological Research sites, Monarch Watch, Hummingbird Monitoring Network, the Global Learning and Observations to Benefit the Environment Program), (2) professionals in agricultural and land-management activities, and (3) citizen scientists from a wide variety of backgrounds and with diverse interests. Indeed, a related effort, "Project Budburst", is highly successful in using the internet and a consistent set of straightforward protocols to both engage citizen scientist observers and provide outreach to a broad range of educators (Project Budburst 2007). 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 and other research and monitoring networks must serve a broad set of end users, including researchers, land managers, and decision makers. A key cyberinfrastructure challenge for 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 and to higher-order products derived from these observations.

A number of recent cyberinfrastructure developments will help the phenological community to achieve these goals. There are now common tools for managing ecological data and metadata (Michener 2006). In addition, research that was aimed at developing virtual astronomical observatories is beginning to migrate into Earth science and progress has been made in combining data from multiple sources 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 (eg Adang 2006).

Research and practical implications

How do these recent advances address key environmental issues of concern? Here, we provide examples in the areas of climate research and land management.

Interactions between changing phenologies and climate change

In the context of global climate change, the "phenology–climate connection" presents a problem to ecologists and climatologists alike. The issue of scale is particularly critical here, as 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 (eg through surface–atmosphere exchanges). Ample evidence suggests that 20th-century climate change has altered phenologies (Schwartz *et al* 2006). Land-surface phenology can be coupled with assimilated meteorological information to explore relationships across large areas (Fisher *et al.* 2006; Zhang *et al.* 2007). Given the increasing rate of climate change projected for the 21st century, there is a pressing need to establish the spatial and temporal phenological responses to climate change. Improving our understanding, across all taxa and scales, of intra- and inter-species phenological sensitivity to climate change will help ecologists to identify vulnerable ecosystems and potential ecological asynchronies (eg Williams *et al.* 2007).

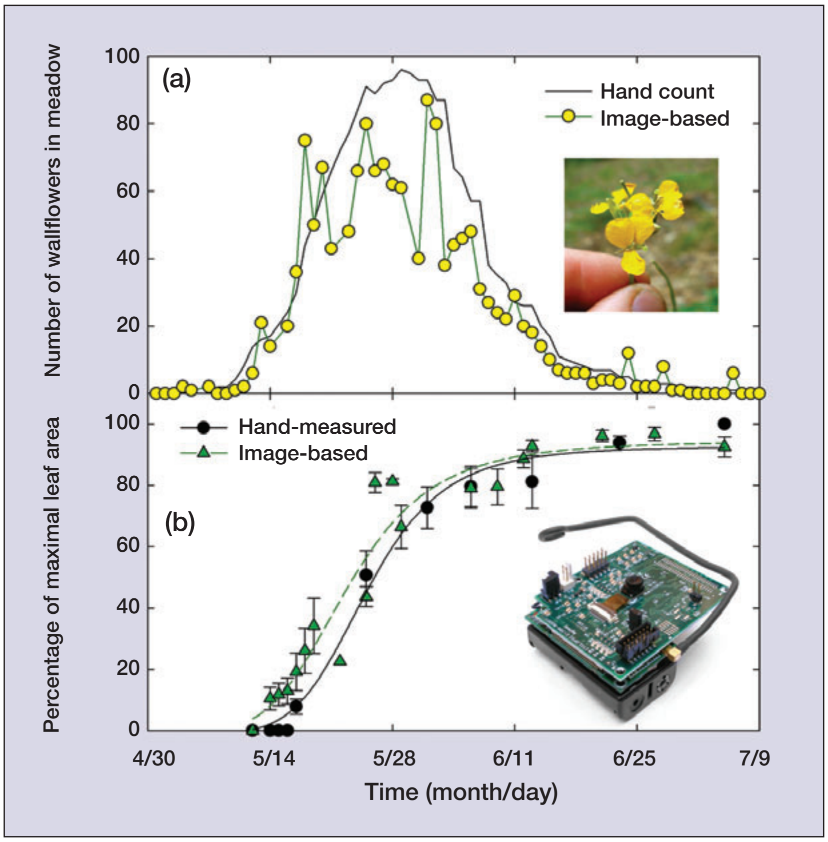

Figure 3. *Examples of (a) automatically identifying and counting individual flowers from images captured in a 5000-m² field with a pan-tilt-zoom camera and (b) calculating leaf areas of rhododendron in a temperate forest using a camera on a mobile platform. Inset in (b) is an example of a small, wireless, battery-powered camera that can be networked for automated image retrieval (http://research.cens.ucla.edu).*

We do not yet know how the multivariate influence of meteorological conditions (eg temperature, precipitation, solar radiation) drives phenology. In addressing these uncertainties, 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 (eg heat waves, hard freezes, drought) and dominant modes of climate variability (eg El Niño–Southern Oscillation, Northern Annular Mode) on phenological events, as well as the "memory" of flora and fauna to previous conditions.

While the causal link between climate and phenology is conceptually straightforward, the potential influence of phenology on climate is less well understood (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 in 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 time scales, from minutes (eg transpiration) to centuries (eg 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 pat-

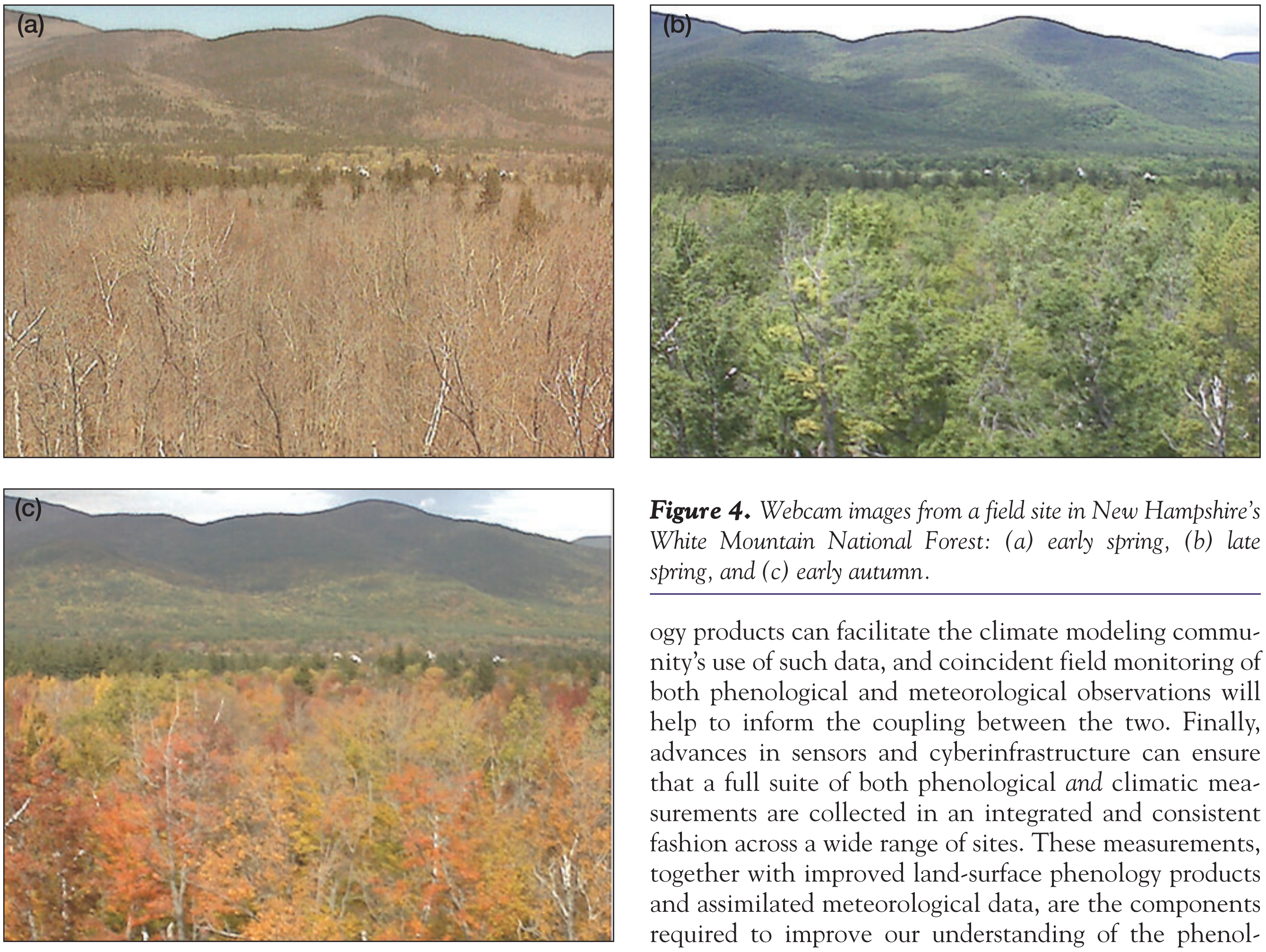

Figure 4. *Webcam images from a field site in New Hampshire's White Mountain National Forest: (a) early spring, (b) late spring, and (c) early autumn.*

terns, soil thermal properties, and levels of atmospheric CO_2 (eg 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 (eg Integrated Biosphere Simulator [IBIS], Simple Biosphere Model, version 2 [SiB2], Community Land Model [CLM]) are inadequate for resolving the complexities of surface–atmosphere exchanges associated with phenology. Currently, climate models either specify a predetermined phenological scheme or produce phenological parameters as output from the model. When predetermined, 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).

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, and coincident field monitoring of both phenological and meteorological observations will help to inform the coupling between the two. Finally, advances in sensors and cyberinfrastructure can ensure that a full suite of both phenological *and* climatic measurements are 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 components required to improve our understanding of the phenology–climate change connection and sensitivities at local to regional scales.

Land use and management

Many ecosystem processes from which we derive economic benefit depend on climate 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 important management implications for grazing, forestry and agriculture, pest management, disease vectors and allergens, energy consumption, water availability and conservation, and tourism and hunting, among others. In each of these disciplines, improved understanding and forecasting of phenologies may improve management techniques and, in some cases, reduce the risk of undesirable outcomes (eg disease outbreaks, crop failure, 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 (eg 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 area of active research in the future.

For land management, the principal challenge relates 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, because ecosystem processes interact, management of one domain will affect others, and understanding phenological response across taxa will be important.

New work on land-surface phenology (Fisher and Mustard 2007; MODIS nd) 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 to connect existing climate forecasts to phenological forecasts. By having predictions of both future climate and future phenology, land managers will have added insight into the ecosystem services relevant to them.

Conclusions

As long as there are living organisms on our planet, we can expect to see seasonal patterns in life-cycle events. The better we understand these cycles, the better we will understand the world around us, and this will help us to adapt to climate change and to 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. Cyberinfrastructure will enable these data to be synthesized and used 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 to make the most of the new information. The USA–NPN, having been established to help coordinate phenological research in the US, will promote such awareness (Betancourt *et al.* 2007). Given the advances and issues presented here, it is certainly a timely idea, currently blooming with possibilities.

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