PERSPECTIVES: PHENOLOGY

Responses to a Warming World

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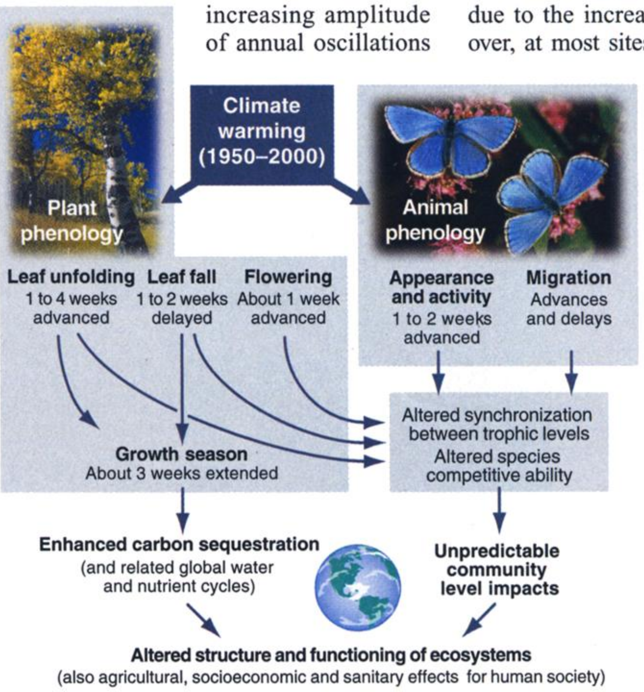
Climate warming (*1*) is expected to alter seasonal biological phenomena such as plant growth and flowering or animal migration, which depend on accumulated temperature, that is, the total heat required for an organism to develop from one point to another in its life cycle. These so-called phenological changes are likely to have a wide range of consequences for ecological processes, agriculture, forestry, human health, and the global economy. An increasing number of studies now report changes in plant and animal cycles from a wide range of regions, from cold and wet to warm and dry ecosystems. These phenological changes are sensitive and easily observable indicators of biospheric changes in response to climate warming.

Phenological changes differ from species to species (*2–12*), but some are substantial (see the figure). In Mediterranean ecosystems, the leaves of most deciduous plant species now unfold on average 16 days earlier and fall on average 13 days later than they did 50 years ago (*7*). In Western Canada, *Populus tremuloides* shows a 26-day shift to earlier blooming over the past century (*9*). Other shifts are smaller but go in the same direction. A 6-day shift to earlier leaf unfolding and a 5-day delay in autumn leaf coloring over 30 years have been described from Scandinavia to Macedonia (*4*). An earlier onset of biological spring by about 8 days has also been reported across Europe for 1969–98 (*10*, *11*) and by about 6 days in North America for 1959–93 (*12*). In marine ecosystems, substantial positive linear trends in phytoplankton season length and abundance have been described in areas of the North Atlantic with warming waters for 1948–95 (*13*).

Remote sensing data validate these ground observations on larger scales. The Normalized Difference Vegetation Index (NDVI), which is derived from infrared and red Earth surface reflectance, scales with green biomass. NDVI satellite data between 45°N and 70°N for 1982–90 showed an 8-day shift to an earlier start of the growing season and a delay of 4 days for the declining phase (*14*). New NDVI data suggest that the growing season has become nearly 18 days longer during the past two decades in Eurasia and 12 days longer in North America (*15*). The data also show a gradual greening of the northern latitudes above 40°N: Plants have been growing more vigorously since 1981, especially in Eurasia.

This lengthening of the plant growing season is likely to contribute to the global increase in biospheric activity, which has been inferred from the increasing amplitude of annual oscillations in the atmospheric CO_2 between 1960 and 1994 (*16*). The atmospheric data also suggest an extension of the growing season by about 7 days in the Northern Hemisphere between the 1960s and the early 1990s, mostly after 1980. Accelerated tree growth across Europe, previously attributed to fertilization by nitrogen compounds and increased CO_2 (*17*), may be driven at least partly by this extended growing season. The lengthening of the growing season thus plays a key role in global carbon fixation, the amount of CO_2 in the atmosphere, and related global water and nutrient cycles.



Ecological consequences of climate warming on plant and animal phenology.

Data on shifts in flowering dates are abundant and show similar trends. Shifts to earlier flowering by about 1 week have been reported in Mediterranean species for 1952 to 2000 (*7*), in Hungary for 1851 to 1994 (*3*), in Wisconsin for 1936–98 (*5*), and in Washington, DC, for 1970–99 (*6*). These observations agree with model results, which indicate that the time of maximum olive pollen concentrations advances by about 6 days per degree Celsius in the western Mediterranean (*18*).

All these plant phenological changes are highly correlated with temperature changes, especially in the months before seasonal life cycle events. Temperature (*1*) as well as phenology has changed most noticeably after the mid-1970s. This correlation does not necessarily imply a causal connection. However, available data and current knowledge of plant phenology, including numerous experimental studies (*4*, *19*, *20*), indicate that the observed changes are mostly due to the increased temperatures. Moreover, at most sites, the number of freezing days has decreased substantially in recent years (*1*, *7*), decreasing the probability of frost damage to young leaves and flowers (*21*).

Animal life cycles also depend on climate. For example, insects are expected to pass through their larval stages faster and become adults earlier in response to warming. Aphid species in the United Kingdom have shown a 3- to 6-day advance in the timing of different phases in their life cycle over the past 25 years (*22*). The date on which the maximum numbers of individuals of the most common Microlepidoptera in the Netherlands were counted shifted forward by 12 days on average between 1975 and 1994 (*23*). Butterflies now appear 11 days earlier than in 1952 in northeast Spain (*7*). British butterflies have not only appeared earlier but have also shown longer flight periods, that is, enhanced activity, over the past two decades (*24*). In other animal groups, frog calling has been reported to occur about 10 days earlier between 1990 and 1999 than between 1900 and 1912 in New York state (*25*), and bird species surveyed in the United Kingdom from 1971 to 1995 showed 9-day shifts toward earlier egg laying (*2*).

The advanced leafing, flowering, fruiting, and appearance of insects are likely to advance the availability of food supplies for

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birds. However, a later arrival in Europe of migratory birds wintering south of the Sahel has been reported (*7*, *26*). For these species, the decision when to start spring migration may become maladaptive when the cue for migration is independent of the environmental change in the breeding area (*7*). Climate change may thus be a serious threat to species that migrate from tropical wintering grounds to temperate breeding areas. They may arrive at an inappropriate time to exploit the habitat and compete with larger numbers of individuals of resident species as more of them survive the winter. These arguments may partly explain the decline of these long-distance migratory species in Western Europe (*8*), although short-distance migrants may be more flexible. These findings support previous results demonstrating that shifts in global climate patterns can affect migratory birds (*27*).

These changes in plant phenology and bird migration show that climate warming may lead to a decoupling of species interactions, for example, between plants and their pollinators or between birds and their plant and insect food supplies (*2*). Changes not only in mean temperatures but also in temperature patterns may affect these interactions even more strongly because they may alter the synchronization between species (*28*). An example of such decoupling was recently reported. The Great Tit still breeds at the same time, but its food supply has been advanced because of earlier plant development in recent years (*29*). Different phenological responses (*7*, *30*) may alter the competitive ability of different species and thus their ecology and conservation, resulting in unpredictable impacts on community structure and ecosystem functioning.

The observed phenological changes have occurred with a warming only 50% or less of that expected for the 21st century (*1*). Many ecological (carbon sequestration, nutrient and water cycles, species competition, pests and diseases, bird migration and reproduction, and species-species interactions), agricultural (crop suitability, yield potential, length of growing season, risk of frost damage, epidemiology of pests and diseases, timing and amount of pesticide use, and food quality), and socioeconomic and sanitary (duration of the pollen season and distribution and population size of disease vectors) factors depend strongly on plant and animal phenology. Phenology is therefore increasingly relevant in the framework of global change studies (*31*).

As in many areas of environmental science, the key requirement is long-term data sets. Today, thousands of people—professionals and volunteers—record phenological changes all over the world, as do international and national phenological monitoring networks such as Global Learning to Benefit the Environment (GLOBE) or the European Phenology Network. Together with remote sensing, atmospheric, and ecological studies, these data will help to answer the many questions raised by the recently reported climate effects on phenology: What are the limits of the lengthening of the plant growth season and the consequent greening of our planet? Will the (less seasonal) tropical ecosystems be less affected than boreal, temperate, and Mediterranean ecosystems? How will different aquatic ecosystems respond? How will responses to temperature and other drivers of global change interact to affect phenology and the distribution of organisms? How will changes in synchronization between species affect population dynamics both in terrestrial and aquatic communities? Will appropriate phenological cues evolve at different trophic levels?

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31. A conference, "The times they are a changing. Climate change, phenological responses and their consequences for biodiversity, agriculture, forestry and human health," will be held in Amsterdam in December 2001; see www.dow.wau.nl/msa/epn/conference.

PERSPECTIVES: PLANT BIOLOGY

A Baroque Residue in Red Wine

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The walls of higher plants contain small amounts of a mysterious polysaccharide known as rhamnogalacturonan II (RGII). RGII is thought to be the most complex polysaccharide on Earth, and its presence and strong conservation in all higher plants suggest that it is important for the structure or growth of plant cell walls. The study by O'Neill *et al.* (*1*) on page 846 of this issue convincingly shows, 23 years after its discovery (*2*), that RGII is essential for plant growth and that minor changes in its structure cause growth defects.

More than 300 years ago, Robert Hooke pointed his primitive microscope at a slice of cork and discovered the cellular basis of organisms. Sadly, since then, plant cell walls, which formed the compartments he actually observed, have never been considered particularly entertaining structures. Indeed, the word wall itself evokes something dull and rigid, built only to enclose, support, divide, and protect. However, a closer look reveals just how erroneous this view is. Walls of growing plant cells are extremely sophisticated composite materials made of dynamic networks of polysaccharides, protein, and phenolic compounds. Cellulose microfibrils with a tensile strength comparable to that of steel provide the plant with a load-bearing framework. These microfibrils are rigid wires made of crystalline arrays of β-1,4-linked chains of glucose residues, which are extruded from little hexameric spinnerets in the plant cell plasma membrane and surround the growing cell like the hoops around a barrel. Because cellulose microfibrils constrain turgor-driven cell expansion in one preferential direction, they control the shape of plant cells and ultimately that of the plants themselves. Hemicelluloses, such as xyloglucans, are tethered by hydrogen bonds to cellulose and form cross-links that may control the separation of the cellulose microfibril hoops. The cellulose-hemicellulose network is embedded in a matrix of complex galacturonic acid–rich pectic

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