The 2007 Eastern US Spring Freeze: Increased Cold Damage in a Warming World?

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Plant ecologists have long been concerned with a seemingly paradoxical scenario in the relationship between plant growth and climate change: warming may actually increase the risk of plant frost damage. The underlying hypothesis is that mild winters and warm, early springs, which are expected to occur as the climate warms, may induce premature plant development, resulting in exposure of vulnerable plant tissues and organs to subsequent late-season frosts. The 2007 spring freeze in the eastern United States provides an excellent opportunity to evaluate this hypothesis and assess its large-scale consequences. In this article, we contrast the rapid prefreeze phenological advancement caused by unusually warm conditions with the dramatic postfreeze setback, and report complicated patterns of freeze damage to plants. The widespread devastation of crops and natural vegetation occasioned by this event demonstrates the need to consider large fluctuations in spring temperatures a real threat to terrestrial ecosystem structure and functioning in a warming climate.

Keywords: extreme temperature fluctuation, frost damage, plant phenology, climate warming, carbon cycle

Unpredictable extreme weather and climate events have the potential to upset the normal exchanges of carbon dioxide (CO_2) among different carbon reservoirs of the Earth system and cause great uncertainty in assessment of the global carbon cycle. For example, the heat wave and drought in the summer of 2003 in Europe effectively eliminated the net terrestrial carbon uptake accumulated by the whole region during the previous four years (Ciais et al. 2005). Alternating warm and freezing weather represents another form of extreme event that can endanger vegetation, as warm conditions induce untimely early plant growth and development, which may be cut short by subsequent frosts (Cannell and Smith 1986, Inouye 2000). Such temporal patterns of temperature constitute an "agent of surprise" for terrestrial ecosystem functioning (i.e., carbon and water cycles) in a warming climate.

This agent of surprise is not a remote possibility. In 2007, both the western and the eastern parts of the United States witnessed its power. In January, an Arctic air mass blanketed the western United States, and in April, a severe frost and freezing event swept across the eastern United States. The events shared two characteristics: they were preceded by unusually warm conditions, and they had disastrous consequences for natural vegetation and many crops. The freezing event in the eastern United States, which occurred 5–9 April (and thus is sometimes called the 2007 Easter freeze), is particularly interesting because it affected a very broad region and occurred during the crucial transition period for plants from dormancy to growth.

In the days and weeks following the 2007 spring freeze, we initiated a sequence of measurements at established research sites in the affected region and analyzed relevant remote-sensing images. These efforts allowed us to evaluate the consequences of the event quantitatively and to develop hypotheses in view of a warming climate. In this article, we report initial findings, discuss the potential implications of the 2007 spring freeze, and call attention to the research opportunities this event offers.

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The event

The 2007 spring freeze was caused by a winter configuration of the jet stream, which brought an Arctic air mass deep into the eastern two-thirds of the conterminous United States, breaking low-temperature records in dozens of locations. The spatial extent of the event is delineated approximately by the daily minimum temperature anomaly as determined by the terrestrial observation and prediction system (TOPS) (figure 1; Nemani et al. 2007). Spring freezing events are not unusual in this part of the United States; it is unusual, however, to have such an extreme freeze event after extended periods of above-normal temperatures.

At an AmeriFlux site in central Missouri (Gu et al. 2006), the daily minimum temperature exceeded 15 degrees Celsius (°C) for a week just before the sustained April freeze, which at its coldest reached –7°C (figure 2a). The daily minimum temperature also exceeded 15°C eight times during the two weeks leading up to the freeze event, which at its coldest reached –5°C, at the Walker Branch watershed station in Tennessee (figure 2b). This stretch of high late-winter temperatures preceding the freeze, coupled with above-normal warmth earlier in March, caused that month in 2007 to be the warmest March on record at the Walker Branch station and also at the nearby Oak Ridge, Tennessee, station (mean temperature of 13.7°C; period of record, 1948–2007).

To help place such extreme early spring temperature fluctuations in context, the next warmest March at Oak Ridge that was followed by a multiday April freezing event was in 1989, with a mean temperature of 11.6°C (the 10th warmest March on record). As shown in the next sec-

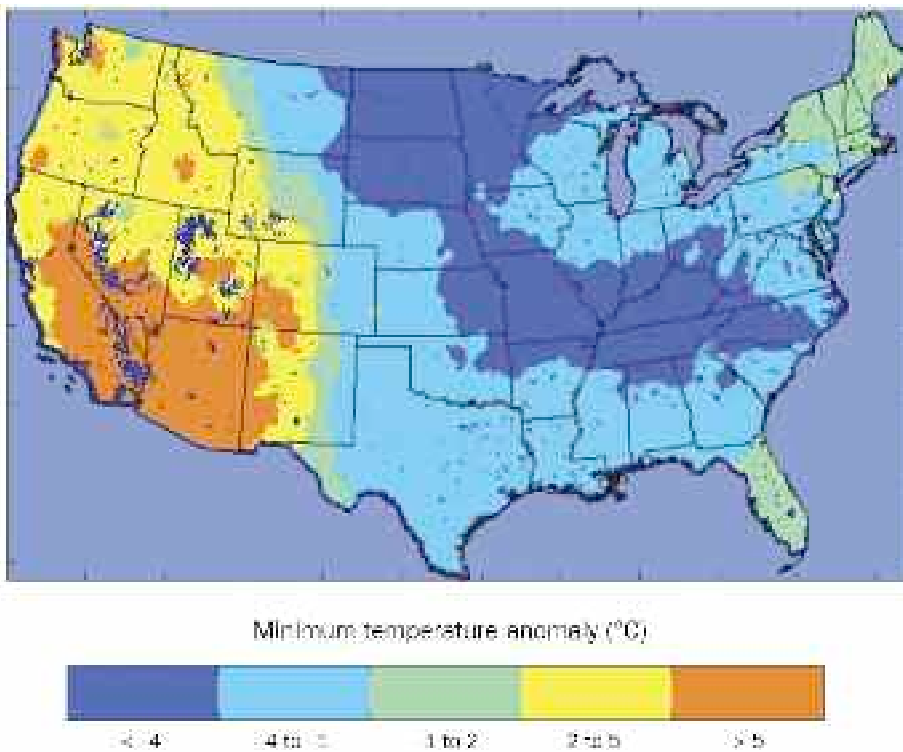

Figure 1. Anomalies of the average daily minimum temperature (degrees Celsius) for the period 5–9 April 2007 relative to the 2000–2006 average computed with the terrestrial observation and prediction system (8-kilometer spatial resolution).

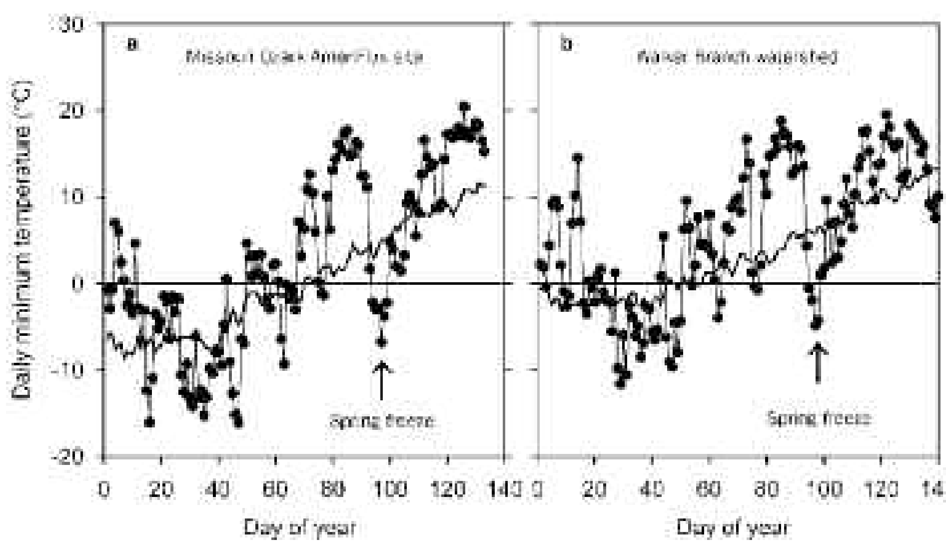

Figure 2. The 2007 daily minimum temperatures (line with circles), in degrees Celsius, versus the long-term mean daily minimum temperatures (line only) at the Missouri Ozark AmeriFlux site in central Missouri (a) and at the Walker Branch watershed site in eastern Tennessee (b). Note the similarity of the 2007 daily minimum temperatures in central Missouri and eastern Tennessee around the time of the freeze, indicating the broad spatial extent of the warm-freeze sequence that was responsible for the large-scale damage to plants. Also note the high temperatures right before the freeze. Long-term mean minimum temperatures for Walker Branch cover the period from 1951 to 2006 (data are from http://walkerbranch.ornl.gov/ *and* http://tde.ornl.gov*). Long-term mean minimum temperatures for Missouri are for the 1971–2000 period, measured at the nearby weather station at the Columbia Regional Airport (data are from the National Climatic Data Center).*

tions, the unusually warm periods before the 2007 spring freeze caused plants to break dormancy early throughout the southern part of the central and eastern United States. When the cold, Arctic air subsequently moved into the region, the stage was set for the freeze to decimate newly grown tissues of crops, horticultural plants, and native forest species.

From a rushing "green wave" to a collapsing "green retreat"

The MODIS (Moderate-resolution Imaging Spectroradiometer) rapid response system (RRS; *http://rapidfire.sci.gsfc.nasa.gov/*) provided timely spatial and temporal information about the impacts of the 2007 spring freeze on vegetation development (i.e., leaf canopy) in the affected region. Images of the Normalized Difference Vegetation Index (NDVI) from the MODIS RRS before the freeze indicated that vegetation in the southeastern United States and the southern part of the Midwest was developing rapidly, and showed the vernal front reaching as far north as northern Missouri. After the freeze, the vernal front was pushed back to mid-state locations in Arkansas, Mississippi, Alabama, and Georgia (figure 3; compare the dark green areas in panels a and b). The regionwide phenological development in 2007 (figure 3a, 3b) also presented a marked contrast to that in 2006 (figure

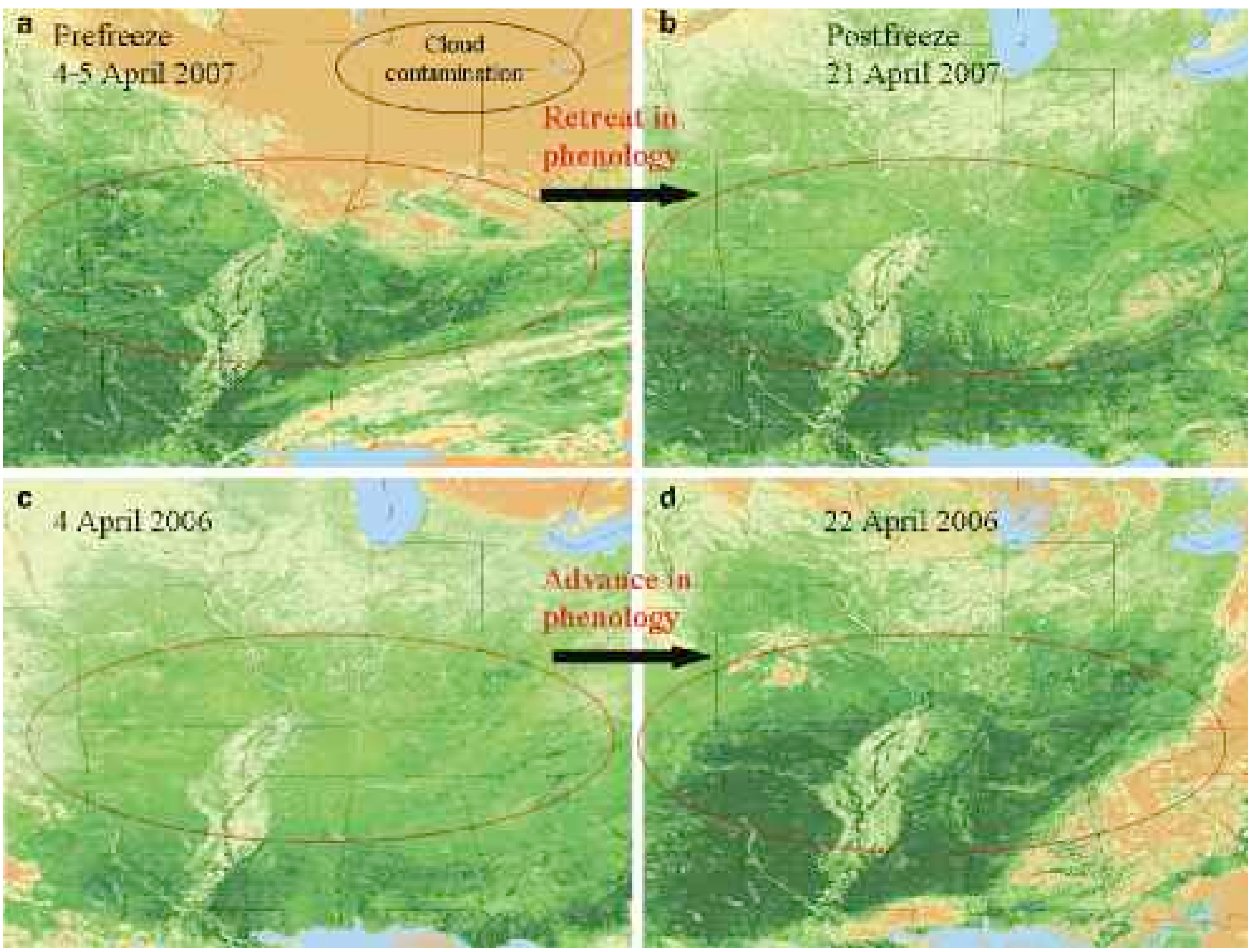

Figure 3. Normalized Difference Vegetation Index (NDVI) images reflecting the impact of the 2007 spring freeze on phenological development. The freeze-induced damage to vegetation is indicated by the reduced greenness from (a) to (b), most noticeably within the oval area bordered by a solid line. The impact can also be inferred by comparing (a) and (b) with the normal spring phenological progression represented by two images from 2006 around the same time (c and d). Note that before the freeze, phenology is more advanced in 2007 than in 2006 (compare a and c), whereas after the freeze, the opposite is true (compare b and d). Each NDVI panel consists of two cuts from the MODIS (Moderate-resolution Imaging Spectroradiometer) rapid response system (RRS) 1-kilometer resolution Terra daily images. Dates were chosen not only to represent times before and after the freeze but also to minimize the presence of clouds identified visually from the true-color images (not shown), indicated by the brownish bands in the NDVI images. The MODIS RRS team produces RRS images, which have been used extensively for monitoring extreme events such as wildfires, floods, dust or snow storms, and, here, freeze damage to vegetation.

3c, 3d). Before the spring freeze in 2007, the southeastern NDVI was developing much faster than in 2006 (figure 3, compare panels a and c). After the freeze, the opposite pattern is clearly evident (figure 3, compare panels b and d). The freeze effectively and nearly instantaneously turned a rushing green wave of vegetation development into a green retreat.

The collapse of the early vegetation development was even more vivid on the ground. The 2007 spring freeze killed newly formed leaves, shoots, and developing flowers and fruits (figure 4), and left entire forest ridges brown, symptomatic of the extreme nature of the freeze. Plant canopies transitioned from elongating shoots and expanding leaves and flowers to dark brown, necrotic, desiccated litter in a matter of days (figures 5, 6). The consequences were not limited to canopy physiognomy. In a temperate deciduous forest in Oak Ridge, Tennessee, we observed increased illumination of the understory (figure 7) during a period when understory conditions normally would have transitioned into deep shade.

The 2007 spring freeze hit agriculture particularly hard. Severe and widespread damage to crops was reported from Nebraska to Maryland in the north, and from Texas to South Carolina in the south. Farmers in several states considered this freezing event "the worst ever seen," and many sought federal farm disaster relief. For example, the agricultural loss in North Carolina alone was estimated at $111.7 million, and Governor Mike Easley requested federal disaster declaration for crop damage in 56 counties (*www.governor.state.nc.us/News_FullStory.asp*).

Postfreeze surveys in eastern Tennessee and northern Georgia revealed that plants had extensive, complex responses to frost. The degree of frost damage among species in the same habitat was very different, ranging from total loss of flowers, fruits, and leaves (e.g., oak [*Quercus*] and hickory [*Carya* spp.]) to largely undamaged crowns (e.g., red maple [*Acer rubrum* L.]). The pace of postfreeze regrowth was also different among species; yellow poplar (*Liriodendron tulipifera* L.) was surprisingly slow to recover. After the freeze, new shoots and leaves grew from dormant lateral buds, and epicormic shoots developed from trunks and branches (figure 8) following the removal of apical dominance, but by midsummer, the normal level of canopy development observed in previous years had not been achieved (figure 7).

Variations in microclimate added to a complicated spatial pattern of plant damage. Plants inside dense canopies suffered less damage because they were protected by the volume of the forests and the associated heat storage (Gu et al. 2007). At higher elevations in the Cumberland and Appalachian mountains of eastern Tennessee, damage was less severe because

Figure 4. Sample photographs showing different degrees of freeze damage to leaves and fruits of natural and horticultural species in Oak Ridge, Tennessee.

Figure 5. A comparison of prefreeze and postfreeze aspects of a switchgrass plantation in Milan, Tennessee. The switchgrass in the lower picture was not dead and grew back subsequently. The summer-style clothing of the two scientists in the upper picture indicates the warmness right before the 2007 spring freeze. Photographs: Tris West (prefreeze picture); Rosier Matamala (postfreeze picture).

plants at those altitudes had not experienced warm enough temperatures before the freeze to advance their phenological development. On lower hills, however, damage was widespread. Interestingly, the high thermal capacities of large bodies of water (lakes and river reservoirs) protected adjacent vegetation; for example, vegetation along the edges of Watts Bar and Chickamauga lakes in eastern Tennessee was undamaged by the spring freeze, in contrast to vegetation away from the lakes (figure 9). Vegetation on islands within these lakes showed no signs of frost damage, but we have not yet investigated whether differences in species composition could contribute to the spatial pattern of damage observed in the lake areas.

The warm-cold sequence as the culprit for damaging plants

Note that the unusual warmth before the 2007 spring freeze (figures 2, 5) was as much of a culprit as the freeze itself for the widespread, severe damage to plants. The regionwide, early phenological development caused by high temperatures before the freeze is apparent in figure 3 (panels a and c). We also surveyed reports on the agricultural impacts of the 2007 spring freeze from a variety of media outlets (e.g., Agriculture Online, North Carolina Cooperative Extension, Southeast Farm Press, *USA Today*). According to our survey, farmers and extension specialists throughout the affected region estimated that the development of crops (e.g., wheat, pecan, apple, peach) before the freeze was two to three weeks earlier in 2007 than in 2006. This premature development made plants more vulnerable to the subsequent devastation by the freeze.

In the temperate deciduous forest mentioned earlier (figure 7), spring leaf-out typically starts around day 100 (from January 1). Because of the record warmth of March, however, in 2007 leaf-out started around day 85 and progressed rapidly until the freeze hit. The damage caused by the freeze was apparently sustained—canopy development was significantly below the average level by midsummer. In contrast, the spring of 1996 was very cold, but consistent (no extreme warm-cold fluctuations); canopy development began late (around day 110), but the consistently cold temperatures that spring did not prevent the canopy from achieving its normal development level. The contrast between 1996 and 2007 in this deciduous forest demonstrates that a swinging warm and cold spring is more harmful to plants than a consistently cold spring.

Potential short-term and long-term effects of the 2007 spring freeze on the terrestrial carbon cycle

All signs have so far indicated that the 2007 spring freeze had at least a short-term, profound effect on the terrestrial carbon cycle in much of the central and eastern United States during the crucial period of spring phenological development. In fact, for the period 7–14 April 2007, the fraction of absorbed photosynthetically active radiation, a sensitive indicator of terrestrial primary production (computed by TOPS), was markedly lower than the 2001–2006 average for the same period (figure 10). At the Missouri Ozark AmeriFlux site (Gu et al. 2006), reduced forest carbon uptake and altered surface energy balance were observed after the freeze. It also appears that regrowth did not yield the normal maximal leaf area indices of major deciduous forest biomes found in the freeze-affected region in previous years (figure 7). Given the severity and spatial extent of the damage in 2007 to managed and natural vegetation throughout the southeast, one might question how strong the terrestrial carbon sink was that year in the United States, and speculate on long-lasting impacts beyond the 2007 growing season.

We hypothesize on the basis of several considerations that this event will evoke both short-term and long-term responses. The level of tissue damage represents a substantial loss of carbon and nutrients that would have been remobilized to internal plant stocks during autumnal senescence. Plants cannot resorb nutrients and carbohydrates from freeze-damaged tissues. The loss of energy-intensive resources disturbs the internal nutrient cycling and carbohydrate

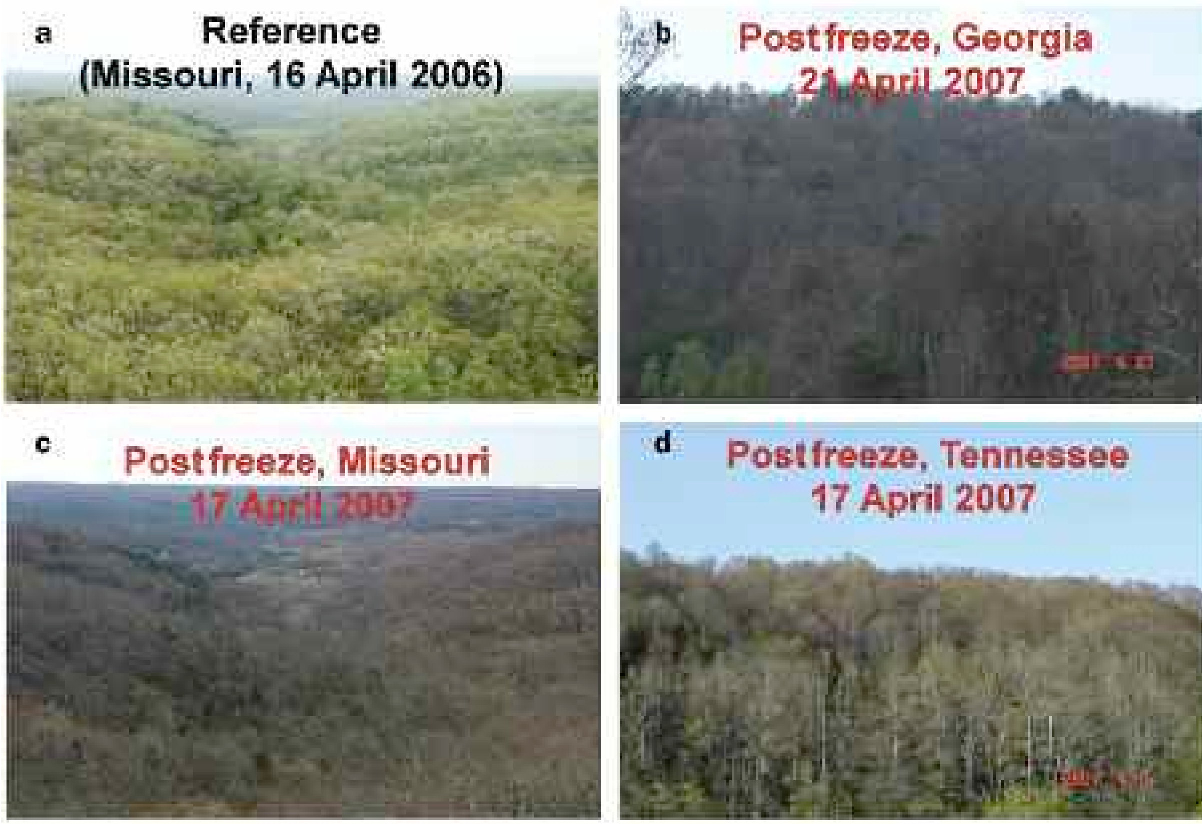

Figure 6. Samples of freeze-damaged canopies in northern Georgia (b), central Missouri (c), and eastern Tennessee (d). A picture from the same period in 2006 on the same spot as the Missouri freeze-damage picture is used as a reference (a). Had the 2007 spring freeze not occurred, all three sites should be at least as green as indicated by (a), because Missouri is the northernmost site of the three.

budgets. These disturbances may have lasting effects—experimental studies have found that resorption of nutrients and carbohydrates, particularly of nitrogen and phosphorus, plays a significant role in shoot growth in the following spring (e.g., Karlsson 1994, Cheng and Fuchigami 2002). Furthermore, some nutrients contained within leaves and terminal stems killed by frost may be leached *in situ* from unabscised tissues, volatilized directly to the atmosphere, or immobilized by microbes after falling onto the ground away from the ecosystem nutrient cycles (Norby et al. 2003).

Plant-community structures may also be affected in the long run by the uneven impacts of the freeze on different species, and by the stimulation of understory growth due to increased canopy light penetration caused by damage to the overstory (figure 7). Plant architecture may be altered by epicormic growth caused by the loss of apical meristems (figure 8), which may have a lasting effect on light interception by plant canopies. Impacts on other trophic levels are also probable. For example, the fruit crop of white oak–group species, which develops in the spring and is a substantial food source for wildlife, very likely failed throughout much of the region in 2007 because frost killed the flowers. Therefore, the spring freeze may have long-term effects on terrestrial ecosystems in the affected region.

Implications of the 2007 spring freeze for a changing climate

The 2007 spring freeze coincided with the release of the fourth assessment report by the Intergovernmental Panel on Climate Change (IPCC). This report concluded that it is "virtually certain" that the 21st century will have "fewer cold days and nights over most land areas" (Solomon et al. 2007). In view of this prediction, what implications does the 2007 spring freeze have for terrestrial ecosystems in a warming global climate?

To address this question, we must first draw a line between frost frequency and risk of frost damage in the context of climate change. As Meehl and colleagues (2000) articulated, reduced frost frequency does not necessarily mean reduced risk of frost damage. Farmers and other land managers may respond to warming and reduced frost frequency by planting earlier or by planting alternative species. Natural plant populations and animal species might advance the development of crucial phenological phases, or with sufficient time, shift their ranges poleward or to higher elevations. With such adjustments and adaptations, the risk of frost damage could remain the same or even become greater.

This argument does not consider the effect of photoperiod on phenology (Schultz and Kay 2003). In theory, this effect

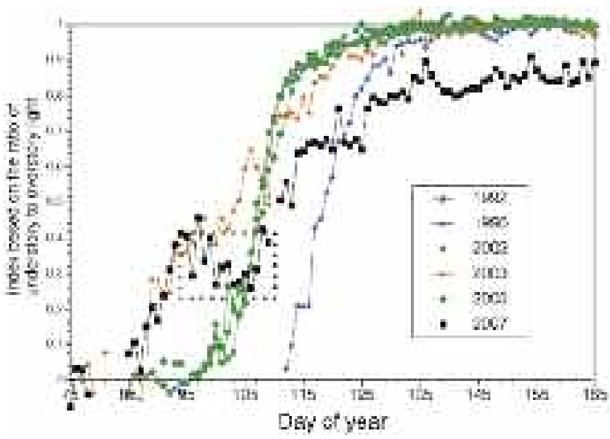

Figure 7. A comparison of canopy development in 2007 with selected previous years for a temperate deciduous forest in Oak Ridge, Tennessee. The y*-axis estimate of canopy development is derived from data on light penetration through the canopy, with low values corresponding to reduced canopy development. Years 1992, 2002, and 2005 all showed "normal" spring canopy phenology. The 2003 leaf-out pattern represents an early spring development without freeze damage, and the 1996 pattern represents a very cold spring with late leaf-out progression. The dashed-line rectangular box shows the impact of freeze-induced foliar damage caused by the 2007 spring freeze. Before the freeze, the canopy in 2007 was developing even faster than in 2003; after the freeze setback, the canopy development resumed but did not achieve the normal level. This is in contrast to 1996, when canopy development started very late but progressed very quickly after the leaf-out, and thus was able to achieve the normal level eventually. This demonstrates that a swinging warm-cold spring is more harmful to plants than a consistently cold spring.*

should eventually limit phenological advancement of plants as the climate continues to warm and thus reduce the risk of frost damage associated with premature onset of plant growth. Observations have shown, however, that phenology of many plant species frequently has an interannual variability of weeks to over a month (e.g., Schwartz 1998, Schaber and Badeck 2005). The sharp contrast between the 2007 and 2006 NDVI images shown in figure 3 (panels a and c) suggests a large, regionwide, interannual variability in plant phenology. As noted earlier, the developmental difference between 2006 and 2007 for crops in the region was about two to three weeks. In Oak Ridge, the timing of spring leaf-out can differ by more than 30 days from year to year (figure 7). The generally large interannual phenological variability means that it will be a long while before photoperiod can play a significant role in the relationship between plant phase development and climate change, and that the constraint of photoperiod on the risk of plant frost damage will be minimal in a warming climate.

Figure 8. An example of postfreeze epicormic growth in Oak Ridge, Tennessee, resulting from the removal of apical dominance by the freeze.

Figure 9. Large thermal capacities of lakes and rivers protect adjacent vegetation against freeze. Note that trees near the water body (Watts Bar Lake, Tennessee) are green whereas those farther away are brown.

In addition to the distinction between frost frequency and risk of frost damage, we must also consider the myriad interactive effects among changing environmental factors crucial for plant growth, including atmospheric CO_2 concentration, temperature, water availability, snow cover, ozone concentration, and ultraviolet-B (UV-B). Without taking these factors into account, we cannot fully appreciate the seemingly paradoxical risk of frost damage to plants in a warming climate.

An obvious issue of concern is the effect that higher atmospheric CO_2 concentrations would have on plant tolerance and resistance to low temperatures both early and late in the growing season. Experimental results suggest that responses are most likely species-specific, but there is a mounting consensus that, for many plant species, growth under elevated CO_2 can reduce their resistance and tolerance to freezing temperatures (Repo et al. 1996, Lutze et al. 1998, Barker et al. 2005, Bertrand et al. 2007). The reduction in tolerance appears to be caused by a slowdown in low-temperature acclimation (Loveys et al. 2006), which is caused by higher daytime leaf temperatures due to reduced stomatal conductance under

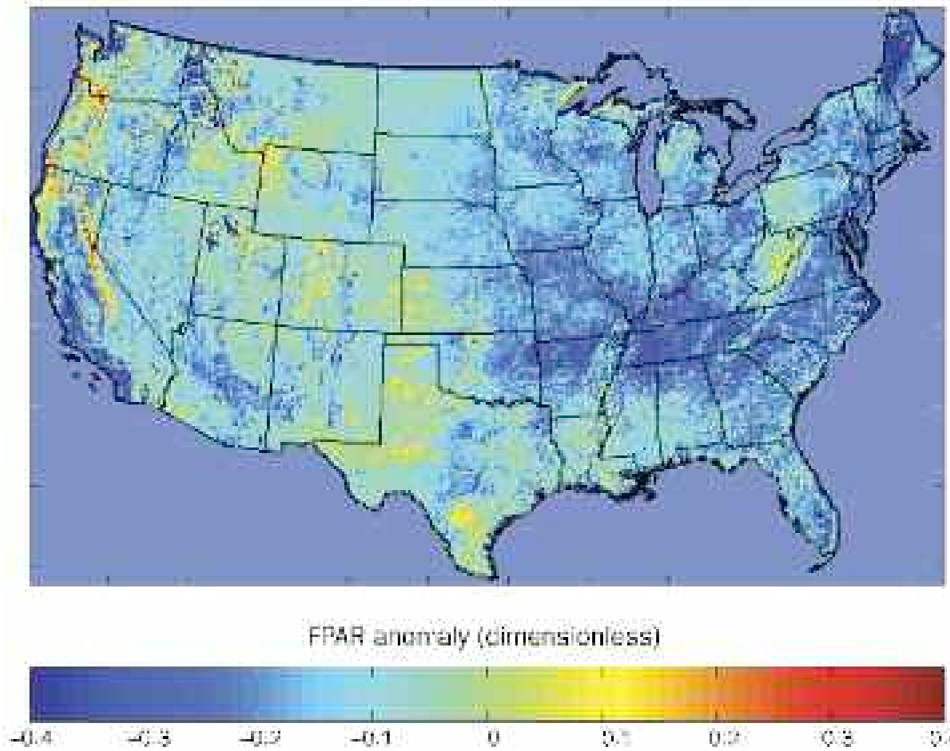

Figure 10. Satellites observed significant reduction in photosynthetic activity as a result of the freeze across the eastern United States. This reduction is shown here as anomalies of the fraction of absorbed photosynthetically active radiation (FPAR) derived from the Moderate-resolution Imaging Spectroradiometer (MODIS) for the period 7–14 April 2007 relative to the 2001–2006 average computed with the terrestrial observation and prediction system (8-kilometer spatial resolution).

elevated CO_2 (Long et al. 2006). Furthermore, elevated CO_2, alone or interacting with UV-B, may increase the foliar ice nucleation temperatures of both evergreen and deciduous species, and thus make them vulnerable even to moderately cold conditions (Beerling et al. 2001).

Although warming may be the general climate trend (Solomon et al. 2007), there is little certainty regarding future temperature variability. If, as predicted, temperatures in winters rise prominently (Meehl et al. 2007, Giorgi and Bi 2005), one may expect more frequent freeze and thaw fluctuations during future winters, a situation that would present several problems for plant growth. These fluctuations may delay plant hardening and hasten dehardening (Cannell and Smith 1986, Leinonen 1996). Many plants' tolerance to freeze increases only after a sustained period of exposure to low temperatures (Thomashow 1999). If temperatures change too quickly, however, plants may not have enough time to acclimate. Additionally, repeated freeze and thaw fluctuations may multiply the risk of xylem embolism and reduce xylem conductivity, leading to crown dieback (Sperry et al. 1994, Zhu et al. 2000). In fact, widespread diebacks of yellow birch (*Betula alleghaniensis* Britt.), paper birch (*Betula papyrifera* Marsh.), and red spruce (*Picea rubens* Sarg.) in eastern North America have been attributed to injuries related to freeze and thaw fluctuations (Strimbeck et al. 1995, Bourque et al. 2005, Lazarus et al. 2006).

In addition to more frequent freeze and thaw fluctuations, changes associated with winter warming will most likely also include reduced snowfall, less snowpack, and early snowmelt. Observations summarized in *Climate Change 2007,* the IPCC's fourth assessment report (*www.ipcc.ch/ipccreports/ar4-syr.htm*), show that snow cover in most regions of the world has been decreasing (Lemke et al. 2007). These changes can deprive plants of thermal protection when it is most needed—a deprivation that not only endangers aboveground overwintering tissues and seeds but also poses a potential freezing stress for near-surface fine roots (Groffman et al. 2001, Inouye et al. 2002).

The IPCC fourth assessment report also predicts that drought will become more frequent in a warmer climate (Meehl et al. 2007). An unfortunate scenario would combine spring freeze damage with prolonged drought, similar to the pattern that developed in 2007 in the eastern United States. Such a scenario can lead to mutually reinforcing damage to vegetation—drought limits postfreeze plant regrowth and recovery while freeze damage weakens plant tolerance to drought.

In addition, frost can interact with ozone to affect vegetation health and growth. In an experiment conducted to examine the effects of frost and ozone on the photosynthesis of birch in Finland, Oksanen and colleagues (2005) found that frost induced significant pigment loss and structural injuries and impaired light capture by photosystems. Furthermore, frost damage was exacerbated by simultaneous exposure to ozone. Forster and colleagues (2007) reported that tropospheric ozone in several developing regions of the world has been increasing recently. Thus, interactive effects of frost and ozone could be another concern for plant growth in the future.

The discussion above suggests that the 2007 spring freeze has important implications for terrestrial ecosystems in a changing climate. This freeze should not be viewed as an isolated event; rather, it represents a realistic climate change scenario that has long concerned plant ecologists. Mild winters and warm, early springs lead to early onset of plant growth, prematurely exposing developing plant parts (sensitive new leaves, flowers, ovaries, and so on) to killing frosts (Cannell and Smith 1986, Inouye 2000). The 2007 spring freeze opens a window of opportunity to study the consequences of this scenario and to observe processes of regional impacts that cannot be reproduced with manipulative experimentation. It also highlights the importance of uninterrupted terrestrial observations through remote sensing and regional ecological networks such as AmeriFlux (*http:/public.ornl.gov/ameriflux/*) and the National Phenological Network (*www.uwm.edu/Dept/Geography/npn/index.html*). Only through these continuous observations can we capture the impacts of unpredictable yet potentially devastating events such as the 2007 spring freeze and obtain much-needed information for evaluating uncertainties in the future global carbon cycle.

Conclusions

The 2007 spring freeze, which caused widespread damage to natural vegetation and agriculture in the southeastern United States, points to the necessity of considering large temperature fluctuations during the crucial spring transitional period as a real threat to terrestrial ecosystem structure and functioning. As the scientific community focuses on climate warming and its potential consequences, the 2007 spring freeze reminds us that Cannell and Smith's warning more than 20 years ago is still valid today: climatic warming may actually increase the risk of frost damage to plants in temperate regions (Cannell and Smith 1986). The 2007 spring freeze has potentially significant implications for the terrestrial carbon cycle in a warming world. Although warming may lengthen the growing season and enhance terrestrial carbon sinks in temperate areas (Keeling et al. 1996, Myneni et al. 1997), the functioning of temperate carbon sinks depends on a number of anthropogenic (Reay et al. 2007) and environmental factors, including temperature regimes during vulnerable periods of plant activities. The damage to vegetation that is associated with large temperature fluctuations may have unexpected consequences for terrestrial ecosystems and their carbon-cycle functioning, and must be fully evaluated to reduce uncertainties in assessing the future global carbon cycle. In particular, in order to predict the responses and feedbacks of the terrestrial carbon cycle to climate change realistically, a proper representation of the impact of alternating warm and freezing weather on plant growth is needed in terrestrial ecosystem models and in coupled carbon-climate models. So far, such a representation has been lacking.

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