

Phenology, Growth, and Allocation in Global Terrestrial Productivity

Robert B. Jackson, Martin J. Lechowicz, Xia Li,
and Harold A. Mooney

I. Introduction

A symposium held in Montpellier, France, in 1965 on the functioning of terrestrial ecosystems and the link to primary production (Eckardt, 1968) was an important milestone in our understanding of the controls and distribution of the Earth's primary productivity. At this symposium Professor M. Monsi presented his classic paper on mathematical models of plant communities (Monsi, 1968). This extraordinarily rich paper contained new and fundamental approaches to understanding the relationships between canopy distribution in time and space and stand productivity. Among the many issues discussed was the relationship between allocation and productivity. Monsi showed, for example, how production was dependent on the proportion of dry matter allocated to photosynthetic tissue, as well as the proportion of time this tissue was active on the plant (its phenology). Because of the analogy of "compound interest," the gain in dry matter is higher for photosynthetic tissue than for nonphotosynthetic tissue when there are no environmental limitations.

The ideas we discuss in this chapter on the importance of phenology, growth, and allocation for terrestrial primary productivity build on the foundation laid by Monsi (1968). The topic is far too broad to be reviewed comprehensively here; consequently, we provide background and examples for a subset of issues relevant to global change. We highlight trees and forest ecosystems because these systems contain the predominant fraction of global terrestrial carbon stores in plants. We end by highlighting several promising areas of research: (1) extension of the present theory of the timing of

allocation to include the phenology of belowground organs and reproduction, (2) techniques for improving estimates of belowground productivity and patterns of global allocation above- and belowground, and (3) the use of remote sensing combined with modeling for estimating global phenology and productivity.

II. Phenology

A. The History of Phenological Studies

Phenology is the study of the seasonal timing of biological events (Lieth, 1974, 1994), typically those that are readily observable such as the timing of bud burst in spring, the ripening of fruit, or the coloring of leaves in fall. Less observable but equally important is belowground phenology, including the seasonal timing of fine root growth. Intimate knowledge of phenology was essential in preindustrial societies because phenological events were used to decide when to plant crops or gather natural products. The aphorism that "seed should be sown when oak leaves are as big as a sow's ear" springs from folk knowledge accumulated over millennia, knowledge held by people throughout north temperate zones where oaks predominate. The species of oak change from place to place, but the wood anatomy that characterizes oaks ensures that in a local forest they will be among the last trees to produce leaves (Lechowicz, 1984, 1995). The leafing of oak is a reliable natural indicator that the danger of late frost is past, and it is not surprising that this phenological event became a benchmark in characterization of the seasons.

Beginning in about the seventeenth century, folk knowledge of phenological events began to be transformed by the ongoing scientific revolution in western societies. There was a great vogue for publishing "calendars of nature" (Stillingfleet, 1791; Aikin, 1799; Howitt, 1835), essentially collations of phenological sequences drawn from folk knowledge. These were superseded as formal records of the phenology of agricultural and natural systems began to be kept, sometimes at the behest of governments (Clarke, 1936) or as a pastime of the aristocracy (Jenyns, 1846; Molesworth, and Ormerod, 1880; Sparks and Carey, 1995). There is an extraordinary number of these historical records of phenology, although many are published obscurely if published at all (Balatova-Tulackova, 1970). These records, which are assuming greater importance as we struggle to assess the possible impacts of climate change on natural ecosystems, are beginning to be collected and made more available in electronic databases (Lieth, 1994; Lechowicz and Koike, 1995; see also links to the International Phenology Network, <http://mmf.math.rsu.ru/phenology/links.en.html>; contact, listserv@nic.surfnet.nl). In the past few decades (see Schnelle, 1955; Lieth, 1974, 1994),

phenology has also emerged as a scientific discipline dedicated to modeling and predicting the seasonal timing of biological events, not simply observing and recording them. It is this science that concerns us here, with an emphasis on woody species in natural ecosystems.

Most of the science has focused on the prediction of the seasonal timing of bud burst for leaves and flowers. The large part of the work is phenomenological and not well rooted in an understanding of the mechanisms underlying a phenological response. Emphasis is often on the prediction of the timing of an event in a given species using readily available data (daily temperature or hours of daylight). The most notable exception to this phenomenological approach is the detailed work on *Pinus sylvestris* by Sarvas (1974) and others who have studied the biochemistry and physiology of phenological responses such as dormancy and flowering (Luomajoki, 1986; Champagnat, 1989; Hänninen *et al.*, 1985; Cannell, 1990). Such detailed work is important for parameterizing future generations of phenological models.

B. Phenology and Phenomenological Models

Three elements are woven together in phenomenological models: a period of chilling in fall and winter, a period of warming in late winter and spring, and photoperiodic signals that may affect responses to temperature (Hunter and Lechowicz, 1992). Differences in the detail and form of the inputs define three types of phenomenological models: warming models, sequential models, and parallel models. The simplest and oldest phenological models use only the daily progression of temperature to predict the timing of events such as bud burst. An event is predicted to occur when a measure of cumulative warming (measured as degree-days) reaches a species- and event-specific threshold; tallying degree-days requires specifying a day of the year when the tally will begin and a base temperature above which temperature increments will be accumulated. Hence, despite the apparent simplicity of their dependence on only a single datum (daily mean temperature), these warming models in fact require the estimation of three parameters: a starting date, a base temperature, and a temperature sum.

A second class of phenomenological models, referred to as sequential (Hänninen, 1987), focuses on what sets the starting date when a plant begins to respond to and accumulate warming temperatures toward its threshold for a particular phenological event. Rather than assume a fixed starting date (e.g., January 1), these sequential models mandate that a chilling requirement be met before the plant responds to warming. By analogy to the accumulation of warmth in late winter and spring, the models tally chilling degree-days through the fall and winter. They also require specification of a day on which the chilling will begin to be tallied, but this is often readily tied to such recognizable events as leaf fall in deciduous species or the day of the first killing frost.

The third model class, parallel (Hänninen, 1987), is so named because these models allow an interaction between chilling and warming (usually more warming is required if less chilling has occurred). A variant in this class of models brings photoperiod into consideration, with the warming requirement reduced as photoperiod lengthens. The net effect of these parallel models is to reduce the likelihood that a period of warmth in midwinter, such as a February thaw, will trigger bud burst when the risk of a return to freezing conditions is still great.

With their focus on the timing of an event in relation to environmental conditions, present phenological models fail to account for the possible dependence of a phenological response on endogenous factors. We might expect coordination of different phenological responses in plants, not simply because they are responding to similar environmental cues but also because they depend on common internal resources. For example, both leafing and flowering of trees draw on stores of carbohydrates, proteins, and minerals (Kozłowski, 1992). There is of necessity some coordination in the timing of these demands on stored resources. Some species produce flowers and leaves simultaneously, whereas others separate these two competing resource demands to different parts of the season (Lechowicz, 1995). Similar differences arise in the timing of root and shoot growth; some species synchronize allocation to above- and belowground growth and others separate them (Lyr and Hoffmann, 1967; Riedacker, 1976; Harris *et al.*, 1995). In this view it is clear that phenology is really a question of the timing of allocation in plants, not simply the prediction of responses to exogenous environmental cues. Phenological responses to exogenous cues are likely to have evolved as a way to coordinate resource allocation for competing plant functions in a seasonal climate. Our understanding of the mechanisms underlying a phenological response cannot be sought solely in the biochemistry of chilling factors or phytochrome-mediated responses to photoperiodic cues. We also need to consider the costs imposed by a phenological event and the return in acquired resources that follows from alternative timing of the event—the legacy of Monsi's (1968) pioneering insight.

C. Toward a Theory of Functional Types in Phenology

Kikuzawa (1991, 1995; Kikuzawa *et al.*, 1996) developed a theory of phenology that begins to move beyond phenomenological models toward an analysis of the costs and benefits that accrue from alternative strategies of phenology and allocation. He focuses on the timing of allocation of resources to leaves, recognizing two alternative strategies in leaf phenology: one favored in high-light environments that are not limited by nutrient or water resources and the other in environments that are more resource limited. He shows that resource-rich environments favor a steady production of short-lived leaves through the growing season and their array in multilayer

canopies with vertically oriented shoots (Kikuzawa *et al.*, 1996). Resource-poor situations conversely favor the production of a single cohort of long-lived leaves each season and their array in a monolayer canopy with more horizontally oriented shoots. These analyses are an important first step toward a general theory that would place the many observations of phenological responses to exogenous factors (e.g., temperature, photoperiod) in the context of alternative plant production strategies. This is the fundamental context of phenology that Monsi (1968) recognized when he identified the consequences of the timing of allocation to different plant functions.

There are some important challenges to be met if we are to come to a comprehensive theory of phenology relevant both to functional ecology and to ecosystem ecology. From the viewpoint of functional ecology, we must extend the rudimentary theory to include allocation to belowground tissues and to reproduction. Kikuzawa's analysis (Kikuzawa, 1991, 1995) emphasizes light resources, which have different temporal patterns of availability compared to water and nutrient resources. Consequently the cost-benefit analysis of allocations to above- versus belowground organs involved in resource acquisition is likely to differ and lead to a greater diversity of phenological strategies at the whole-plant level. The same argument applies to reproduction, whereby the seasonality of pollinator availability and suitable conditions for seedling establishment will influence the timing of allocation to reproduction within and among years. If we secure a more comprehensive theory of the timing of allocation to different vegetative organs and to reproduction, we will also serve the needs of ecosystem ecologists interested in global change. For example, our relative ignorance of the contribution of belowground biomass to net primary productivity is a significant problem in the analysis of ecosystem responses to global change. If we have a sound theoretical basis to link the wealth of observational data on the timing of aboveground production to belowground production, then we can refine our estimates of seasonal production in diverse ecosystems.

D. Phenology and Climate Change

It is clear that the timing of phenological events can directly and significantly affect plant growth and reproduction. Tree breeders recognize that genotypes of deciduous trees with earlier leafing and/or later leaf senescence (longer periods of annual production) have higher rates of growth (e.g., Wang and Tigerstedt, 1993 for *Betula*; Farmer, 1996 for *Populus*). The loss of flowers in a late spring frost and the failure to mature fruit before an early fall frost are problems familiar to growers of fruit and nut trees (Alston and Tobutt, 1989; Germain, 1990).

As climate at a location changes, the timing of a particular phenological response may shift, as may the costs and benefits associated with the phe-

nological response. Photoperiodic cues on ecological time scales and in a specific location are stable, whereas temperature regimes are not. Consequently, trees under climate change could end up responding to environmental cues that are poorly synchronized with local seasonal cycles (i.e., climate change could decouple existing photoperiod/climate relationships). On the other hand, though the phenology of some trees is apparently influenced by photoperiod (Nizinski and Saugier, 1988; Heide, 1993), in general it appears that tree phenology responds predominantly to thermal cues rather than to photoperiodic ones (Hunter and Lechowicz, 1992; Kramer, 1995a).

There is a fairly large, but somewhat inconsistent, literature on the effects of phenology when trees are moved hundreds of kilometers within or close to the limits of their present geographic range. Most commonly, trees moved to higher latitudes respond with an earlier phenology than do the local stock—they leaf out and flower earlier (Kramer, 1995a; Deans and Harvey, 1995; Farmer, 1996). In general, displacements of a few hundred kilometers seem to be without penalty and often lead to growth advantages (Farmer, 1996), at least in fairly short provenance trials. In the longer term, climatic extremes that occur only very infrequently may pose problems for the displaced stock compared to the local provenance.

Excellent examples of the importance of phenology for ecosystem productivity come from recent eddy covariance and satellite studies in forests. Goulden *et al.* (1996) examined changes in productivity at the Harvard Forest in response to interannual climate variability. In 2 years of the study, leaves emerged 6–10 days earlier than in other years, leading to a cumulative increase in net ecosystem exchange of 20–40%. The timing of the end of the growing season was also important. Canopy senescence occurred 5–10 days later in 1992 and 1993 than in the other years of the study, increasing annual gross production by 50 g C m⁻² (Goulden *et al.*, 1996). Such a lengthening of the growing season may be likely during the next few centuries, with large potential consequences for ecosystem productivity. In fact, recent atmospheric and satellite analyses show up to a 12-day advancement in the initiation of CO₂ uptake from 45°N to 70°N latitudes in the past few decades (Keeling *et al.*, 1996; Myneni *et al.*, 1997).

Storage poses a significant complication in viewing phenology as an expression of the timing of allocation in that the production and utilization of stored resources are uncoupled. In general there is a regular annual cycle of movement of photosynthate into and out of storage pools. In both coniferous and hardwood trees, stored carbohydrate reserves are highest in winter, drop to a low midway through the growing season, and then gradually recover to winter levels (Wargo, 1971; Essiamah and Eschrich, 1985; Egger *et al.*, 1996; Hansen *et al.*, 1996). There can also be short-term cycling into and out of storage reserves within the growing season that is associated with

rhythmic shoot growth (Alaoui-Sosse *et al.*, 1994). In many trees there are also interannual cycles of storage buildup, transformation (e.g., the conversion of starch to soluble sugars in winter), and depletion associated with intervals between reproductive events (Silvertown, 1980; Monselise and Goldschmidt, 1982; Kozlowski, 1992).

Phenological studies traditionally emphasize the timing of leaf emergence in spring, but in fact this only marks the onset of the annual production cycle in deciduous trees. In temperate forests the timing of leaf-out typically spans 3–6 weeks (Lechowicz, 1984) and it is this “green wave” that most satellite indices track (Schwartz, 1994). To put this green wave in the context of seasonal patterns of actual production, it helps to consider the different ways that trees organize the actual timing of shoot extension growth through the warm season, a phenological character that applies equally to evergreen and deciduous species. There are fewer data of this sort available, but we can draw on a careful report by Anic (1964) to illustrate the diversity of shoot growth phenology among European forest trees. Between 1948 and 1960, Anic regularly observed thousands of trees growing in the vicinity of Zagreb and recorded their shoot extension every few days throughout the growing season. He monitored 9 gymnosperm and 30 angiosperm tree species that occurred naturally. The local forests, which are described by phytosociologists as a *Querceto roboris*–*Carpinetum betuli* type, occur on brown forest soils in a region with a continental climate showing strong seasonality. The mean annual temperature is 10.6°C with an annual mean maximum temperature of 34.9°C in summer and a minimum of –15.7°C in winter. Mean annual precipitation is 871 mm and is evenly distributed throughout the year. The forests are part of the Balkan refugium from which trees recolonized northern Europe after the Quaternary glaciations (Bennett *et al.*, 1991; Willis, 1994). Anic’s (1964) observations of the seasonality of shoot growth are therefore relevant to a broader geographic range in Europe than might initially be apparent.

The annual cycle of shoot growth of trees in this region may be characterized primarily by (1) the time at which the shoot growth begins and (2) how long it proceeds (Fig. 4-1). The onset of shoot growth spans about 4–5 weeks in spring, beginning in early April for some species but as late as early May for others. There is a much greater difference among species in their duration of shoot growth, which ranges from 44 to 127 days. Such interspecific variation in the duration of shoot growth is correlated with annual height growth (Fig. 4-1), which is a good indicator of tree productivity. These different seasonal patterns of shoot growth could indicate important differences among species in their responses to climate change. We might assume, for example, that the productivity of species with longer periods of shoot extension would be subject not only to adverse climatic events such as late spring frosts, but also summer droughts. With a few exceptions, however,

Forest saplings near Zagreb, 1948-1960

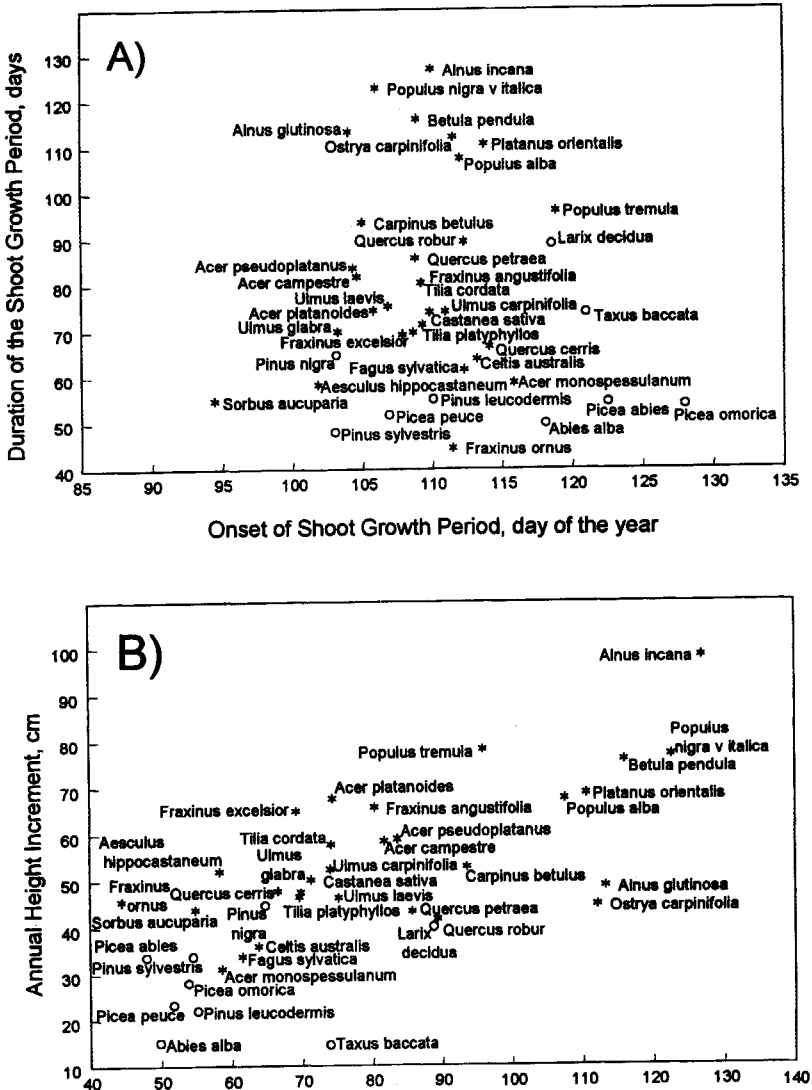


Figure 4-1 The seasonality of shoot growth in 30 angiosperm and 9 gymnosperm tree species growing near Zagreb in former Yugoslavia (data from Anic, 1964). (A) The relationship between the timing of the onset of shoot growth and its duration; (B) the correlation between annual height growth and the duration of shoot growth. Open symbols are needle leaf gymnosperms; asterisks are broadleaf angiosperms. The values are the means of observations made between 1948 and 1960.

that may be an unwarranted assumption because most species achieve the majority of their annual height increase in an initial flush of growth.

The diversity of phenological responses and associated variation in growth among this broad sample of European trees is an indication that the forests we have now are not necessarily the forests of the future. If climate change alters seasonality sufficiently, the competitive interactions among these species will likely shift and lead to forests of different composition and different predominant phenology. In the previous interglacial period *Picea omorica* was dominant throughout Europe, but in the current interglacial it is restricted to a small part of former Yugoslavia (Bennett *et al.*, 1991). This species has the latest onset and one of the shortest durations of shoot growth of any of the European forest trees (Fig. 4-1). *Picea abies*, the dominant European spruce today, is similar in phenology to *P. omorica*. At the ecosystem scale, should we take the shifting dominance in the European spruces as an indication that the part of the annual cycle in which the forest functions as a carbon sink might be altered under climate change? We do not know, but the possibility that forest composition may differ in a future climate, with effects on the seasonality of production, is an important unknown. This possibility also illustrates the potential longer term importance of biodiversity to ecosystem functioning: species that are a minor component of present systems may become more important under climate change, and their elimination now might limit ecosystem functioning in the future.

III. Growth and Allocation

A. Growth Models

Ecosystem productivity depends not only on the timing of allocation to different aspects of plant growth, but also the nature of the growth functions that determine future rates of production. A critical issue is balancing allocation to belowground tissues involved in soil resource uptake with allocation to shoots involved in the capture of carbon and energy. For forest trees, growth models fall into two broad categories, those emphasizing the development of tree form and those emphasizing the process of growth. Models of tree form define rules for branching architecture in considerable detail, but devote less attention to productivity processes that determine how much material is available for growth. Conversely, there are a number of detailed models of the physiological processes underlying growth that adopt simplified tree forms (e.g., root/stem/leaf without explicit architectural detail). Models such as LIGNUM (Pertunnen *et al.*, 1996) and AMAPpara (Forcaud *et al.*, 1998) set out to combine models of form and process to more realistically mimic tree growth.

This is not the place for a full review of whole-tree growth models, but it is useful to consider how the available models treat allocation processes. If we consider phenology as essentially the timing of resource allocation, then the way such models deal with allocation is important (Nikinmaa, 1992; Cannell and Dewar, 1994). Approaches to modeling the allocation of photosynthate to competing functions or structures in whole-plant growth models basically fall into two classes. One group uses the observed forms of trees to dictate allocational rules that lead to similar tree form; the other attempts to identify allocational rules with reference to actual physiological processes. In general, there are far too few data on the mechanisms governing the partitioning of biomass, and no compelling reason at this time to favor one modeling strategy over another.

The models that depend on observed form to guide allocation are easier to parameterize and were generally developed earlier. The simplest approach (partitioning rules) is to assign fixed partitioning coefficients that define the allocation of photosynthate. The effect of this fixed partitioning is a changing ratio in the accumulated investment in different structures and functions over time. A second approach (allometric rules) posits fixed ratios between certain structural parts of the plant, with photosynthate partitioned to maintain those ratios. A variant of this approach (functional rules) posits the maintenance of some functional balance in the plant that is maintained through appropriate allocation of photosynthate. The former variant emphasizes form, and the latter, function, but both act to keep a fixed set of proportions among plant parts and activities. All these approaches are essentially descriptive and do not allow much dynamic response to changing environmental conditions. The proportionate investments among competing structures are set by empirical measurements of existing plants rather than by general physiological processes.

Two other approaches to modeling allocation build on processes that might affect changes in allocation during plant development or across environments. The first of these (priority rules) assigns priorities to each structure or function through a series of equations describing allocation when photosynthate is insufficient to meet all demands. The steeper the allocation curve for a particular structure or function, the more likely that demand will be met even when photosynthate is in short supply. On the other hand, this approach allows some photosynthate to be allocated to most structures or functions in all but the most adverse situations. Competing demands are met in parallel, not sequentially. The other more mechanistic approach (transport rules) determines the resistances to movement of photosynthate between sources and sinks and assumes that these resistances determine partitioning to competing structures or functions. These two approaches are really variants on a common theme. Both try to define the ba-

sis for allocation by measurements of allocational process, rather than by simple measurements of the plant.

B. The Coupling of Root and Shoot Growth

Had we a more complete understanding of allocation, we would be better able to predict the general patterns of coordination between root and shoot growth. Despite the difficulties of studying belowground systems, the importance of root phenology and its coupling to shoot phenology have been recognized for centuries (see Lyr and Hoffmann, 1967). Belowground phenology is less likely to be useful as an indicator of global change than aboveground phenology because monitoring roots is more difficult and because there are fewer discrete events in root systems, such as flowering. But there can be no doubt that the effects of global change on belowground phenology and allocation will have important consequences for global productivity. Global warming may extend the length of the belowground growing season, and phenological differences among species may lead to important changes in species composition in response to global change.

The initiation of root growth in the spring generally occurs before the initiation of shoot growth, a fact observed by Theophrastus more than 2000 years ago (Lyr and Hoffmann, 1967). Roots of *Acer saccharinum* resume growth at a cooler temperature than do shoots (5° and 10°C, respectively), but root and shoot growth are not independent; an auxin signal from shoot buds of *Acer* appears necessary for the initiation of spring root growth (Richardson, 1958). In addition to beginning earlier, root growth also tends to extend longer into the fall and winter than does shoot growth, even after leaf abscission in deciduous forests (Hendrick and Pregitzer, 1996). In general, root growth slows or ceases during winter, but it may continue at soil temperatures very near freezing (Bhar *et al.*, 1970). It may also continue in deep soil layers when roots of the same individual plant are in frozen soil layers near the surface (Fernandez and Caldwell, 1975). Soil warming can extend the active period of root growth (Lyr and Hoffmann, 1967) and roots have been shown to grow 2–4 months longer in unfrozen soil covered in snow than in frozen soil (Kolesnikov, 1971). Clearly global warming has the potential to alter belowground productivity through an extended growing season.

In addition to generalizations about the initiation and timing of root and shoot growth, there are strong species effects on the coupling of above- and belowground phenology. The timing of root and shoot growth in seedlings of *Robinia pseudoacacia* was relatively synchronous, whereas that of *Pinus sylvestris* was almost completely segregated (Lyr and Hoffmann, 1967). Other trees studied in the experiment showed intermediate coupling. For cold-desert shrubs in the field, more than half of all root growth of *Artemisia tri-*

dentata occurred before any shoot growth was visible, and root growth was minimal during fruit development (Fernandez and Caldwell, 1975). For the co-occurring shrub *Atriplex confertifolia*, there was much greater overlap in the timing of root and shoot growth and almost all root growth in deeper layers occurred during fruit development. Although such phenological differences are important for niche partitioning, it not clear to what degree such differences are genetic compared to environmental. The greater the role of genetics in controlling phenology, the greater the potential for large changes in community composition with global warming and other aspects of environmental change.

IV. Future Directions

Estimating patterns of global phenology and productivity have been priorities since the efforts of the International Biological Programme. Refining current estimates is especially important for identifying the missing carbon sink and for establishing an accurate baseline for measuring the effects of global change. Two areas of pressing importance are (1) the use of remote sensing coupled with global models to refine estimates of phenology and aboveground net primary production (NPP), and (2) improving estimates of carbon turnover in roots and the soil.

A. Remote Sensing and Modeling of Global Phenology and Productivity

Remote sensing provides a powerful new tool for addressing patterns of global phenology, particularly when combined with global models. Satellite data from the Advanced Very High Resolution Radiometer (AVHRR) and normalized difference vegetation indices (NDVIs) have been used successfully to examine regional and global vegetation types and phenology for more than a decade (Tucker, 1986; Townshend and Justice, 1986; Moulin *et al.*, 1997). NDVIs are based on the normalized ratio of the visible and near-infrared (IR) spectral bands, because photosynthesizing vegetation reflects proportionally more radiation in the near-IR range than at visible wavelengths. Higher NDVI values indicate greater photosynthetically active leaf area (Hobbs, 1990). A framework for using the seasonality of NDVI to estimate phenology and productivity was developed by Running *et al.* (1995) (Fig. 4-2). These satellite data essentially integrate the tree-to-tree and place-to-place variation in observational records of phenological events.

Although satellite data can be used successfully for determining regional phenology, they are more useful in regions with pronounced phenological changes (e.g., temperate deciduous forests) than in regions without (e.g., tropical evergreen forest). Li *et al.* (unpublished observations) investigated

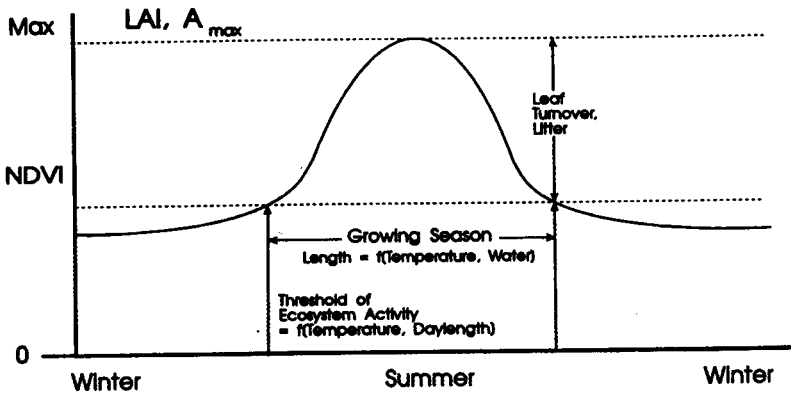


Figure 4-2 NDVI seasonality analysis. The potential use of satellite-derived NDVI data for determining phenology and primary productivity. The idealized curve shows how the amount of productivity (ΔNDVI), the length of the growing season, and the timing of leaf onset and offset are all potentially available from satellite data (from Running *et al.*, 1995). LAI, Leaf area index.

the use of changes in the NDVI [$\Delta\text{NDVI} = \text{NDVI}(t - 1) - \text{NDVI}(t)$, where t is a monthly time period] as an indicator or correlate of litterfall. They found that the metric worked well for systems with clear on/off leaf cycles (Fig. 4-3), but was not universally good at predicting litterfall (Fig. 4-4). The NDVI typically has a relatively poor temporal resolution for most grasslands and evergreen systems (though the relationship for the Spanish coniferous forest in Fig. 4-4 is relatively good, analyses for three other coniferous forests showed poor correlations).

White *et al.* (1997) developed a method of using satellite data to determine phenological development at the continental scale. The raw NDVI is used as an input to create a smoothed index that defines the beginning and end of the green period (Fig. 4-5). Based on this method they mapped the onset and offset of greenness for the vegetation of the United States (excluding shrubland and evergreen forests). From their analyses they noted that during a 3-year period from 1990 to 1992 the continentally averaged length of the growing season varied by 17 days, an amount that could have a large effect on regional productivity.

Remotely sensed data are especially useful for clarifying global patterns of phenology and productivity when combined with ecosystem and global modeling (Running, 1990). Phenology is becoming increasingly integrated into such models. Jorg and Heimann (1996) were among the first to address the role of phenology in regulating vegetative growth in a global ecosystem model. Their model simulated two phenological sequences, bud burst and

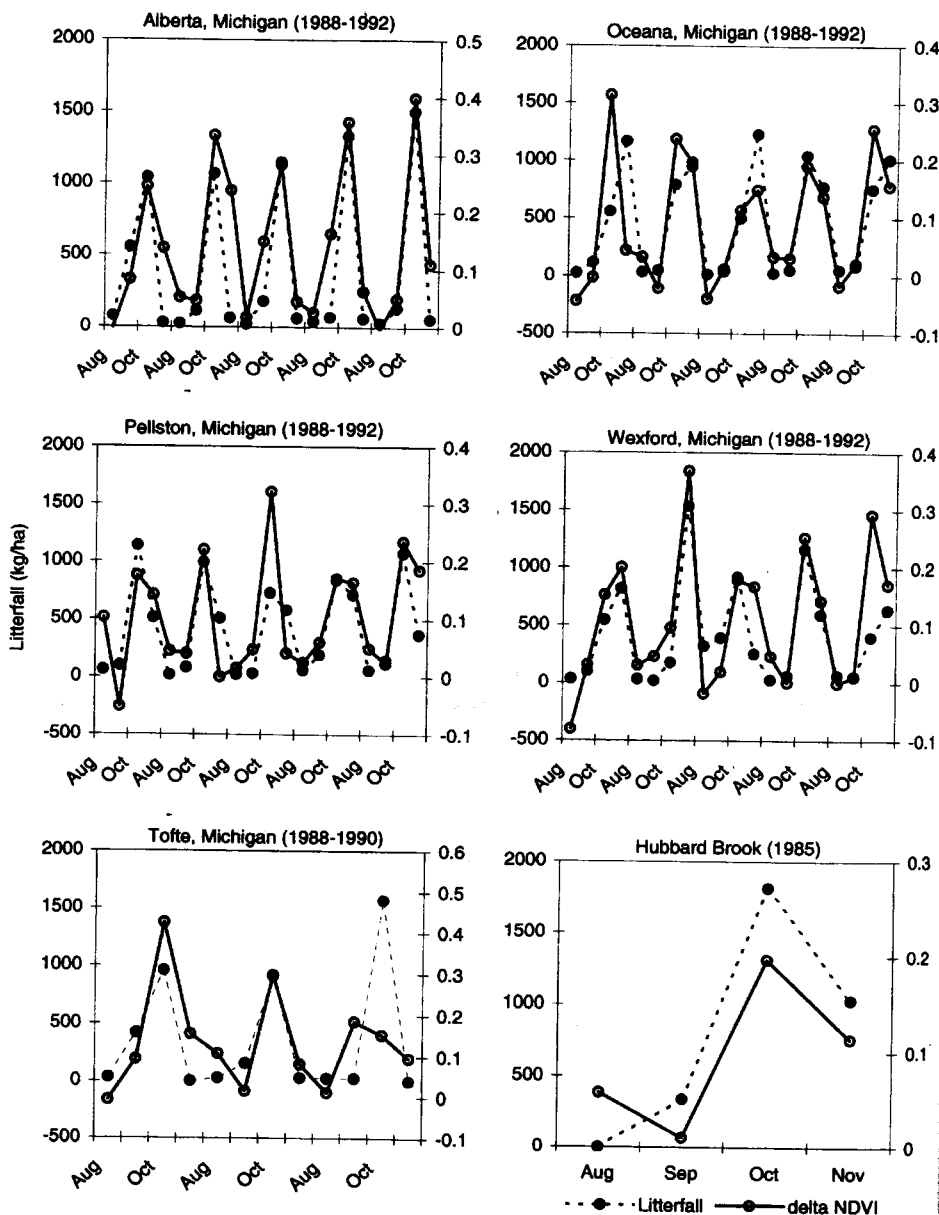


Figure 4-3 Correlations between Δ NDVI and litterfall for six deciduous forests sites (Li et al., unpublished data). ●—●, litterfall; ○—○, Δ NDVI. Δ NDVI = NDVI($t-1$) - NDVI(t), where t is a monthly time period. Each year has four measurement dates of NDVI (Aug 15, Sept 15, Oct 15, and Nov 15) and the Δ NDVI value for each August measurement is approximately zero.

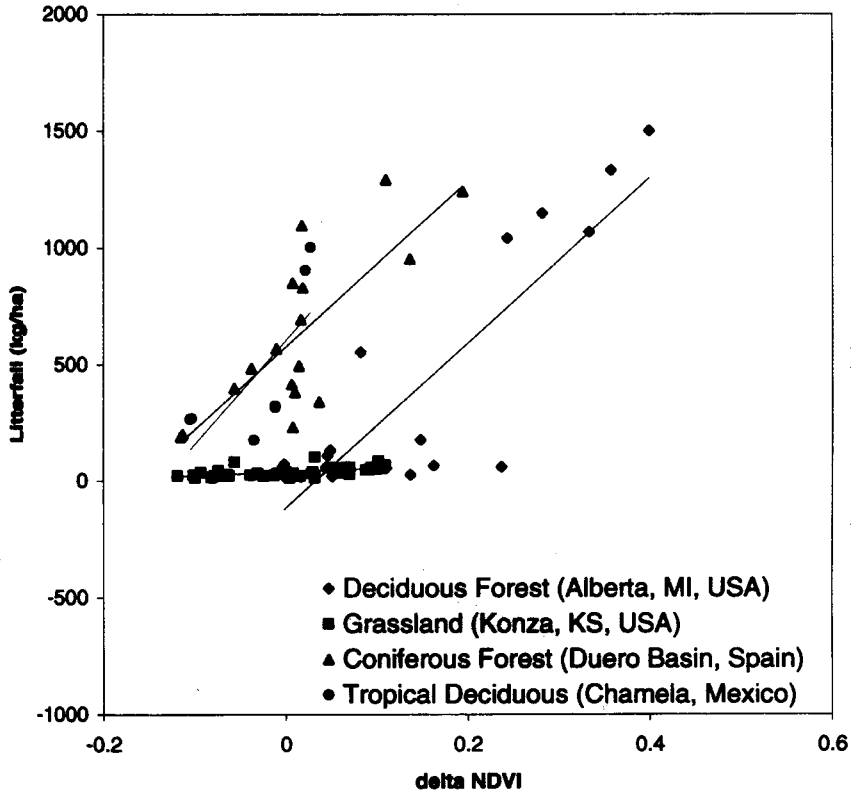


Figure 4-4 Relationships between litterfall and ΔNDVI for a hardwood forest and a temperate grassland in the United States, a coniferous forest in Spain, and a tropical deciduous forest in Mexico (Li *et al.*, unpublished data). $\Delta\text{NDVI} = \text{NDVI}(t-1) - \text{NDVI}(t)$, where t is a monthly time period.

leaf fall, based on a set of climate-dependent, biome-specific rules. Bud burst was predicted after the growing-degree-day requirements were satisfied. Litterfall was predicted based on the temperature below 5°C (for temperate deciduous ecosystems), the ratio of actual to potential evapotranspiration for tropical deciduous ecosystems, or a constant litterfall production for evergreen ecosystems. Because of almost universal limitations in knowledge of the timing of belowground allocation, their analysis did not explicitly consider root turnover or biomass; this limited the success of the model in systems with relatively large belowground allocation, such as grasslands (Jorg and Heimann, 1996). Burton and Cumming (1995) simulated plant response to global change using a forest patch model that integrates species-specific phenology and site-specific frost events. The simulations showed

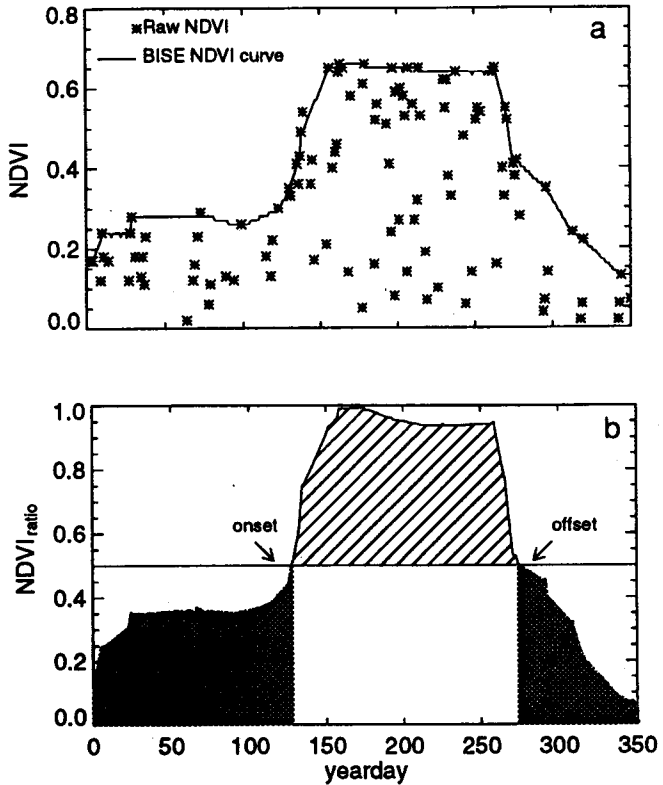


Figure 4-5 Daily AVHRR observations of a 1-km² pixel in a deciduous, broadleaf forest in the northeast United States (a) and 400 NDVI curves for the same site averaged and transformed to generate the best fit to the NDVI data (b). (a) The solid line represents the Best Index Slope Extraction (BISE) of the phenological time course. (b) The striped area corresponds to the growing season, the dark area corresponds to the nongrowing season, and the points where the curve crosses NDVI = 0.5 represent leaf onset and offset (from White *et al.*, 1997).

major shifts in equilibrium forest composition and productivity. Kramer (1995b, 1996) carried out a comprehensive analysis of the potential impact of altered phenology on the productivity of European trees under climate change. He compared estimates from a number of different models of tree growth and forest productivity involving contrasting assumptions about allocation and controls on net primary productivity. Phenological effects were important in all instances, about the same order of magnitude as changes in other key parameters influencing net production. By using remote-sensing data to establish regional estimates of production and litterfall, and to

parameterize global models, significant progress should be forthcoming for global estimates of aboveground phenology and productivity. The challenge is to generate climate-driven phenological models that are applicable at the global scale.

B. Belowground Productivity and Its Distribution in the Soil

A second area where progress is needed is in refining estimates of belowground productivity and allocation to above- and belowground structures (Casper and Jackson, 1997; Jackson, 1998). Despite the difficulty in estimating belowground production, several relatively new techniques offer promise for improving our understanding of belowground phenology and production. Minirhizotrons have made the *in situ* study of root growth and demography feasible for field studies, highlighting the role of fine roots in ecosystem functioning (Taylor, 1987; Hendrick and Pregitzer, 1993). Although the technique is not new, the use of increasingly small rhizotron tubes, the ability to place these tubes in almost any field setting, and improvements in video technology have made the technique more widespread and much more fruitful. A second promising approach is the use of stable isotopes (e.g., ^{13}C , ^2H , and ^{18}O) for partitioning ecosystem carbon fluxes. In the next decade great strides will likely be made in using these isotopes to separate root respiration from microbial decomposition, to partition soil fluxes from canopy fluxes, and to estimate the coupling of CO_2 and H_2O fluxes in plant canopies (Broadmeadow and Griffiths, 1993).

A database of climate, soil, and root attributes was constructed to examine patterns of root biomass, length, and surface area with depth in the soil and their relationship to environmental variables globally (Jackson *et al.*, 1996, 1997; Canadell *et al.*, 1996). Based on results from hundreds of field studies, the data were used to examine patterns of global root biomass and annual belowground NPP. Total root biomass is approximately 290×10^{15} g globally (or approximately 140×10^{15} g C) (Table 4-1). Global fine root biomass is approximately 80×10^{15} g, equivalent in size to 5% of the atmospheric carbon pool, and the live fine root fraction is approximately half the total fine root pool (Table 4-1). If one assumes that fine roots turn over on average once a year, then 20×10^{15} g C of net primary production cycles through fine roots annually, one-third of total net primary production for plants globally (Jackson *et al.*, 1997).

Such an analysis necessarily glosses over many important phenomena, particularly spatial and temporal variation in ecosystems. Temporal variation is in part a synonym for phenology, and, as discussed above, such phenological data are especially lacking for root systems. Minirhizotrons, stable isotopes, and other techniques should go a long way to filling in such gaps and improving global estimates of belowground primary productivity.

Table 4-1 Global Classification Scheme^a

Biome	Land area (10 ⁶ km ²)	Total root biomass (10 ⁹ Mg)	Total fine root biomass (10 ⁹ Mg)	Live fine root biomass (10 ⁹ Mg)
Tropical rainforest	17.0	83	9.7	5.7
Tropical seasonal forest	7.5	31	4.3	2.1
Temperate evergreen forest	5.0	22	4.1	2.5
Temperate deciduous forest	7.0	29	5.6	3.1
Boreal forest	12.0	35	7.2	2.8
Woodland and Shrubland	8.5	41	4.4	2.4
Savanna	15.0	21	14.9	7.7
Temperate grassland	9.0	14	13.6	8.5
Tundra/alpine	8.0	10	7.7	2.7
Desert	18.0	6.6	4.9	2.3
Cultivated	14.0	2.1	2.1	1.1
Totals	121	292	78.2	40.8

^aScheme of Whittaker (1975); estimates are based on data in Jackson *et al.* (1996, 1997).

V. Summary and Conclusions

We have emphasized that phenology is best viewed as the timing of resource allocation to different plant functions (above- and belowground growth, reproduction, etc.) that in turn set the long-term trajectory of plant growth and productivity. Various models of phenology, allocation, and growth are available, but there is as yet no comprehensive theory to integrate such models. Our empirical and theoretical analysis of belowground growth is especially deficient given the importance of belowground biomass and turnover for primary production. Both the literature on tree breeding and ecosystem models incorporating measures of aboveground phenological events show that the phenology of vegetation is important to ecosystem net primary production. In addition, satellite data using the greening of the landscape as an indication of production are increasingly important in global models of the carbon cycle. It would be especially useful if we could relate these remotely sensed data of aboveground events to seasonal patterns of belowground production. Our ability to use such global satellite data and to adjust the regional signals for vegetation heterogeneity should advance our understanding of the roles of phenology, growth, and allocation in global plant productivity.

Acknowledgments

This research was supported by grants from the National Science Foundation (DEB 97-33333), NIGEC/DOE (Tul-038/95-98), and the Andrew W. Mellon Foundation to RBJ; the Natural Sciences and Engineering Research Council of Canada to MJL; and NASA-EOS (NAS 5-31726) to HAM. We thank T. Hinckley, W. Hoffmann, and S. Thomas for helpful comments on the manuscript.

References

- Aikin, A. (1799). "The Natural History of the Year," 2nd Ed. J. Johnson, London.
- Alaoui-Sosse, B., Parmentier, C., Dizengremel, P., and Barnola, P. (1994). Rhythmic growth and carbon allocation in *Quercus robur*: 1. Starch and sucrose. *Plant Physiol. Biochem.* **32**, 331-339.
- Alston, F. H., and Tobutt, K. R. (1989). Breeding and selection for reliable cropping in apples and pears. In "Proceedings of the 47th University of Nottingham Easter School in Agricultural Science," pp. 329-339. Sutton Bonington, England.
- Anic, M. (1964). Il dinamismo di crescita longitudinale di alcune specie arboree durante il periodo vegetativo. *Annal. Accad. Ital. Sci. Forestal.* **30**, 317-354.
- Balatova-Tulackova, E. (1970). Bibliographie der phanosppektrum—Diagramme von pflanzen-gesellschaften. *Excerpt. Botan. Sec. B Bd.* **10** 243-257.
- Bennett, K. D., Tzedakis, P. C., and Willis, K. J. (1991). Quaternary refugia of north European trees. *J. Biogeogr.* **18**, 103-115.
- Bhar, D. S., Mason, G. F., and Hilton, R. J. (1970). *In situ* observations of plum root growth. *J. Am. Soc. Hort. Sci.* **95**, 237-239.
- Broadmeadow, M. S. J., and Griffiths, H. (1993). Carbon isotope discrimination and the coupling of CO₂ fluxes within forest canopies. In "Stable Isotopes and Plant Carbon-Water Relations" (J. R. Ehleringer, A. E. Hall, and G. D. Farquhar, eds.), pp. 102-129. Academic Press, San Diego.
- Burton, P. J., and Cumming, S. G. (1995). Potential effects of climate change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. *Water Air Soil Pollut.* **84**, 401-414.
- Cannell, M. G. R. (1990). Modelling the phenology of trees. *Silva Carelica.* **15**, 11-27.
- Cannell, M. G. R., and Dewar, R. C. (1994). Carbon allocation in trees: A review of concepts for modelling. *Adv. Ecol. Res.* **25**, 59-104.
- Canadell, J., Jackson, R. B., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E.-D. (1996). Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**, 583-595.
- Casper, B. B., and Jackson, R. B. (1997). Plant competition underground. *Annual Review of Ecol. Systemat.* **28**, 545-570.
- Champagnat, P. (1989). Rest and activity in vegetative buds of trees. *Ann. Sci. For.* **46** (suppl.) 9s-26s.
- Clarke, J. E. (1936). The history of British phenology. *Q. J. Roy. Meteorol. Soc.* **62**, 19-23.
- Deans, J. D., and Harvey, F. J. (1995). Phenologies of sixteen European provenances of sessile oak growing in Scotland. *Forestry* **68**, 265-273.
- Eckardt, F. E. (ed.) (1968). "Functioning of Terrestrial Ecosystems at the Primary Production Level." UNESCO, Paris.
- Egger, B., Einig, W., Schlereth, A., Wallenda, T., Magel, E., Loewe, A., and Hampp, R. (1996). Carbohydrate metabolism in one- and two-year old spruce needles, and stem carbohydrates from three months before to three months after bud break. *Physiol. Planta.* **96**, 91-100.

- Essiamah, S., and Eschrich, W. (1985). Changes of starch content in the storage tissues of deciduous trees during winter and spring. *Int. Assoc. Wood Ana. Bull.* **6**, 97–106.
- Farmer, R. E., Jr. (1996). The geneecology of *Populus*. In "Biology of *Populus* and its Implications for Management and Conservation" (R. F. Stettler, H. D. Bradshaw, Jr., P. E. Heilman, and T. M. Hinckley, eds.), pp. 33–55.
- Fernandez, O. A., and Caldwell, M. M. (1975). Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *J. Ecol.* **63**, 703–714.
- Forcaud, T., Blaise, F., Bartholemy, D., Houllier, F., and deReffye, P. (1998). A physiological approach to tree growth modelling in the software AMAPpara. In "Connection Between Silviculture and Wood Quality through Modelling." Proc. IUFRO Workshop, Kruger National Park, South Africa. In press.
- Germain, E. (1990). Inheritance of late leafing and lateral bud fruitfulness in walnut (*Juglans regia* L.), phenotypic correlations among some traits of the trees. *Acta Hort.* **284**, 125–135.
- Goulden, M. L., Munger, J. W., Fan, S.-M., Daube, B. C., and Wofsy, S. C. (1996). Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science* **271**, 1576–1578.
- Hänninen, H. (1987). Effects of temperature on dormancy release in woody plants: Implications of prevailing models. *Silva Fenn.* **21**, 279–299.
- Hänninen, H., Kanninen, M., and Smolander, H. (1985). The annual cycle of forest trees: The Sarvas approach revisited. In "Crop Physiology of Forest Trees" (P. M. A. Tigerstedt, P. Puttonen, and V. Koski, eds.). Helsinki University Press, Helsinki.
- Hansen, J., Vogg, G., and Beck, E. (1996). Assimilation, allocation and utilization of carbon by 3-year-old Scots pine (*Pinus sylvestris* L.) trees during winter and early spring. *Trees* **11**, 83–90.
- Harris, J. R., Bassuk, N. L., Zobel, R. W., and Whitlow, T. H. (1995). Root and shoot growth periodicity of green ash, scarlet oak, turkish hazelnut, and tree lilac. *J. Am. Soc. Hort. Sci.* **120**, 211–216.
- Heide, O. M. (1993). Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiol. Planta.* **88**, 531–540.
- Hendrick, R. L., and Pregitzer, K. S. (1993). Patterns of fine root mortality in two sugar maple forests. *Nature (London)* **361**, 59–61.
- Hendrick, R. L., and Pregitzer, K. S. (1996). Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *J. Ecol.* **84**, 167–176.
- Hobbs, R. J. (1990). Remote sensing of spatial and temporal dynamics of vegetation. In "Remote Sensing of Biosphere Functioning" (R. J. Hobbs, and H. A. Mooney, eds.), pp. 203–219. Springer Verlag, New York.
- Howitt, William (1835). "The Book of the Seasons, or The Calendar of Nature," 3rd Ed. Bentley, London.
- Hunter, A. F., and Lechowicz, M. J. (1992). Predicting the timing of budburst in temperate trees. *J. Appl. Ecol.* **29**, 597–604.
- Jackson, R. B. (1999) The importance of root distributions for hydrology, biogeochemistry, and ecosystem functioning. In "Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes" (J. Tenhunen and P. Kabat, eds., Dahlem Conf.), pp. 219–240. John Wiley and Sons, Chichester.
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E.-D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**, 389–411.
- Jackson, R. B., Mooney, H. A., and Schulze, E.-D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci. U.S.A.* **94**, 7362–7366.
- Jenyns, L. (1846). "Observations in Natural History." John van Voorst, London.
- Jorg, K., and Heimann, M. (1996). A prognostic phenology scheme for global terrestrial carbon cycle models. *Climate Res.* **6**, 1–19.

- Keeling, C. D., Chin, J. F. S., and Whorf, T. P. (1996). Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature (London)* **382**, 146–149.
- Kikuzawa, K. (1991). A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *Am. Naturalist* **138**, 1250–1263.
- Kikuzawa, K. (1995). Leaf phenology as an optimal strategy for carbon gain in plants. *Can. J. Bot.* **73**, 158–163.
- Kikuzawa, K., Koyama, H., Umeki, K., and Lechowicz, M. J. (1996). Some evidence for an adaptive linkage between leaf phenology and shoot architecture in sapling trees. *Funct. Ecol.* **10**, 252–257.
- Kolesnikov, V. (1971). "The Root System of Fruit Plants." Izdatelstvo Mir, Moscow.
- Kozlowski, T. T. (1992). Carbohydrate sources and sinks in woody plants. *Bot. Rev.* **58**, 107–222.
- Kramer, K. (1995a). Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. *Plant Cell Environ.* **18**, 93–104.
- Kramer, K. (1995b). Modelling comparison to evaluate the importance of phenology for the effects of climate change on growth of temperate-zone deciduous trees. *Climate Res.* **5**, 119–130.
- Kramer, K. (1996). Phenology and growth of European trees in relation to climate change. Thesis, Landbouw Universiteit, Wageningen. CIP-Data Koninklijke Bibliotheek, Den Haag, Netherlands.
- Lechowicz, M. J. (1984). Why do temperate deciduous trees leaf out at different times? Adaptation and the ecology of forest communities. *Am. Natural.* **124**, 821–842.
- Lechowicz, M. J. (1995). Seasonality of flowering and fruiting in temperate forest trees. *Can. J. Bot.* **73**, 175–182.
- Lechowicz, M. J., and Koike, T. (1995). Phenology and seasonality of woody plants: An unappreciated element in global change research? *Can. J. Bot.* **73**, 147–148.
- Lieth, H., ed. (1974). "Phenology and Seasonality Modelling." Springer-Verlag, New York.
- Lieth, H. (1994). Aims and methods in phenological modelling. *G. Bot. Ital.* **128**, 151–182.
- Luomajoki, A. (1986). Timing of microsporogenesis in trees with a reference to climatic adaptation: A review. *Acta For. Fenn.* **196**, 1–33.
- Lyr, H., and Hoffmann, G. (1967). Growth rates and growth periodicity of tree roots. *Int. Rev. For. Res.* **2**, 181–235.
- Molesworth, C., and Ormerod, E. A. (1880). "Cobham Journals: Abstracts and Summaries of Meteorological and Phenological Observations in 1825 to 1850." E. Stanford, London.
- Monselie, S. P., and Goldschmidt, E. E. (1982). Alternate bearing in fruit trees. *Hort. Rev.* **4**, 128–173.
- Monsi, M. (1968). Mathematical models of plant communities. In "Functioning of Terrestrial Ecosystems at the Primary Production Level" (F. Eckardt, ed.), pp. 131–149. UNESCO, Paris.
- Moulin, S., Kergoat, L., Viovy, N., and Dedieu, G. (1997). Global scale assessment of vegetation phenology using NOAA/AVHRR satellite measurements. *J. Climate* **10**, 1154–1170.
- Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., and Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature (London)* **386**, 698–702.
- Nikinmaa, E. (1992). The allocation of carbohydrates. In "Simulation of Forest Development" (H. Salminen and T. Katerman, eds.), pp. 21–34. Finnish Forestry Research Institute Paper 407, Helsinki.
- Nizinski, J. J., and Saugier, B. (1988). A model of leaf budding and development for a mature *Quercus* forest. *J. Appl. Ecol.* **25**, 643–652.
- Perttunen, J., Sievanen, R., Nikinmaa, E., Saarenmaa, H., and Vakeva, J. (1996). LIGNUM: A tree model based on simple structural units. *Ann. Bot.* **77**, 87–98.
- Richardson, S. D. (1958). Bud dormancy and root development in *Acer saccharinum*. In "The Physiology of Forest Trees" (K. V. Thimann, ed.), pp. 409–425. Ronald Press, New York.

- Riedacker, A. (1976). Growth and regeneration rhythms of ligneous species. *Ann. Sci. For. (Paris)* **33**, 109–138.
- Running, S. W. (1990). Estimating terrestrial primary productivity by combining remote sensing and ecosystem simulation. In "Remote Sensing of Biosphere Functioning" (R. J. Hobbs and H. A. Mooney, eds.), pp. 65–86. Springer Verlag, New York.
- Running, S. W., Loveland, T. R., Pierce, L. L., Nemani, R. R., and Hunt, E. R., Jr. (1995). A remote sensing based vegetation classification logic for global land cover analysis. *Remote Sens. Environ.* **51**, 39–48.
- Sarvas, R. (1974). Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Comm. Instit. Forestal. Fenn.* **84**.
- Schnelle, F. S. (1955). "Probleme der Bioklimatologie. Band 3. Pflanzen-Phanologie." Akademische Verlagsgesellschaft Geest und Portig K-G, Leipzig.
- Schwartz, M. D. (1994). Monitoring global change with phenology: The case of the spring green wave. *Int. J. Biometeorol.* **38**, 18–22.
- Silvertown, J. W. (1980). The evolutionary ecology of mast seeding in trees. *Biol. J. Linn. Soc.* **14**, 235–250.
- Sparks, T. H., and Carey, P. D. (1995). The response of species to climate over two centuries: An analysis of the Marsham phenological record, 1736–1947. *J. Ecol.* **83**, 321–329.
- Stillingfleet, B. (1791). The calendar of flora, Swedish and English. In "Miscellaneous Tracts Relating to Natural History, Husbandry, and Physick," pp. 223–337. J. Dodsley, London.
- Taylor, H. M. (1987). "Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics." American Society of Agronomy, Madison, Wisconsin.
- Townshend, J. R. G., and Justice, C. O. (1986). Analysis of the dynamics of African vegetation using the normalized difference vegetation index. *Int. J. Remote Sens.* **7**, 1435–1445.
- Tucker, C. J. (1986). Maximum normalized difference vegetation index images for sub-Saharan Africa for 1983–1985. *Int. J. Remote Sens.* **7**, 1383–1384.
- Wang, T., and Tigerstedt, P. M. A. (1993). Variation of growth rhythm among families and correlation between growth rhythm and growth rate in *Betula pendula* Roth. *Scand. J. For. Res.* **8**, 489–497.
- Wargo, P. M. (1971). Seasonal changes in carbohydrate levels in roots of sugar maple. USDA Forest Service Research Paper NE-213, Northeastern Forest Experiment Station.
- White, M. E., Thornton, P. E., and Running, S. W. (1997). A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochem. Cycles* **11**, 217–234.
- Whittaker, R. H. (1975). "Communities and Ecosystems." Macmillan, London.
- Willis, K. J. (1994). The vegetational history of the Balkans. *Q. Sci. Rev.* **13**, 769–788.