

Research review

Responses of spring phenology to climate change

Author for correspondence:
Franz-W. Badeck
Tel: +49 331 2882675
Fax: +49 331 2882695
Email: badeck@pik-potsdam.de

Franz-W. Badeck, Alberte Bondeau, Kristin Böttcher, Daniel Doktor,
Wolfgang Lucht, Jörg Schaber and Stephen Sitch
Potsdam Institute for Climate Impact Research (PIK), Pf 60 12 03, 14412 Potsdam, Germany

Received: 23 September 2003
Accepted: 20 January 2004

doi: 10.1111/j.1469-8137.2004.01059.x

Summary

Climate change effects on seasonal activity in terrestrial ecosystems are significant and well documented, especially in the middle and higher latitudes. Temperature is a main driver of many plant developmental processes, and in many cases higher temperatures have been shown to speed up plant development and lead to earlier switching to the next ontogenetic stage. Qualitatively consistent advancement of vegetation activity in spring has been documented using three independent methods, based on ground observations, remote sensing, and analysis of the atmospheric CO₂ signal. However, estimates of the trends for advancement obtained using the same method differ substantially. We propose that a high fraction of this uncertainty is related to the time frame analysed and changes in trends at decadal time scales. Furthermore, the correlation between estimates of the initiation of spring activity derived from ground observations and remote sensing at interannual time scales is often weak. We propose that this is caused by qualitative differences in the traits observed using the two methods, as well as the mixture of different ecosystems and species within the satellite scenes.

© *New Phytologist* (2004) **162**: 295–309

Introduction

Phenology is the science of recurring events in nature. A working group of the International Biological Program proposed the definition: 'Phenology is the study of the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species' (Lieth, 1974). The name of the science has generally also been used to address the object – the term 'phenology' is applied to the annual course of developmental events. It is applied in biological and geosciences (e.g. phenology of glaciers, lake ice). In the biological

sciences, the core of phenological research addresses the timing of switches between recurrent developmental or behavioural phases of organisms. However, some researchers stretch the term to cover continuous changes in traits, e.g. growth of organs (termed phenometry by Schnelle, 1955). Used as an analogy, continuous changes in the reflectance of vegetative covers are often addressed as phenological changes in the field of remote sensing.

Based on its well known variation with the annual course of weather elements, plant phenology might be expected to be one of the most responsive and easily observable traits in nature that change in response to climate. Trends in the

timing of plant developmental phases that are brought about by the current anthropogenic global climate change can have major impacts on plant productivity, competition between plant species, and interactions with heterotrophic organisms. In addition to direct effects in the biosphere, these impacts can have consequences for goods and services extracted from ecosystems for human use. Production of food, fibre and extractable chemical substances are affected, with nonnegligible effects on the economic value of agricultural and forestry products. Shifts in phenology are relevant for nature conservation planning and the seasonal suitability of landscapes for recreational activities. It has been shown that phenology plays a crucial role in the carbon balance of terrestrial ecosystems (Keeling *et al.*, 1996); in determining shifts in agricultural zoning (Fischer *et al.*, 2002); in vegetation feedback onto the atmospheric boundary layer (Schwartz & Crawford, 2001); in plant competition (Rathcke & Lacey, 1985); in pest and disease control (Penfound *et al.*, 1945); and in pollen flight forecasts (Traidl-Hoffmann *et al.*, 2003).

If the pivotal role of plant phenology as a response factor to climate change is to be proven, quantification of the effects mentioned so far and attribution of changes in phenology to climatic change are required. The close link between the seasonal course of temperature and water availability on the one hand, and the timing of phenological phases on the other, engenders good qualitative arguments in favour of a climate-change effect on phenology, as well as difficulties in obtaining statistically significant evidence for the causal link. Inter-annual variation in the timing of phenological events is large (with SD often ≈ 5 to > 10 d between earliest and latest dates of occurrence spanning ≈ 1 month). This variation has repeatedly been explained by variations in temperature sums for many phenological phases, especially in temperate and boreal systems. Hence there is ample evidence that the timing of many phenological phases is a function of temperature. Therefore, given the well documented increase in regional and global temperatures (IPCC, 2001), there are good reasons to expect changes in plant phenology. However the high inter-annual variation related to circulation patterns, solar cycles, and oscillations such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) render the detection of a trend in phenology and the attribution to global warming a complicated task.

Here we briefly review evidence for changes in terrestrial plant phenology stemming from ground observations, remote sensing and analyses of the seasonality of atmospheric CO₂-mixing ratios. We mainly focus on bud-burst of deciduous trees in temperate and boreal ecosystems. We address the complementary information provided by ground observation and remote-sensing data, and discuss the factors that determine the correlation between these two data sets. If the causes of changes in surface greenness throughout the year derived from satellite observations are to be understood, the area-averaged signal needs to be decomposed into the classes of

properties that induce changes in reflectance. And if predictive models are to be developed, the elementary processes that lead to changes in area-averaged light absorption need to be analysed and modelled. Therefore the challenge in comparing ground observations and satellite data is twofold. Ground observations at the level of individual plants need to be extrapolated in space. This will also allow for integration of detailed physiological knowledge in predictive schemes. Methods to identify individual sources of variation of the area-averaged satellite signals need to be evaluated. We discuss some first steps along these lines.

Trends in plant phenology

Temperature is a main driver of many developmental processes in biology. The rates of chemical reactions are temperature-dependent and generally increase with increasing temperature. In living systems this is especially true for enzyme-catalysed reactions. Temperature-sensitive biological processes include denaturation of enzymes at high temperatures, enzyme kinetics, the fluidity of membranes, and freezing and formation of ice crystals and consequent destruction of cellular structures (Johnson & Thornley, 1985). In many cases, higher temperatures have been shown to speed up plant development (Saxe *et al.*, 2001 and references therein) and lead to earlier incidence of switches to the next ontogenetic stage. The general expectation in a warming climate is therefore to find time trends in the phenological switches that determine the length of the vegetation period in temperature-limited, cold-deciduous plants. A correlation between the date of onset of the phenophase and antecedent heat sums, mainly temperatures of the preceding months, is to be expected. In water-limited systems where plants enter into dormant stages or die when soil water is depleted, changes in precipitation patterns are expected to modify the annual cycle of plant activity.

Indeed, the documented advance in spring leaf bud burst and flowering dates in middle and higher latitudes could well be an effect of concurrent anthropogenic climate change and associated increasing temperatures. Evidence for the expected trends in plant phenology comes from long-term ground observations and from more recent remote-sensing time series of greenness of the earth's surface, discussed in the following subsections.

Environmental factors other than temperature also modify plant phenology. The second most important trigger of spring phenological phases is photoperiod length. This has been shown in experimental studies (Saxe *et al.*, 2001). The weight of this factor is species-specific. This has also been concluded from fits of phenological models to large data sets of phenological observations (Schaber & Badeck, 2003). Evidence for effects on spring phenology of precipitation, nutrients and soil physical properties are scarce, and where effects have been found the effect is small relative to the temperature effect (Sparks *et al.*, 1997). In addition to changes in the physical

climate, an increasing CO₂-mixing ratio is a dominant trait of climate change.

Can CO₂ potentially have a direct effect on spring phenology such as bud burst in cold-deciduous species? Conceptually, we propose that there is a continuum of phenological phases for which the timing is more-or-less dependent on the plant carbon balance. At one extreme there are phases that are switched on independently of plant growth. Bud burst of leaves and flowering of many cold-deciduous plant species probably belong to this group. The evolutionary significance of such a response can be seen in the synchronization of the onset of photosynthetic and flowering activities with favourable thermal conditions and late frost risks. At the opposite extreme, there are switches to phenological phases that respond to precedent accumulation of sufficient reserves. On the basis of this conceptual model, we do not expect to find effects of CO₂ on the timing of spring phenophases if CO₂ acts on plant traits via photosynthesis and subsequent source-sink relationships. Experimentally, no effect of elevated CO₂ was detected on the bud break of *Acer rubrum* and *Acer saccharum* (Norby *et al.*, 2003), *Fagus sylvatica* (Forstreuter, 2002; F.-W.B., unpublished results), *Liquidambar styraciflua* (Herrick & Thomas, 2003), *Populus trichocarpa* (without increased CO₂ during the leafless period; Sigurdsson, 2001), *Populus alba*, *Populus nigra* (in one of two observation years a slightly earlier bud break of 3 d was observed in the control treatment, SD = 1 d) and *Populus × euramericana* (Calfapietra *et al.*, 2003). It remains to be confirmed if the response of mature trees is the same as that of seedlings, saplings and young trees reported in most of these studies. With this reservation, we conclude that there is a low probability for a significant direct effect of rising atmospheric CO₂-mixing ratios on observed trends in the spring phenology of cold-deciduous trees. However, effects on bud break of evergreen trees (Sigurdsson, 2001 and references therein) and later phase switches such as flower initiation, start of seed filling or onset of senescence are more complex.

Ground observations: treasures to be discovered

Long time series of phenological observations can be found in many scientific disciplines and historical documents, because of the many uses of phenological observations for synchronization of human interventions in nature that take into account the seasonality of the activities of plants and animals. Such data are collected (a) in forestry provenance studies; (b) to parameterize phenology models that are a central element for predicting productivity in agriculture, crop suitability in a region, and the timing of application of fertilizers, herbicides, insecticides and pesticides, as well as irrigation and to assist hybridization and selection; and (c) for prediction of pollen flight seasons. Information on observation networks is collected by the European Phenology Network which provides a web page (www.dow.wau.nl/msa/e/pn/) giving access to the

worldwide phenological research community. To our knowledge, the most detailed account of the roots and history of phenological research up to the mid-20th century is given by Schnelle (1955). Several papers updating this information can be found in a recent book edited by Schwartz (2003).

With rising public and scientific interest in the impacts of climatic change, phenology has been identified as one of the most responsive traits in nature. The second International Panel on Climate Change (IPCC) report, issued in 1996, illustrates the unequal role phenological research had played in agricultural and ecological research in the preceding decades. A chapter on agriculture in a changing climate (Reilly *et al.*, 1996) discusses aspects of the responses of crop phenology to climatic conditions that have been studied intensively, including accelerated crop development and the associated risk of decreasing yields, the wide range of temperature requirements of different cultivars of the same species and associated adaptive capacities, and modelling of expected shifts in regions suitable for cultivation of different crops. As opposed to this phenological responses of forest trees were discussed in less detail due to scarcity of published results. However, the need for more studies on this topic has been stressed (Kirschbaum *et al.*, 1996). In the latter half of the past decade the scientific community began to reap the harvest of long phenological time series, documented by a rapidly increasing number of published papers.

Historical time series: witnesses of global change effects

By the mid-20th century several authors were already reporting on changes in phenology that mirrored the observed warming trend (Erkamo, 1953; von Rudloff, 1967; Lauscher & Schnelle, 1986). Erkamo (1953) stated that 'a distinct rise in temperature has occurred in our climate during the last few decennial periods'. He showed that this trend had been accompanied by earlier foliation of *Betula alba* and *Acer platanoides* in Finland and by an extension of the vegetation period.

Walther *et al.* (2002) review studies on climate-change impacts on shifts in species range, invasions, community shifts and phenology. For all these traits, many examples were reported of changes in the direction expected to occur under ongoing climate change. From their Figure 2, which shows anomalies of observational time series of phenophases for animal and plant species during the period 1950–2000, no strong trend can be detected (by qualitative visual inspection) in the early years, but a clear trend for advancement in the spring phenophases emerges from about 1985 onwards.

Recently, in two studies (Parmesan & Yohe, 2003; Root *et al.*, 2003) meta-analysis techniques were applied to test if a coherent fingerprint of global warming on wild plants and animals could be detected. References to nearly 100 individual studies reporting trend analysis on phenological phases are given in these two papers and in Walther *et al.* (2002).

Root *et al.* (2003) analysed results from 143 studies on changes in species densities and ranges; morphology; genetic

frequencies; and phenology. Vote-counting analysis showed that where changes in the first three categories occurred, they significantly changed in the direction expected for the given climatic-change trends. For the studies on spring phenology within the past 50 yr, linear trends were calculated and the regression slopes analysed. The analysis is based on 61 studies reporting results on 694 plant and animal species. The studies included had to meet the following three criteria: they examined a time series of at least 10 yr; they found a change for at least one trait analysed; and they found either a temporal trend in temperature or a strong association between the trait and site temperature. The estimated mean number of days of advancement in the phenological phases per decade was 5.1 (± 0.1 SE). Because the warming trend is higher in higher latitudes, separate analyses were performed for the latitudinal belts 32–49.9° and 50–72°N that resulted in trends per decade of 4.2 (± 0.2 SE) and 5.5 (± 0.1 SE), respectively. Trees, on average, responded less (3.0 ± 0.1 SE) than nontree plants that had a response ratio close to 5 as the overall result.

Parmesan & Yohe (2003) analysed results on more than 1700 species on changes in species abundance; range boundary shifts; and phenology. Observations of birds, butterflies and alpine herbs resulted in an overall significant trend for northward and upward elevational shifts in range boundaries at the poleward and upper distribution limits. Trends in phenology were analysed for 172 species, for which time series of at least 17 yr and observations over large geographical regions were available. Meta-analysis resulted in a mean advancement of spring phases by 2.3 d per decade (95% confidence interval, 1.7–3.2).

The differences in trend estimates provided by these two studies could be related to differences in the relative number of observations in higher and lower latitudes, different taxa or groups of phases (flowering vs leafing; early vs late) and/or to the length of the time series analysed. These potential sources of disagreement need to be studied in detail, thus here we discuss only the effect of varying length of time series.

There is ample evidence that trends in spring phenology changed during the course of the 20th century. This is to be expected given the high fraction of variance in spring phases that is explained by temperature. The evolution of the global warming signal in the 20th century deviates substantially from the monotonous, exponential increase that would result from a direct proportionality to the increase in greenhouse gas-mixing ratios (IPCC, 2001). Two periods of temperature rise (1910–mid-1940s and late 1970s onwards) were interrupted by a 30 yr period with stable temperatures. This pattern in temperature rise can, to a large extent, be explained by the combined action of natural and anthropogenic forcing factors (IPCC, 2001). Therefore, based on the basic, robust hypothesis about the causal link between temperatures and spring phenology, a deceleration in the advancement of spring phenology in the middle of the 20th century is to be expected. However, this coarse-grained pattern should be further

modified by deviations of seasonal from annual warming trends, and by deviation of regional patterns from the global mean.

Observations on changes in the trend, as evident in the review by Walther *et al.* (2002), confirm this expectation of an acceleration of spring phenology advancement in the late 20th century. Peñuelas *et al.* (2002) made the same observation in analysing time series for a mesic Mediterranean site in northern Spain. Scheifinger *et al.* (2002), in systematically varying start and end years for trend calculations, established a trend matrix. Their results are consistent with a trend reversal in 1984 for pollination of *Corylus avellana*.

Schaber (2002) defined standard periods for which different trends in phenological dates can be expected by analyses of the trend reversal in the March and April temperatures recorded for stations of the German Weather Service (DWD). He identifies 1890–1931, 1931–48, 1948–84 and 1984–99 as periods with no change, warming, cooling and warming trends, respectively. When linear trends were calculated for combined phenological time series in natural regions of Germany within these periods, significant trend reversals were identified. For three natural regions, 120 yr time series of phenological data could be reconstructed and analysed. During the period 1880–1931 some phenophases showed significant trends for advancement, others were retarded, and the majority did not show significant trends. From 1931 to 1948 many phases were progressively advanced and the rest were not significantly changed. In the 1948–84 period positive as well as negative trends were again observed, with only some of the trends for advancement being significant and the rest nonsignificant. After 1984, 22 out of 23 series displayed significant trends for advancement, six of these being greater than 10 d per decade.

These results fit well to earlier findings that had been published in the mid-20th century. von Rudloff (1967) identified a warm and dry period, 1942–53, that he called ‘climatic optimum’. In this period relatively early flowering phenology of cherry, lilac and locust tree was observed compared with the period 1928–34 in Austria. Lauscher & Schnelle (1986) analysed 11 long time series and found that during the warmest decade, 1941–50, phenological phases were also earliest. Erkamo (1953) found a trend for earlier bud burst of birch and maple in Finland in the first four decades of the 20th century.

The examples of an early bud-burst phase (birch) and a late bud-burst phase (oak) illustrate the general patterns (Fig. 1) in the second half of the 20th century: (a) a small trend for advancement in the early spring phase up to 1984; (b) trends for retarded or unchanged onset of the phase in late spring phases in the same period; and (c) a clear trend for advancement in both early and late spring phases after 1984. Menzel *et al.* (2001), who analysed data from the same database, found less advancement for late spring than for early spring phases. Schaber (2002) showed that the difference in trends between early and late spring phases is explained by differences in seasonal warming trends. April temperatures in the late 1940s were higher than in the last (and generally warmest)

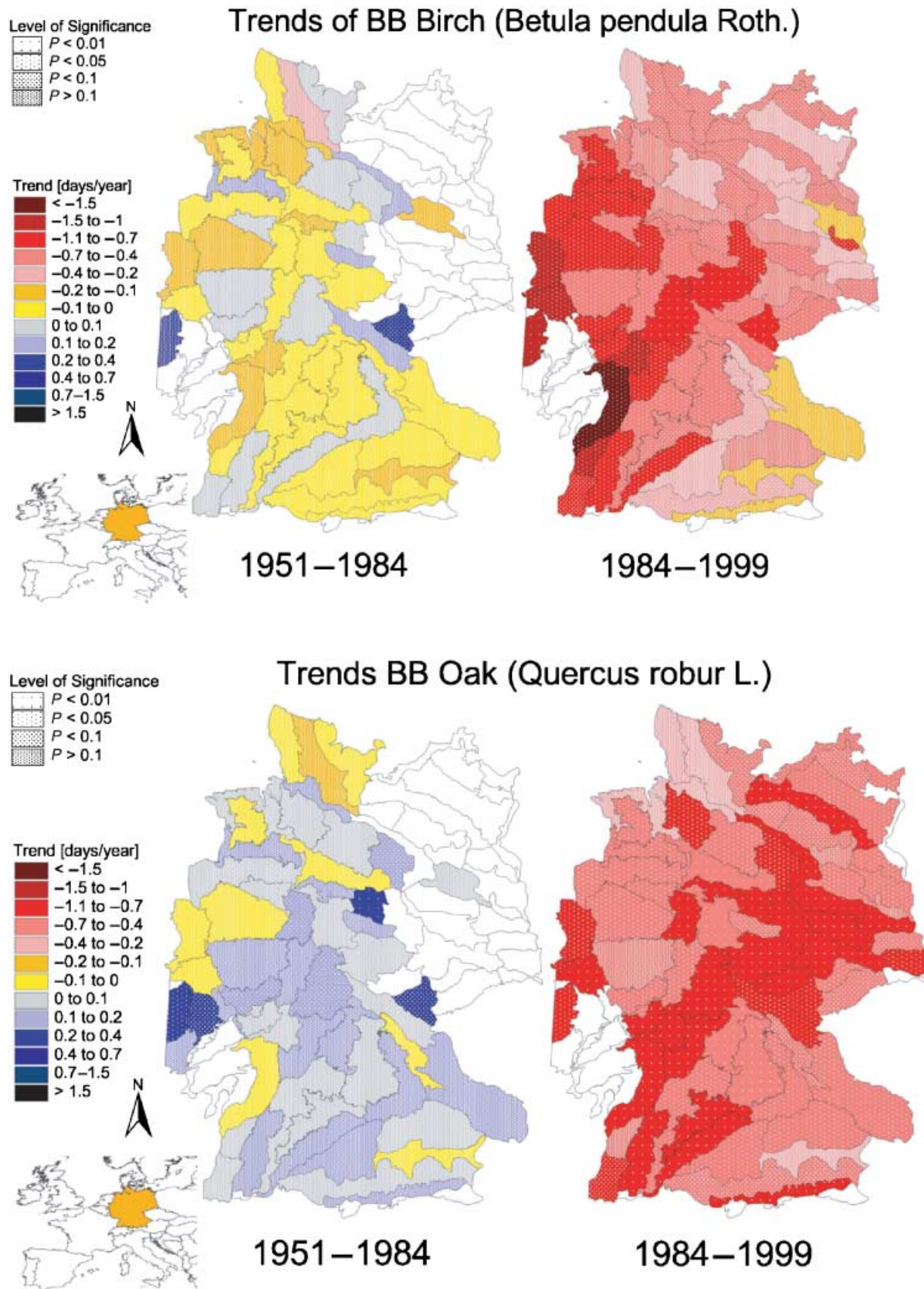


Fig. 1 Trends in bud burst of birch and oak in Germany in the periods 1951–84 and 1984–98.

decade of the 20th century, while temperatures in February and March are closer to the plateauing pattern found for the global temperature rise. Phenology mirrors this pattern. Observations of contrasting trends of monthly temperatures correspond with the trends reported by Scheifinger *et al.* (2002) for the period 1951–98 in the Alpine region, with a warming trend in February/March and no change in April.

Several analyses of the interannual variability in phenophases (Forchhammer *et al.*, 1998; Chmielewski & Rötzer, 2001; D'Odorico *et al.*, 2002; Scheifinger *et al.*, 2002) demonstrated a correlation with the NAO Index. In positive phases of the NAO, when winters are warmer in northern and middle Europe, phenological phases tend to be triggered earlier.

In conclusion, ground observations of phenology not only bear a clear and consistent warming signal, but also indicate parallelism in the phases of warming and advancement of phenology. However, it remains to be analysed how far phases of accelerated and unchanged phenology were related to modifications of the pace of global warming by forcing factors such as solar and volcanic activity and aerosols; regional natural variability (e.g. NAO); or modifications of regional climate oscillatory patterns by global warming.

Satellite observations: a powerful tool to monitor phenology from space

Shortly after the launch of the first operational Earth-observing systems in the 1970s, satellite measurements of surface radiation in the short wavelengths were used to monitor the phenological cycle of deciduous ecosystems. Analysis of the normalized difference vegetation index (NDVI) temporal cycle (Reed *et al.*, 1994) provides an indication of the seasonal greenness (range -1 – 1 ; in practice the NDVI of terrestrial surfaces is generally > 0) of the vegetation as seen from space. This has two important consequences: (a) as data are available for over 20 yr, observed interannual variability and temporal trends in the phenology (as well as spatial contrasts) can be investigated for the entire globe; and (b) especially in places without any ground observations, phenological models can be tested (Botta *et al.*, 2000), calibrated and validated for the

climate of the past 25 yr, which might eventually display some trends. This provides more reliability when these models are applied with future climate change scenarios.

At the continental scale, vegetation types that differ in their phenology could easily be classified using daily satellite observations of the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer (NOAA/AVHRR) series, e.g. the various types of the West African savannah along the north–south precipitation gradient (Viovy, 2000). As expected, spatial variations in phenological behaviour observed from space are well related to the seasonal features of climate such as temperature and precipitation (Justice *et al.*, 1985; Moulin *et al.*, 1997; Suzuki *et al.*, 2003). For example, the use of a daily 1 km spatial resolution NOAA/AVHRR data set for western Europe to estimate the date of green-up for the deciduous forests produces the expected results (Fig. 2): the growing season starts earlier in the mild oceanic south-west (Portugal) and later in the cold continental north-east (Poland). The later bud burst of deciduous forests related to a higher elevation is also clearly visible over the mountainous areas (Pyrenees, Alps, Apennines).

Consequently, it is logical to expect that temporal trends in phenology in correlation with recent climatic trends could be found from the > 20 yr of available global satellite data. This point is highly debated: the relatively poor quality of the NOAA/AVHRR data, and the lack of knowledge and experience at the time of the processing of the first data set, have led several authors to question the significance of the 'observed trends' computed from satellite observations (Gutman, 1999). After a careful comparison of the trends detected in the NDVI seasonal profile over the 1982–99 period for different methods of data processing (including consideration of the perturbations caused by atmospheric and directional effects), Slayback *et al.* (2003) conclude that the northern hemisphere (35 N–75 N) is experiencing a significant positive increase in the average May–September NDVI.

The few published studies that quantify the observed trend by the increase of the active growing season in the temperate/boreal northern hemisphere provide similar trends: the growing season is longer, mainly because of an earlier start (Table 1).

Table 1 Yearly increases in length of growing season (L_{GS}) and yearly advances in start of green-up (d_{GU}) as seen from space for northern latitudes

Observation period	Geographic range	Trend* d_{GU}	Trend* L_{GS}	Reference
1981–91	45 N–70 N	8	12	Myneni <i>et al.</i> (1997a)
1981–99	40 N–70 N, Eurasia	3.5	9.4	Zhou <i>et al.</i> (2001)
1981–99	40 N–70 N, North America	4.3	6.3	Zhou <i>et al.</i> (2001)
1982–2001	25 W–60E; 27 N–72 N, Europe	5.4	9.6	Stöckli & Vidale (2004)

*Measured in d per decade.

Deciduous forests greening date 1992

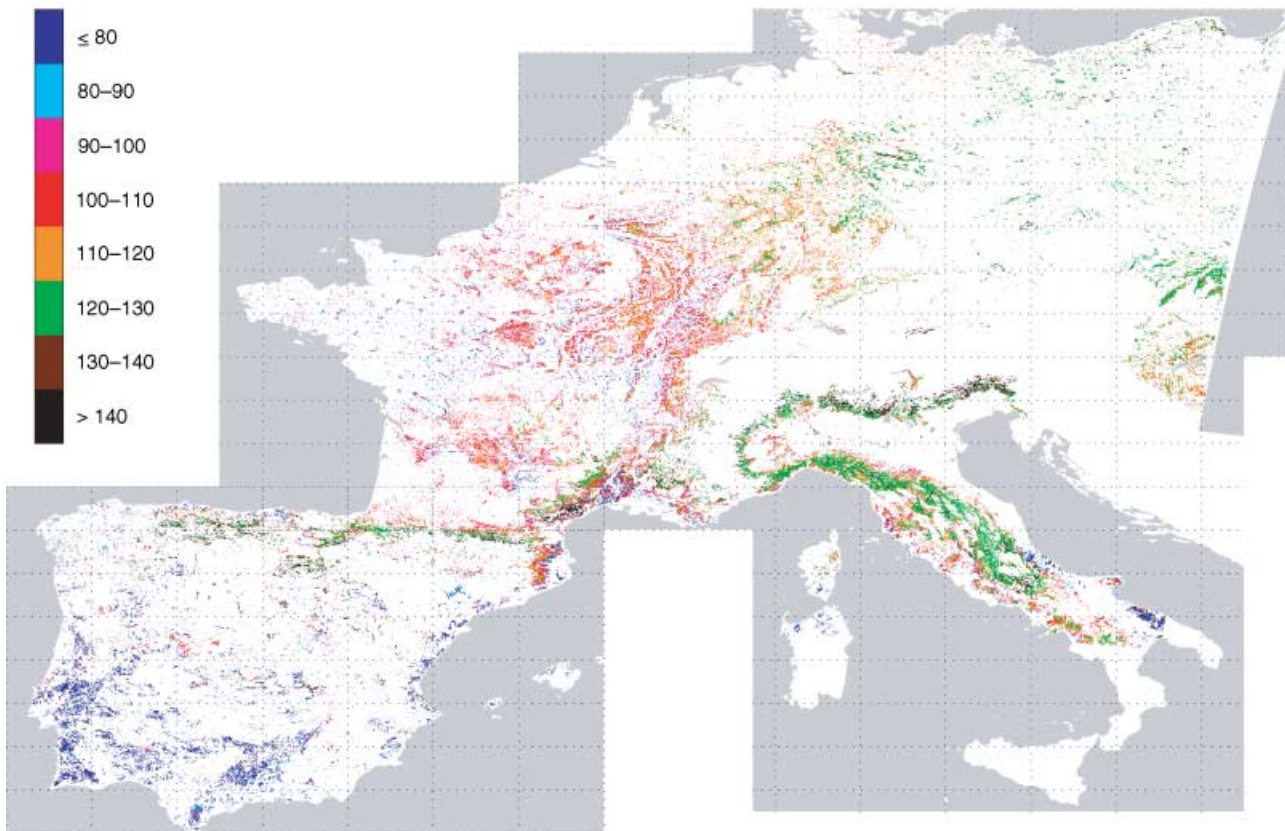


Fig. 2 Map of satellite-detected green-up date over Europe in 1992 (deciduous forests only).

Lucht *et al.* (2002) found that the Lund–Potsdam–Jena biogeochemical vegetation model reproduces satellite-observed leaf area index anomalies well, even in the case when seasonal, intra-annual and decadal variations in temperature only are taken into account. This suggests that temperature control of these variations in the boreal zone is a dominant factor over other effects, such as nutrient supply, forest management or postdisturbance dynamics. An interesting aspect of this study is its investigation of the consequences of the eruption of Mount Pinatubo in the Philippines in June 1991. The eruption caused a global cooling of 0.5°C caused by aerosols injected into the stratosphere. Both the greening trend and the trend toward an advanced spring were interrupted by the event for 1–2 yr, but both continued afterwards. Spring occurred several days later, and maximal leaf area of the vegetation declined.

Using methods of correlation analysis, Buermann *et al.* (2003) show that the spatial patterns of covariability of spring temperature and greenness in the northern hemisphere are associated with the influence of large-scale atmospheric circulation patterns. Particularly, the effect of ENSO is that of a general warming at northern latitudes, while the Arctic Oscillation (AO) in its positive phase, which has been predominant

in past decades, adds additional warming in Eurasia but not in eastern North America. The additive effect of these patterns may explain differences between vegetation activity in Eurasia and North America visible in greening trends and spring timing, where Eurasia is seen as being affected more.

Atmospheric CO₂: the carbon-exchange perspective

In conclusion, both studies of trends in spring phenology observed on the ground, and analyses of the greening of the earth's surface in mid- and high-latitude spring as seen from space, provide evidence for an advancement in the start of the growing season. Variations in quantitative estimates of this trend (2–5 d per decade averaged over the response rates of many species observed on the ground; 4–8 d based on satellite data) demonstrate the need for a better understanding of the exact nature of these estimates. However, given this considerable range of uncertainty, it must be stressed that both lines of evidence support the expectations of a significant change in spring phenology in response to the warming trend of the past two decades. A third, independent source of information stemming from atmospheric CO₂ measurement supports this conclusion.

Keeling *et al.* (1996) found strong indications for a change in the seasonality of the global metabolism of terrestrial ecosystems when analysing changes in phasing and amplitude of the seasonal cycle of the atmospheric CO₂-mixing ratio. The timing of the drawdown of CO₂ caused by CO₂ uptake by photosynthesis of terrestrial plants showed no trend from 1959 up to the mid-1970s at the Mauna Loa Observatory, Hawaii. It then advanced irregularly, becoming ≈ 7 d earlier in the mid-1990s. At Point Barrow a comparable advancement of ≈ 7 d was detected for the same period. These observations were interpreted as indicating an advanced start of the vegetation period. Keeling *et al.* (1996) also postulated that a major fraction of the observed increase in amplitude of the seasonal CO₂ cycle can be explained only by a lengthening of the vegetation period of mid- and high-latitude ecosystems. The change trend of 3.5 d per decade falls within the range of the estimates cited above. The implication of a higher annual gross and net primary production caused by a prolonged vegetation period, as suggested based on the analyses of the seasonal amplitude, is paralleled by inferences drawn from the inter-annual variation of carbon-exchange rates measured at eddy flux towers (Chen *et al.*, 1999); from calculations of the change in potentially absorbed radiation with a change in the length of the vegetation period (Schaber, 2002); and from the modelled change in annual production simulated with forest and ecosystem models forced with different phenologies (Kramer, 1995; White *et al.*, 1999; Schaber, 2002). However, an earlier start of the period during which plants are actively photosynthesizing does not necessarily mean increased annual production. If the plants use scarce water resources earlier in the year, the gains in spring might be compensated by losses in dry summer months (White & Nemani, 2003). These potential interactions need to be investigated further.

Ground observations and satellite data: complementary views

Ground observations of phenology and satellite-derived measures of surface greenness provide complementary information. Ground observations describe the onset of phenophases at the level of the individual plant, and can be scaled to the level of varieties, provenances and species given that the biological variability and confounding microclimatic influences are assessed. Individual plants are observed in a given, more-or-less well known microenvironment. Hence ground observations generally do not provide a spatially integrated response pattern that depends on the mixture of species in the landscape, but rather focus on developmental switches of individual species. Remote sensing, in turn, provides area-averaged information emphasizing dominant vegetation elements and focuses on the greenness, leaf-area index (LAI) and related reflectance. If the significance of the observed changes in reflectance is to be interpreted in terms of causes, the problem arises of decomposition into individual

landscape elements. Remote sensing observes temporally variable objects because of slight variation in the geolocation of the scenes, and because it traces any disturbance and change in land use. There is great potential for a better understanding of phenological effects in landscapes by combining the strengths of both approaches.

If NDVI derived from satellite observations is to be used for monitoring the length of the vegetation period, it is desirable to test estimates of the onset of greening, senescence and leaf shedding by comparison with ground observation data. This is especially necessary because the metrics of NDVI and threshold values applied in its interpretation do not *a priori* correspond to ground truth data. The same need for comparison arises if local ground observation data are to be extended spatially with the use of remote-sensing data, and the surface greening signal interpreted in terms of the phenological development of the individual species that make up the vegetation cover. Therefore an important requirement of phenological research is to establish relationships between the annual course of greenness observed by remote-sensing techniques and the leafing out, senescence and leaf shedding of vegetation elements.

However, in addition to the differences mentioned so far, ground observations and remote-sensing vegetation indices monitor qualitatively different traits. Vegetation indices that are derived from reflectance in the near-infrared and far-red are closely correlated with the absorption of photosynthetically active photons by plants in the visible spectrum. This is the case because the change of reflectance across the so-called red edge is a characteristic feature of photosynthetically active, chlorophyll-bearing plant organs. High reflectance of tissues with high water content in the infrared region, and high absorbance (hence low reflectance) in the red absorption maximum of chlorophyll, are the causes of the good correlation mentioned above (Myneni *et al.*, 1995). This property of the reflectance spectra of vegetated surfaces is the basis for numerous applications of vegetation indices (notably NDVI) that deduce the fraction of absorbed photosynthetically active photons from satellite observations (Myneni *et al.*, 1997b). The latter trace the change in total absorbance of a surface element in the course of time, thus recording seasonal changes in the activity of the vegetation cover.

NDVI signals allow us to estimate overall seasonal changes in light absorption of a given surface element that result from phenological switches *sensu strictu*, further changes in the cover fraction via leaf and shoot growth, and variation in the chlorophyll content of developing and senescing leaves. The strength of remote-sensing approaches resides in providing this integrated measure of energy input to the photosynthetic processes. However, if the relation of absorbed radiation with actual photosynthesis (e.g. changes in energy partitioning with drought) is to be evaluated, and if individual sources of variation in absorbance are to be analysed and described with predictive models, then the integrated signal needs to be decomposed. The challenge is to distinguish the sources of

variance related to bud break, leaf and shoot growth, changes in chlorophyll, and senescence for a given combination of species (individuals) of varying cover fractions. While ground observation of bud break phenology determines the date of an event (the date of bud burst, d_{BB}) in the analysis of NDVI, an estimate of a characteristic change in reflectance (the date of green-up, d_{GU}) is retrieved from the time course of the signal. Subsequently, we discuss methods used and some first steps that have been taken along the line of comparison of ground observation and remote-sensing data.

Several authors have investigated different methods to derive phenological indicators, such as the beginning of active growth or the start of senescence for deciduous forests, from the NDVI temporal profile. The NOAA/AVHRR data were used at first (Lüdeke *et al.*, 1996; Moulin *et al.*, 1997; White *et al.*, 1997); more recent studies deal with the use of new sensors of higher quality such as MODIS or Végétation (Kang *et al.*, 2003; Zhang *et al.*, 2003).

First, the satellite data must be processed to eliminate data from cloudy scenes and to correct for directional and atmospheric effects. Especially when using data from the long-term NOAA/AVHRR archive, the resulting temporal NDVI signal remains very noisy because of daily changes in the orbital and atmospheric conditions. A dynamic filtering is then applied to interpolate the missing dates and smooth the signal, and to restore a temporal signal as representative as possible of the vegetation seasonal cycle (e.g. best index slope extraction, BISE; Viovy *et al.*, 1992).

The 'clean' NDVI curve is an indication of greening of the landscape as seen from space, at a typical spatio-temporal resolution of 8 km/10 d for global studies (1 km/1 d for regional studies). Over homogeneous deciduous ecosystems, we can expect to identify clearly on the NDVI curve critical periods such as the start of the NDVI increase, the period where the maximum NDVI is reached, and the beginning of the NDVI decrease. Therefore these dates of change in NDVI dynamics can be determined with the maxima/minima in the NDVI

derivative (subsequently called slope method). However, this method does not always work: for most deciduous forests in temperate/boreal zones the satellite first sees the greening of the understorey that occurs several weeks before bud burst of the tree leaves (Fig. 3). In many cases the landscape is heterogeneous: several species are present, and sometimes agricultural fields or pastures are mixed with forest within the satellite signal. Consequently, it is not clear to which event on the surface a change in the NDVI profile relates; and often the NDVI shows a rather regular increase from minimum to maximum values without any marked changes in slope. It is therefore easier to use some NDVI absolute threshold value, or a threshold value defined as a fraction of the annual amplitude, that can be empirically related to the beginning or the end of the phenological phases determined on the ground (subsequently called absolute and relative threshold method).

Duchemin *et al.* (1999) tested the estimation of the green-up date (d_{GU}) over an oak deciduous forest in France estimated for 4 yr NOAA/AVHRR satellite data (daily/1 km). They found a strong NDVI seasonal signal, with a nearly linear increase in spring that lasts about 30 d and d_{GU} occurring at NDVI = 0.55. They fitted a linear line segment of fixed length to the NDVI time series in this period and extracted the date when NDVI reached the fixed threshold value of 0.55 (modified absolute threshold method equivalent to a calibration to local conditions). Comparison to only 4 yr of ground observations in an oak forest (nearby) yielded a correlation coefficient of $r = 0.89$, a mean error of 4 d, and no bias, where the interannual range in d_{GU} of 29 d and in ground observations of 25 d was large. Chen & Pan (2002) found no significant correlation between the NDVI (10 d/8 km) value reached at the date identified as start date of the vegetation period and this date across 12 yr at three locations in China. They defined the start of vegetation period from a fixed number of spring phenophases of several plant species that have been triggered. The comparison of the average date of bud burst for 33 tree species in Harvard forest with NDVI

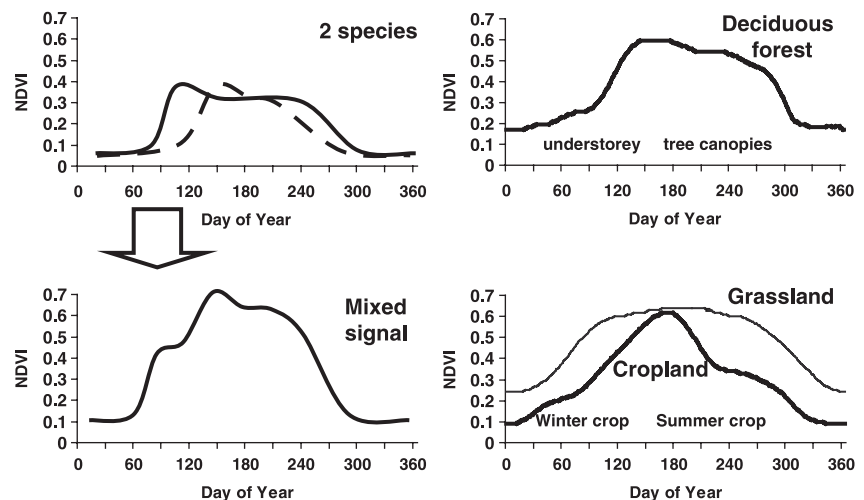


Fig. 3 Typical NDVI profile for three deciduous ecosystems in Germany (right: grassland, crops, deciduous forest). Periods when different vegetation cover elements contributed to the signal are indicated. Left, schematic illustration of the contribution of different species phenology to the NDVI time course.

(biweekly/1 km)-derived dates of bud burst for nine observation years did not yield significant correlation either with a half-maximum or with a change in slope method (Schwartz *et al.*, 2002). In the studies of both Chen & Pan (2002) and Schwartz *et al.* (2002), significant correlations were found between ground observations and phenology models, indicating that the date of bud burst could be predicted better from climatic variables than from area average satellite observations.

Can the low correlation be improved if the resolution of satellite data is increased and the vegetation composition is better constrained? To investigate this question, we use 9 yr (1989–97) of a daily high spatial resolution (1 km) NOAA/AVHRR archive for western Europe to monitor the seasonal NDVI cycle for selected homogeneous deciduous forests. We compare it to ground observations of bud burst from the extensive observational network of the DWD and data for the Fontainebleau forest (Eric Dufrêne, personal communication). We used only data from nearby ground observation stations with no significant difference in elevation, and averaged the data where several stations met the criteria. For the Fontainebleau forest, where beeches and oaks are equally dominant, we took the arithmetic mean of the species bud-burst dates. The satellite data were received and processed at the meteorological institute of the Freie Universität Berlin, including precise geolocation, calibration and cloud screening (Koslowky *et al.*, 2001). We interpolated the missing dates and filtered using an adaptation of the BISE algorithm (Viovy *et al.*, 1992). For deciduous vegetation, the resulting NDVI temporal profile captures the annual phenological cycle, as illustrated in Fig. 3 for three different German land-cover types. For the deciduous forests we tested a version of the relative threshold method that determines the date of bud burst as the date when the NDVI has reached half its annual amplitude. First, this algorithm was applied for the NDVI profile of five deciduous forests (Table 2), chosen for their spatial homogeneity and the availability of ground phenological observations in the vicinity for the period 1989–97.

The date of green-up derived from the NDVI profile and the observed bud-burst dates show a good correlation within the 9 yr time series (Table 2, $r^2 \geq 0.5$ at each site). The use of

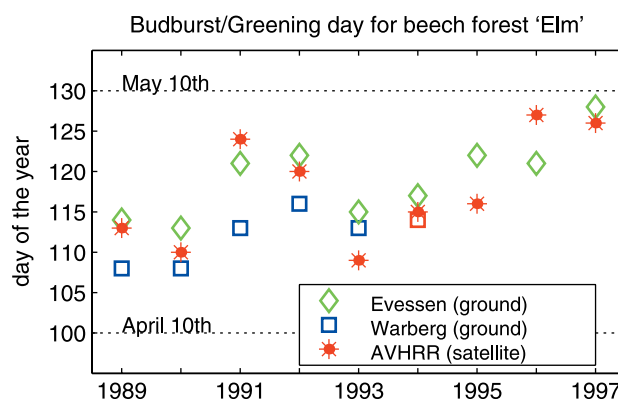


Fig. 4 Observed and estimated bud-burst dates for the Elm forest (Germany) for the period 1989–97.

an originally daily satellite NDVI provides an estimation of d_{GU} that agrees reasonably well with the observed d_{BB} (Fig. 4).

We then relax the conditions for the comparison and use all contingent deciduous forests in Germany (44% of which are covered with beech and 25% with oak). Only those with 1×1 km NDVI pixels were selected for comparison, of which the mid-point was inside a 0.25×0.25 km CORINE (Coordinated Information on the European Environment; land cover data set) deciduous forest pixel that was surrounded by at least three rows of deciduous forest pixels on any side. Thus a buffer of ≈ 0.375 km around the NDVI pixel had to be covered by deciduous forests if the pixel was to be included in the comparison. We used elevation as variable, together with average elevational gradients in d_{BB} for interpolation of beech bud-burst days by detrended kriging. The difference of d_{BB} and d_{GU} for the 9 yr period is shown in Fig. 5 for three of the forested landscapes discussed above.

For the whole of Germany we can compare a total of 2853 (317 pixels \times 9 yr) dates of bud burst interpolated from ground observations (d_{BB}) to NDVI-derived dates of mid-point green-up (d_{GU}). Mean, modus and median of the frequency distribution of $d_{BB} - d_{GU}$ are 3.3, 2.0 and 2.0, respectively, indicating that satellite-derived green-up preceded observed tree bud-burst dates on average by 3.3 d. The distribution is slightly skewed to the right, indicating that much

Table 2 Locations of deciduous forests, dominant species (beech, *Fagus sylvatica*; oak, *Quercus petraea*; or mixture of both), source for ground phenological observations and number of NOAA/AVHRR pixels

Forest	Mid-point	Species	Data source	R^2	No. pixels
Elm (Germany)	10.48 E 52.12 N	<i>F. sylvatica</i>	DWD	0.76	80
Hainich (Germany)	10.24 E 51.06 N	<i>F. sylvatica</i>	DWD	0.79	67
Hainleite (Germany)	10.42 E 51.24 N	<i>F. sylvatica</i>	DWD	0.68	90
Hardt (France)	7.30 E 47.48 N	<i>Q. petraea</i>	DWD	0.50	97
Fontainebleau (France)	2.42 E 48.25 N	Mixed	E. Dufrêne pers. comm.	0.77	56

DWD, German Weather Service. R^2 = squared coefficient for correlation between d_{BB} and d_{GU} .

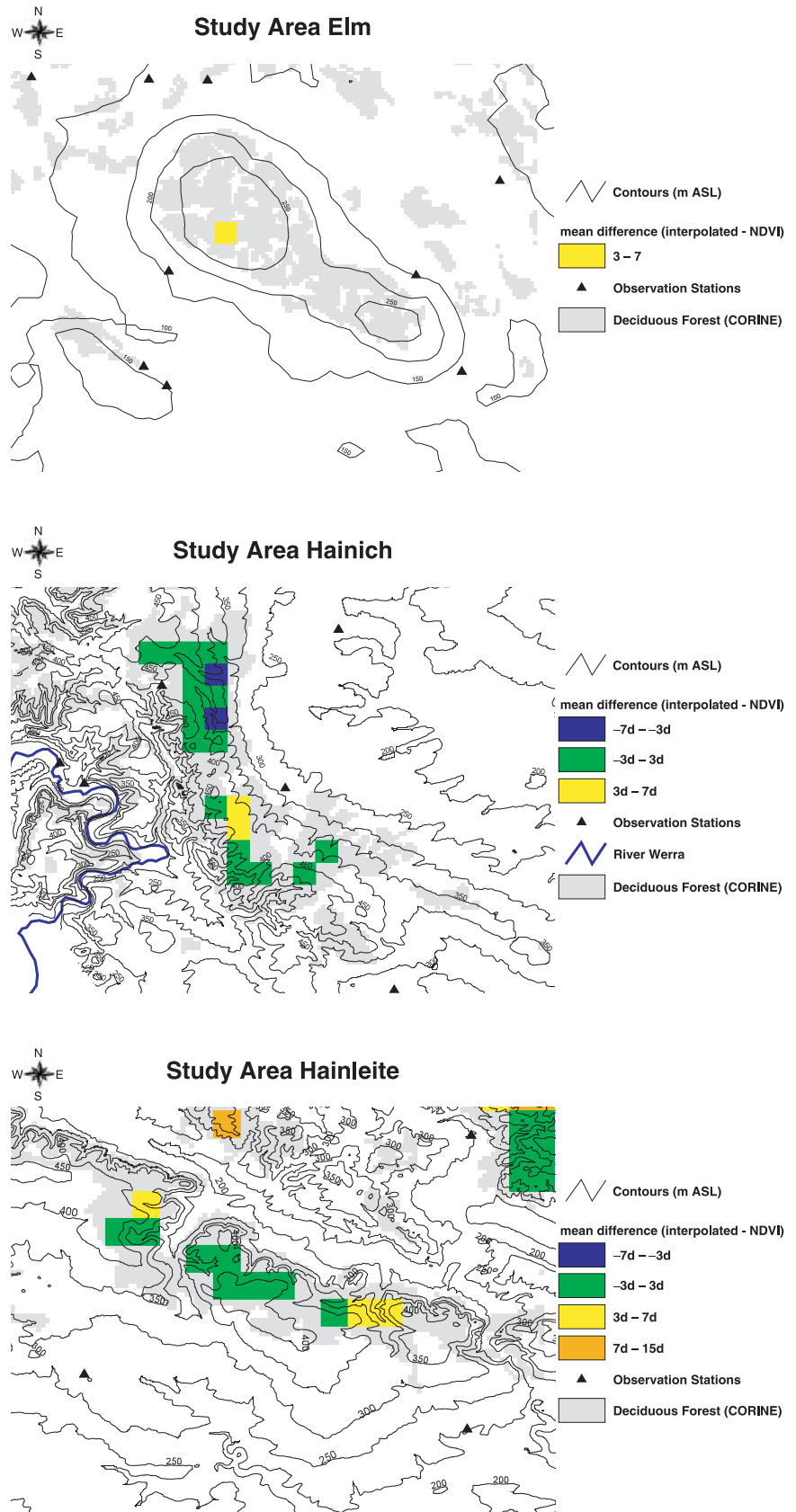


Fig. 5 Maps of the difference between d_{BB} interpolated from ground observation data and d_{GU} for the study areas Elm, Hainich and Hainleite (see text for further details).

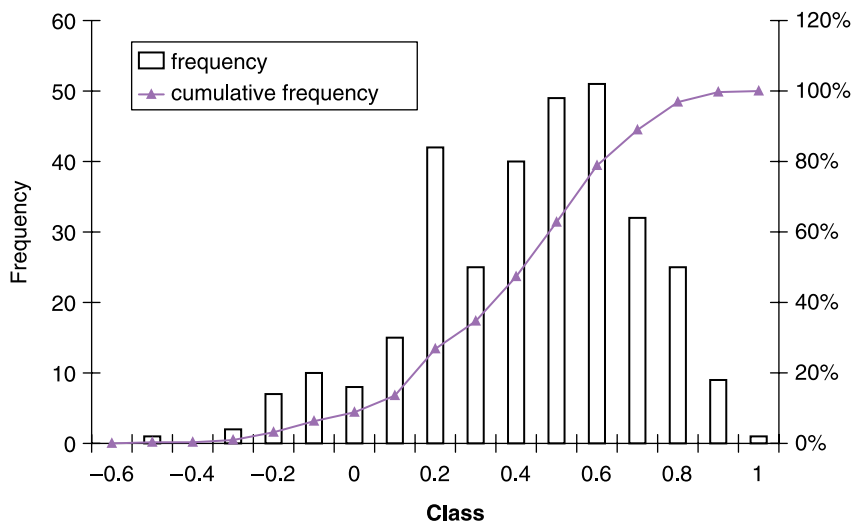


Fig. 6 Frequency distribution of correlation coefficients for the comparison of 9 yr time series of d_{BB} and d_{GU} at 317 deciduous forest sites.

earlier d_{GU} is observed more often than the opposite. This first approximate comparison shows that ground observations and remote-sensing data produce analogue estimates of the spring green wave. However, the correlation between d_{BB} and d_{GU} is low at the level of the deciduous forests under study here. The average correlation coefficient is $r = 0.38$. The distribution of the correlation coefficients (Fig. 6) shows that pixels with high, as well as with no, correlation are abundant.

Several factors can potentially contribute to mismatches between d_{GU} and d_{BB} : (a) inter-individual variability in d_{BB} ; (b) error in the spatial interpolation of d_{BB} ; (c) systematic time lags between d_{BB} and the trait derived from the satellite signal; and (d) heterogeneity in the terrain and vegetation cover.

(a) We estimated the components of variability (SD) associated with ground observations to be ≈ 2 d for observer error, 8 d between the biological objects within the species, and 2.5 d caused by variations of micro-climate at spatial scales of several kilometres and differences in elevation < 50 m (Schaber, 2002; unpublished results). These sources of variation are not expected to introduce a systematic bias into the comparison of d_{GU} and d_{BB} .

(b) Spatial extrapolation propagates the biological variance. An additional source of error comes from the model used implicitly to account for spatial variation of the climatological driving forces. We used elevation as variable for detrended kriging together with average elevational gradients in d_{BB} . Our spatial interpolation cannot account for effects of cold air lakes or thermal belts. A mean absolute error of the interpolation of 5.35 d (SD = 7.2) was determined by cross-validation for 12 yr of observations on beech in Germany. The total error has not yet been partitioned into biological and interpolation components.

(c) The observed date of bud burst should systematically be earlier than the green-up observed on the same vegetation elements. According to the observer instructions, d_{BB} corresponds to the start of leaf unfolding, when only some buds have broken throughout the tree crowns. The mid-point

green-up should occur some days later when a substantial fraction of leaves have already unfolded. From studies by Baumgartner (1952); Hengst (1965); Lausi & Pignatti (1973) we conclude that, in beech, the time span between first buds breaking and complete foliation is < 1 wk for individual trees and ≈ 2 wk for entire stands. It is prolonged when the weather is cool during leaf expansion and hastened under summer day conditions, faster in lowlands and slower in the mountains.

If the NDVI was linearly related to LAI, this period would correspond to the period of increasing NDVI in spring. However, the NDVI signal saturates around LAI = 3. Duchemin *et al.* (1999) estimated that the LAI at the mid-point of the springtime rise of NDVI should be close to 1. Therefore we conclude that d_{GU} is probably delayed less than 1 wk relative to d_{BB} when looking at the same vegetation element, and estimate that d_{GU} can be expected to occur 1–2 d after d_{BB} in hot periods and can be delayed up to several weeks if intermittent cold spells intervene. Finally, all methods used for extraction of d_{GU} from NDVI time series are empirical. Their sensitivity to different sources of variation still needs to be quantified.

(d) Heterogeneity in vegetation cover will tend to advance the satellite measure relative to the bud-burst dates of trees. Many forest understorey plants, grasslands and plants used in agriculture and gardening unfold their leaves earlier than the dominant European forest tree species. In the highly fragmented European landscapes this effect needs to be further investigated and its relationship to different algorithms for the determination of d_{GU} needs to be analysed.

In a last step of generalization, we used the same algorithm to compute the bud-burst date over all deciduous forests. The results (Fig. 2, 1992) display the expected south-west/north-east trend: the earliest bud-burst dates occur in Portugal, the latest in Poland, and the altitude influence is clearly visible for the Alps and the Pyrenees.

From the comparison of d_{BB} and d_{GU} reviewed above, we conclude that the heterogeneity of vegetation cover is a main source of disagreement between satellite-derived green-up

dates and ground observations of bud burst of the dominating tree species. The better the vegetation cover is known, and the more homogeneous it is, the higher the correlation. The example from Duchemin *et al.* (1999) illustrates this hypothesis where ground observations not in the same forest, but in a forest with the same species composition, were compared with NDVI data. In Chen & Pan's (2002) study the contribution of the individual species for which d_{BB} has been observed on the ground to the total landscape LAI is not known. Thus, again, the lack of correlation is consistent with the hypothesis that landscape heterogeneity needs to be taken into account if the seasonal signal of NDVI is to be explained through species phenology. Also, the lower correlation found in our study where the species composition of deciduous forests is not known, as compared with forests with well known species composition, backs up our claim. Ground observation of the main vegetation elements growing within a satellite scene, in combination with a detailed vegetation map, will allow for better interpolation and averaging of ground observations at the scale of satellite pixels. However, the different nature of bud break and green-up sets limits to the improvements that can be achieved with higher spatial and botanical resolution. Strictly speaking, comparison of the two data types does not allow for mutual testing. The reconstruction of the NDVI signal from phenology, growth and chlorophyll content of individual vegetation elements is a challenge for further progress in the analysis of seasonality in ecosystems.

Conclusions and perspectives

Many phenological observations, including long time series which are a valuable source of information for climate change-impact studies, were made in the context of diverse applications of phenology (e.g. agrometeorology, fundamental ecological research). Stimulated by concerns about climate-change impacts, a fraction of this rich asset of information has been collected and analysed for trends in the course of the last decade of the 20th century. The value of sustained efforts in nature observation is demonstrated by this development. Compilation of old series should be continued; reduction of this important, 'old-fashioned', low-tech element of earth observation under rising budgetary constraints should be avoided. In parallel, the time series of satellite-derived measures of surface greenness have grown over a sufficient period to allow the first time-series analyses of spring green-up and length of vegetation period. A powerful new tool for the study of integrated landscape-level phenological development has emerged.

These two sources of information complement each other, but do not observe the same traits. While ground observations provide information about responses of individual species (and sometimes also the biological variability within the species) at a given (micro)-site, satellite measures allow study of the composite responses of phenological switches, LAI development and cover fraction for many vegetation elements

integrated over landscape fractions. The rather modest correlations reported so far between estimates of interannual variation in d_{BB} and d_{GU} are to be expected, based on these differences. The challenge is to improve spatial interpolation of ground observation data and to derive tested algorithms that allow for analysis of satellite signals. The combination of the two approaches has great potential in addressing scaling issues between individual plant and ecosystem responses.

Progress along the latter line can probably be increased if the rich wealth of results accumulated within phenological studies in phytocoenology (Tüxen & Wojterska, 1977) is included in future studies. Further progress can be expected from the use of new generations of satellites (MODIS, Végétation) with higher spatial, temporal and spectral resolution. Nesting of finer-resolution images in high temporal resolution images, in combination with higher-resolution biotope mapping, has a lot of prospects.

The analyses of spring phenology in middle and high latitudes showed vegetation responses that are consistent with expectations based on climate-change trends. Ground observations have shown advancement of spring bud burst and flowering dates in parallel with the global warming trend, and NDVI time series show a trend for advanced green-up in spring. The detected trends are of the order of magnitude of several days per decade. These trends parallel the advanced drawdown of atmospheric CO_2 in spring/summer. This also holds for the time course of the respective changes, with a plateau phase until the 1970s and then an accelerated advancement. Hence three independent measures – local-scale observations of individual species; spatially integrating satellite-based monitoring of surface greenness; and the fingerprint of seasonal activity of vegetation on the atmospheric record – qualitatively yield the same result.

However, differences in trend estimates varying in the range 2–5 d per decade still need to be resolved. These differences may be related in part to variation of the trends in time. Some first indications suggest that trends in spring phenology roughly follow the temporal evolution of the global warming trend (IPCC, 2001), with a period of warming from the end of the 19th century through to the 1950s, followed by a period of stabilization and then a second phase of accelerated warming from the late 1970s onward. However, spring phenology does not respond to global mean temperatures, but rather to regional changes in winter and spring temperatures with a high weight of temperatures in weeks immediately preceding the triggering of the phenological switches. The causes of regional and temporal variation of trends in phenology need to be studied further.

Acknowledgements

We are indebted to the German Weather Service (DWD), Dr Eric Dufrêne (Université de Paris XI) and Dr D. Koslowsky (Technical University of Berlin) who kindly provided ground

observation data and NDVI products, respectively. We are grateful for helpful comments of the reviewers. The work of J.S. was supported by a grant from the Hochschulsonderprogramm of the State of Brandenburg. W.L. was supported by the German Ministry of Education and Research, Climate Research Programme DEKLIM under project CVECA. Further funding was provided within the European project ATEAM (EVK2-2000-00075).

References

- Baumgartner A. 1952. Zur Phänologie von Laubböhlzern und ihre Anwendung bei lokalklimatischen Untersuchungen. *Berichte des DWD in der US-Zone* 42: 69–73.
- Botta A, Viovy N, Ciais P, Friedlingstein P, Monfray P. 2000. A global prognostic scheme of leaf onset using satellite data. *Global Change Biology* 6: 709–725.
- Buermann W, Anderson B, Tucker CJ, Dickinson RE, Lucht W, Potter CS, Myneni RB. 2003. Interannual covariability in Northern Hemisphere air temperatures and greenness associated with El Niño–Southern Oscillation and the Arctic Oscillation. *Journal of Geophysical Research – Atmospheres* 108: 4396.
- Calfapietra C, Gielen B, Sabatti M, De Angelis P, Miglietta F, Scarascia-Mugnozza G, Ceulemans R. 2003. Do above-ground growth dynamics of poplar change with time under CO₂ enrichment? *New Phytologist* 140: 305–318.
- Chen XQ, Pan WF. 2002. Relationships among phenological growing season, time-integrated normalized difference vegetation index and climate forcing in the temperate region of eastern China. *International Journal of Climatology* 22: 1781–1792.
- Chen WJ, Black TA, Yang PC, Barr AG, Neumann HH, Nestic Z, Blanken PD, Novak MD, Eley J, Ketler RJ, Cuenca A. 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Global Change Biology* 5: 41–53.
- Chmielewski FM, Rötzer T. 2001. Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology* 108: 101–112.
- D'Odorico P, Yoo J, Jaeger S. 2002. Changing seasons: an effect of the North Atlantic Oscillation? *Journal of Climate* 15: 435–445.
- Duchemin B, Goubier J, Courrier G. 1999. Monitoring phenological key stages and cycle duration of temperate deciduous forest ecosystems with NOAA/AVHRR data. *Remote Sensing of Environment* 67: 68–82.
- Erkamo V. 1953. On plant-biological phenomena accompanying the present climatic change. *Fennia* 75: 25–37.
- Fischer G, Shah M, van Velthuizen H. 2002. *Climate Change and Agricultural Vulnerability*. IASA report for the World Summit on Sustainable Development, Johannesburg. Vienna, Austria: IASA Publications Department.
- Forchhammer MC, Post E, Stenseth NC. 1998. Breeding phenology and climate. *Nature* 391: 29–30.
- Forstreuter M. 2002. *Auswirkungen globaler Klimaänderungen auf das Wachstum und den Gaswechsel (CO₂/H₂O) von Rotbuchenbeständen (Fagus sylvatica L.)*. Berlin, Germany: TU Berlin.
- Gutman GG. 1999. On the use of long-term global data of land reflectances and vegetation indices derived from the advanced very high resolution radiometer. *Journal of Geophysical Research* 104: 6241–6255.
- Hengst E. 1965. Phänologische Untersuchungen im Laubholzbestand. *Forstwissenschaftliches Centralblatt (Hamburg)* 84: 293–309.
- Herrick JD, Thomas RB. 2003. Leaf senescence and late-season net photosynthesis of sun and shade leaves of overstory sweetgum (*Liquidambar styraciflua*) grown in elevated and ambient carbon dioxide concentrations. *Tree Physiology* 23: 109–118.
- IPCC ed. 2001. *Climate Change 2001: The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the International Panel on Climate Change. Cambridge, UK: Cambridge University Press.
- Johnson IR, Thornley JHM. 1985. Temperature dependence of plant and crop processes. *Annals of Botany* 55: 7–24.
- Justice CO, Townshend JRG, Holben BN, Tucker CJ. 1985. Analysis of the phenology of global vegetation using meteorological satellite data. *International Journal of Remote Sensing* 6: 1271–1985.
- Kang S, Running SW, Lim J-H, Zhao M, Park C-R, Loehman R. 2003. A regional phenology model for detecting onset of greenness in temperate mixed forests, Korea: an application of MODIS leaf area index. *Remote Sensing of Environment* 86: 232–242.
- Keeling CD, Chin JFS, Whorf TP. 1996. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* 382: 146–149.
- Kirschbaum MUF, Fischlin A, Cannell MGR, Cruz RVO, Cramer WP. 1996. Climate change impacts on forests. In: Watson RT, Zinyowera MC, Moss RH, eds. *Climate Change 1995. Impacts, Adaptation and Mitigation of Climate Change: Scientific–Technical Analyses*. Contribution of WGII to the Second Assessment Report of the IPCC. Cambridge, UK: Cambridge University Press, 95–129.
- Koslosky D, Billing H, Eckardt M. 2001. Sensor degradation and inter-calibration of the short wave channels of the AVHRR–NOAA 11/14/16 satellites. *Proceedings of the 2001 EUMETSAT Meteorological Satellite Data Users' Conference* 31: 107–113.
- Kramer K. 1995. Modeling comparison to evaluate the importance of phenology for the effects of climate-change on growth of temperate-zone deciduous trees. *Climate Research* 5: 119–130.
- Lauscher F, Schnelle F. 1986. Beiträge zur Phänologie Europas V. Lange Phänologische Reihen und ihre Beziehung zur Temperatur. *Berichte Deutscher Wetterdienst* 169: 1–24.
- Lausi D, Pignatti P. 1973. Die Phänologie der europäischen Buchenwälder auf pflanzensoziologischer Grundlage. *Phytocoenologia* 1: 1–63.
- Lieth H. 1974. *Phenology and seasonality modelling*. Berlin, Germany: Springer.
- Lucht W, Prentice IC, Myneni RB, Sitch S, Friedlingstein P, Cramer W, Bousquet P, Buermann W, Smith B. 2002. Climatic control on the high-latitude vegetation greening trend and Pinatubo effect. *Science* 296: 1687–1689.
- Lüdeke MKB, Ramge PH, Kohlmaier GH. 1996. The use of satellite NDVI data for the validation of global vegetation phenology models: application to the Frankfurt biosphere model. *Ecological Modelling* 91: 255–270.
- Menzel A, Estrella N, Fabian P. 2001. Spatial and temporal variability of the phenological seasons in Germany from 1951 to 1996. *Global Change Biology* 7: 657–666.
- Moulin S, Kergoat L, Viovy N, Dedieu G. 1997. Global-scale assessment of vegetation phenology using NOAA/AVHRR satellite measurements. *Journal of Climate* 10: 1154–1170.
- Myneni RB, Hall FG, Sellers PJ, Marshak AL. 1995. The interpretation of spectral vegetation indexes. *IEEE Transactions on Geoscience and Remote Sensing* 33: 481–486.
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR. 1997a. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698–702.
- Myneni RB, Nemani RR, Running SW. 1997b. Estimation of global leaf area index and absorbed PAR using radiative transfer models. *IEEE Transactions on Geoscience and Remote Sensing* 35: 1380–1393.
- Norby RJ, Hartz-Rubin JS, Verbrugge MJ. 2003. Phenological responses in maple to experimental atmospheric warming and CO₂ enrichment. *Global Change Biology* 9: 1792–1801.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Penfound WT, Hall TF, Hess AD. 1945. The spring phenology of plants. *Ecology* 26: 332–352.

- Peñuelas J, Filella I, Comas P. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* 8: 531–544.
- Rathcke B, Lacey EP. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16: 179–214.
- Reed BC, Brown JF, Van der Zee D, Loveland TR, Merchant JW, Ohlen DO. 1994. Measuring phenological variability from satellite imagery. *Journal of Vegetation Science* 5: 703–714.
- Reilly J, Baethgen W, Chege FE, van de Geijn SC, Erda L, Iglesias A, Kenny G, Patterson D, Rogasik J, Rötter R, Rosenzweig C, Sombroek W, Westbrook J. 1996. Agriculture in a changing climate: impacts and adaptation. In: Watson RT, Zinyowera MC, Moss RH, eds. *Climate Change 1995. Impacts, Adaptation and Mitigation of Climate Change: Scientific–Technical Analyses*. Contribution of WGII to the Second Assessment Report of the IPCC. Cambridge, UK: Cambridge University Press, 427–467.
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.
- von Rudloff H. 1967. *Die Schwankungen und Pendelungen des Klimas in Europa seit dem Beginn der regelmäßigen Instrumenten-Beobachtungen (1670)*. Braunschweig, Germany: Vieweg & Sohn.
- Saxe H, Cannell MGR, Johnsen B, Ryan MG, Vourlitis G. 2001. Tree and forest functioning in response to global warming. *New Phytologist* 149: 369–399.
- Schaber J. 2002. Phenology in Germany in the 20th century: methods, analyses and models. PhD thesis. Potsdam, Germany: University of Potsdam. <http://pub.ub.uni-potsdam.de/2002/0022/schaber.pdf>
- Schaber J, Badeck FW. 2003. Physiology-based phenology models for forest tree species in Germany. *International Journal of Biometeorology* 47: 193–201.
- Scheffinger H, Menzel A, Koch E, Peter C, Ahas R. 2002. Atmospheric mechanisms governing the spatial and temporal variability of phenological phases in central Europe. *International Journal of Climatology* 22: 1739–1755.
- Schnelle F. 1955. *Pflanzenphänologie*. Leipzig, Germany: Akademische Verlagsgesellschaft.
- Schwartz MD. 2003. *Phenology. An integrated environmental science*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Schwartz MD, Crawford TM. 2001. Detecting energy balance modifications at the onset of spring. *Physical Geography* 22: 394–409.
- Schwartz MD, Reed BC, White MA. 2002. Assessing satellite-derived start-of-season measures in the conterminous USA. *International Journal of Climatology* 22: 1793–1805.
- Sigurdsson BD. 2001. Elevated [CO₂] and nutrient status modified leaf phenology and growth rhythm of young *Populus trichocarpa* trees in a 3-year field study. *Trees – Structure and Function* 15: 403–413.
- Slayback DA, Pinzon JE, Los SO, Tucker CJ. 2003. Northern hemisphere photosynthetic trends 1982–99. *Global Change Biology* 9: 1–15.
- Sparks TH, Carey PD, Combes J. 1997. First leafing dates of trees in Surrey between 1947 and 1996. *London Naturalist* 76: 15–20.
- Stöckli R, Vidale PL. 2004. European plant phenology, climate as seen in a 20 year AVHRR land-surface parameter dataset. *International Journal of Remote Sensing* (In press.)
- Suzuki R, Nomaki T, Yasunari T. 2003. West–east contrast of phenology and climate in northern Asia revealed using a remotely sensed vegetation index. *International Journal of Biometeorology* 47: 126–138.
- Traidl-Hoffmann C, Kasche A, Menzel A, Jakob T, Thiel M, Ring J, Behrendt H. 2003. Impact of pollen on human health: more than allergen carriers? *International Archives of Allergy and Immunology* 131: 1–13.
- Tüxen R, Wojterska M. 1977. Bibliographie der Phänospektrum-Diagramme von Pflanzengesellschaften. Pars II. *Excerpta Botanica* 16: 306–317.
- Viovy N. 2000. Automatic classification of time series (ACTS): a new clustering method for remote sensing time series. *International Journal of Remote Sensing* 21: 1537–1560.
- Viovy N, Arino O, Belward AS. 1992. The best index slope extraction (BISE): a method for reducing noise in NDVI time series. *International Journal of Remote Sensing* 13: 1585–1590.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- White MA, Nemani RR. 2003. Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest. *Global Change Biology* 9: 967–972.
- White MA, Thornton PE, Running SW. 1997. A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochemical Cycles* 11: 217–234.
- White MA, Running SW, Thornton PE. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology* 42: 139–145.
- Zhang X, Friedl MA, Schaaf CB, Strahler AH, Hodges JCF, Gao F, Reed BC, Huete A. 2003. Monitoring vegetation phenology using MODIS. *Remote Sensing of Environment* 84: 471–475.
- Zhou L, Tucker CJ, Kaufmann RK, Slayback D, Shabanov NV, Myneni RB. 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981–99. *Journal of Geophysical Research* 16: 20069–20083.