Seasons and Life Cycles

A conceptual framework explains how individual species' responses to climate warming affect the length of the growing season.

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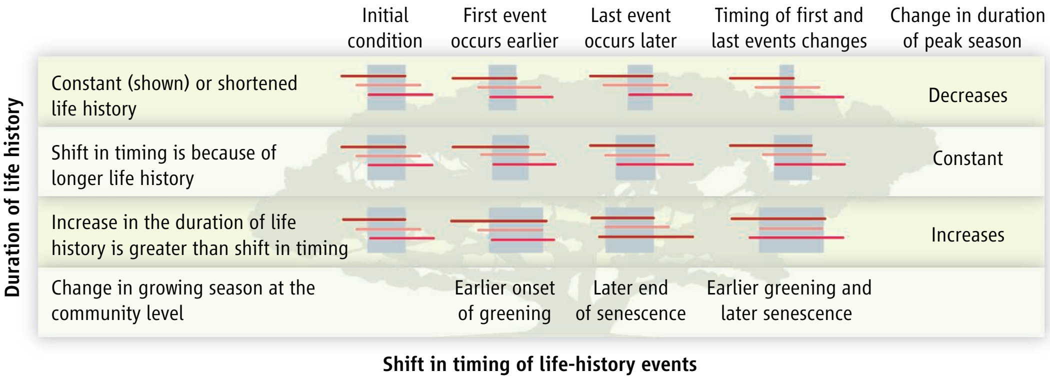
An apparent contradiction has arisen in studies of plant phenological response to climatic warming: Field and satellite data at the community and biome levels indicate a lengthening of the growing season across much of the Northern Hemisphere (*1*–*6*) and—where data exist—in the Southern Hemisphere (*5*, *7*, *8*), yet life history observations of individual species suggest that many species often shorten their life cycle in response to warming (*9*–*12*). Here, we pair evolutionary and ecological viewpoints to resolve this conundrum.



A conceptual framework. This table is a guide to determining how individual species are responding to an extended growing season by observing the duration of peak season. The life history of a species—from the onset of greening through the end of senescence—is illustrated by the length of the solid lines. Each case represents a shift in the timing (columns) and duration (rows) of one or more species in a hypothetical three-species community that includes an early-, mid-, and late-season species. The growing season begins when the first species greens and ends when the last species senesces. The peak season (gray shaded area) occurs when all species have started and none have completed their life history. Reproductive life history events likely begin before the peak season and are completed before its end. The final row and column list changes that can be observed through frequent observations of surface greenness.

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If a plant starts to green earlier, subsequent events in the plant's life cycle often occur earlier as well (*9*–*12*). Advancing the timing of early-season events in this way may increase plant fitness by ensuring that reproduction occurs before loss of reproductive tissues to, for example, herbivory or drought (*13*, *14*). An extended life cycle can also improve fitness if it leads to more or larger offspring, but exposes plants to the risk of damage to flowers or fruits before maturation (*13*). The prevalence of these divergent strategies at the community level will depend on the responses of individual plant species to climatic trends and interannual variation in climatic conditions.

Within a community of several species, life history strategies typically vary, increasing the probability that the length of the growing season quantified at the community level will increase with climate warming. For example, the length of the community's growing season will rise even if early-season species green but also senesce earlier while the timing of events for late-season species remains stable or advances less in response to warming. Thus, ecological constraints on the length of the community's growing season may be eased by climate warming, whereas evolutionary constraints on the life-cycle durations of individual species may limit their response and explain the diverse responses of different species to warming (*9*–*12*).

A longer growing season has been one of the most widely observed biological changes in response to climatic warming across temperate to polar latitudes during the 20th century (*1*–*6*). This change in growing season length has been occurring in regions where temperatures have increased (*5*) and in passive warming experiments that have been replicated across the Northern Hemisphere (*15*–*17*). A nearly universal advance in spring temperature indices of first leaf and bloom dates for cloned lilac and honeysuckle across temperate areas of the Northern Hemisphere has also been reported (*18*). In the Southern Hemisphere, a recent passive warming study in an Australian subalpine meadow showed an advance in spring events for 7 of 14 species (*19*). Predictions from phenological models that use temperature data to estimate the timing of spring events suggest that comparable changes in growing season length have not taken place over the past two centuries in boreal Eurasia (*1*) and that the expected warming in the 21st century will further lengthen the growing season by 5.0 to 9.2 days in North America (*20*).

Few studies on the effects of temperature on growing season length have been conducted in the tropics because of the expectation that temperature does not constrain growing season length there, but the absence of data should not be considered a lack of response (*5*). In two of the three tropical regions studied in Africa, the growing season has lengthened since the early 1980s (*7*). However, earlier budburst in warmer urban areas relative to nearby rural areas was found only in one-third of tropical cities versus three-fourths of temperate cities (*21*).

In contrast to the observed changes in the overall length of the growing season, warming often shortens the duration of life histories of individual species. For many species, climate warming leads not only to earlier greening but also to earlier flowering and senescence (*9*–*12*). Although life histories of individual species may thus be shortened, a longer growing season could still result if the responses of different species in a community diverge, possibly as a result of seasonal niche divergence (see the table). Earlier springs could be caused by an advance in the life history of early-season species in response to warmer air temperatures. Later falls could result from a delay in the life history of late-season species because of extreme mid-season temperatures and low water availability.

These divergent responses by different species to gradual climate warming and to extreme warming events have been seen in forest, grassland, and tundra communities in North America (*9*, *11*, *12*), Europe (*14*), and

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Australia (*19*). Thus, the widespread increase in growing season length may be a result of shortened and more divergent life histories.

Monitoring of the peak season duration through observations of surface greenness can be used to determine how individual species respond to an extended growing season (see the table). Changes in the duration of species' life histories have consistent effects on the peak season duration. Constant or shortened life histories decrease the peak season duration. Alternatively, if the shift in timing occurs because of a longer life history, the duration of the peak season will remain constant. Finally, the peak season duration will only increase if species extend their life cycles by more days than the growing season is lengthened.

Daily measurements of surface greenness from ground-based platforms are increasingly used in phenological studies (*22*, *23*), including those in the tropics (*24*). These data may be sufficient to characterize the duration of peak season in regions where canopy closure corresponds with the onset of peak leaf area. However, models that relate leaf density to greenness may be needed where this does not occur. Piecewise linear models can be fit to the data to determine the duration of peak season via the onset of peak leaf area and senescence. Observations of surface greenness in phenological networks would create continental-scale data sets that could be compared to regional trends in climate and to satellite data.

Although an extended growing season may lead to increased plant production, this is less likely if individual species shorten their life histories. Shortened, more divergent life histories may lead to gaps in the availability of resources for pollinators and herbivores (*11*) and may facilitate the establishment of invasive species (*12*). Nutrient losses during the growing season could also increase through decreased species complementarity (*9*). Thus, the contrasting changes in the duration of the growing season and species' life cycles are consistent, but increase the likelihood that climate warming is altering the structure and function of ecological communities, perhaps adversely.

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ECOLOGY

Phenology Feedbacks on Climate Change

A longer growing season as a result of climate change will in turn affect climate through biogeochemical and biophysical effects.

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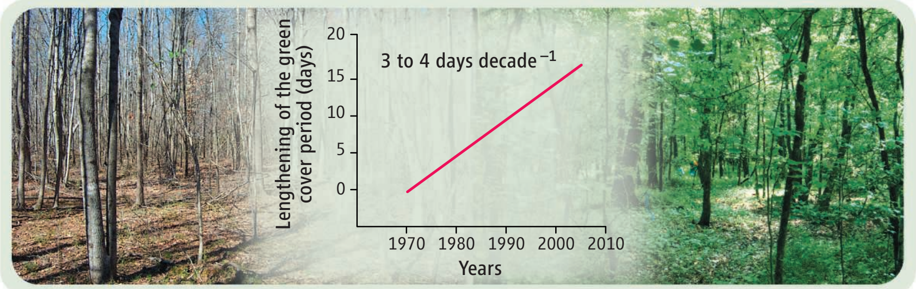
Climate warming has advanced the biological spring and delayed the arrival of biological winter (*1*, *2*). These changes in the annual cycle of plants and the lengthening of the green-cover season have many consequences for ecological processes, agriculture, forestry, human health, and the global economy (*3*). Studies on vegetation-atmosphere interactions (*4*) and particularly on the impact of leaf emergence on climate (*5*–*9*) suggest that the phenological shifts in turn affect climate. The magnitude and sign of this effect are unknown but depend on water availability and regional characteristics.

The earlier presence of green land cover and the delay in autumnal senescence and leaf fall of deciduous canopies may alter the seasonal climate through the effects of biogeochemical processes (especially photosynthesis and carbon sequestration) and physical properties (mainly surface energy and water balance) of vegetated land surfaces.

CO_2 uptake is the main biogeochemical effect. An extended plant activity season increases biospheric CO_2 uptake (*3*) and thus decreases the current rise of atmospheric CO_2 concentration and its influence on the greenhouse effect (*1*). The extended plant activity also further increases the total annual emission of biogenic volatile organic compounds (BVOCs) (*10*). These increased emissions may also contribute to the complex processes associated with global warming (*10*).

Although the atmospheric lifetime of BVOCs is short, they have an important influence on climate through aerosol formation and



Phenology and climate. The change from a dormant winter to a biologically active spring landscape has numerous biogeochemical and biophysical effects on climate. Earlier leaf unfolding and delayed leaf fall as a result of global warming (graph) (*3*, *17*) will thus affect climate change itself.

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