Climate-Induced Tree Mortality: Earth System Consequences

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One of the greatest uncertainties in global environmental change is predicting changes in feedbacks between the biosphere and the Earth system. Terrestrial ecosystems and, in particular, forests exert strong controls on the global carbon cycle and influence regional hydrology and climatology directly through water and surface energy budgets [Bonan, 2008; Chapin et al., 2008].

According to new research, tree mortality associated with elevated temperatures and drought has the potential to rapidly alter forest ecosystems, potentially affecting feedbacks to the Earth system [Allen et al., 2010]. Several lines of recent research demonstrate how tree mortality rates in forests may be sensitive to climate change—particularly warming and drying. This emerging consequence of global change has important effects on Earth system processes (Figure 1).

Observations and Patterns of Tree Mortality

Reports of tree mortality associated with heat and drought from around the world have increased in the past decade, and although each cannot be conclusively linked to climate change, they collectively illustrate the vulnerability of many forested ecosystems to rapid increases in tree mortality due to warmer temperatures and more severe drought [Allen et al., 2010]. Recent examples include extensive “die-offs” in which high proportions of trees die at regional scales [Breshears et al., 2005].

In the southwestern United States, widespread drought and insect-driven mortality of piñon pine in the early 2000s affected more than 12,000 square kilometers in less than 3 years, killing 40–97% of those trees at some sites [Breshears et al., 2005; McDowell et al., 2008]. Although episodic tree mortality is an intrinsic process in many forests, the recent mortality in the southwestern United States occurred during an unusually warm drought and appears to have been more severe than mortality associated with a cooler yet drier drought in the 1950s. In western Canada, drought and unusually warm temperatures weakened trees and accelerated mountain pine beetle population growth and range expansion, causing a massive outbreak that killed millions of trees across 130,000 square kilometers of pine forest in 6 years [Kurz et al., 2008a]. Other
extensive insect outbreaks triggered at least in part by climate have been documented in North America from Alaska to Mexico, with drought and warming appearing as common drivers [Rafya et al., 2008]. Instances of extensive tree mortality also have recently been reported from Africa, Asia, Australia, Europe, and South America [Allen et al., 2010].

In addition to extensive, insect-mediated tree mortality, slower, less obvious changes in tree mortality are equally concerning. Over the past few decades in old forests of the western United States, background (non-catastrophic) tree mortality rates have more than doubled, an apparent consequence of rising temperatures [van Mantgem et al., 2009]. Changes in mortality rates associated with rising temperatures and drought also may be driving elevation shifts in tree species, especially through mortality at lower forest boundaries, effectively pushing tree species uphill and into smaller geographic ranges [Allen and Breshears, 1998; Kelly and Goulden, 2008].

The possibility of rising tree mortality rates in tropical and boreal forests is of particular interest because tropical forests contain more than half of the total stored carbon in global forests, and boreal forests play a critical role in Earth’s surface albedo, which is the ratio of reflected to total incoming solar radiation [Bonan, 2008]. Observations in boreal ecosystems suggest that forests may become increasingly vulnerable to insect outbreaks because of warmer temperatures and elevated drought stress in host trees [Berg et al., 2006]. In the Amazon, modeling studies have raised concerns that forests may approach a tipping point in the coming century where climatic thresholds are exceeded, triggering widespread tree mortality [Phillips et al., 2008; Malhi et al., 2009]. Long-term data from pan-Amazonian forest surveys recently documented effects from a severe drought in 2005, with reduced growth and increased tree mortality driving a marked shift in forest carbon balance [Phillips et al., 2009]. Uncertainty surrounding the responses of forests that greatly influence global climate points to a need for a better understanding of tree mortality.

**Mechanisms of Mortality**

Scientists are far from understanding the specific vulnerabilities of different tree species or forest types that are needed to predict climatically induced changes in tree mortality. Current studies lack a fundamental mechanistic understanding of mortality at all spatial scales, from the level of individual trees, through forest stands, to regional landscapes. Accurate model forecasts of the effects of changing tree mortality on the Earth system require a more robust understanding of the causal links between climate and tree death.

Recent research targeting gaps in this mechanistic understanding has provided insight into the role of drought in tree mortality. Two nonexclusive mechanisms—carbon starvation and hydraulic failure—have been proposed to explain drought-induced tree mortality, based on differing tree strategies [McDowell et al., 2008]. Carbon starvation occurs when isohydric species, which strongly regulate transpiration through stomatal closure to avoid excessive water loss when water-stressed, forgo access to the atmospheric carbon dioxide (CO₂) necessary for photosynthesis. Isohydric plants must then exhaust the drought while relying primarily on stored carbon for the respiratory demands of tissue maintenance. If this respiratory consumption exceeds stored resources, death results from carbon starvation. In contrast, anisohydric species only weakly regulate transpiration to continue photosynthesizing, yet this strategy risks mortality via hydraulic failure if sufficient xylem cavitation occurs, rupturing water transport structures under tension and preventing needed water flow.

Warmer temperatures during drought can exacerbate hydraulic failure via higher evaporative demand or especially carbon starvation via elevated respiration. A recent experimental assessment of drought-induced mortality in pine stands, an isohydric species, found that elevated temperatures increased respiratory load and reduced survival time during drought by 28%, consistent with carbon starvation (Adams et al. [2009a, 2009b, 2009c]; but see Leuzinger et al. [2009] and Sala [2009]). However, mortality also could be caused by a lack of access to stored carbon resources within the plant [Sala et al., 2010]. Thus research into metabolic and carbon transport limitations is needed to determine if starvation occurs from reduced photosynthesis or a water-stress-induced inability to use stored carbon. Increased temperatures also can enhance the success of tree pests (e.g., bark beetles or fungi) directly, by encouraging pest reproduction, growth, survival, and dispersal, and indirectly, by reducing tree defensive capabilities during drought [Rafya et al., 2008].

**Effects on Earth System Processes**

The observations and experimental results summarized above highlight the vulnerability of global forests to widespread mortality, which in turn could affect carbon, energy, and water cycles (Figure 1). Forests are important sinks for anthropogenic CO₂ emissions and exert disproportionately strong controls on Earth system processes relative to their geographic extent [Bonan, 2008]. Forests contain close to 55% of the carbon in terrestrial ecosystems and contribute substantially to the terrestrial sink, absorbing 33% of anthropogenic carbon emissions during the 1990s [Bonan, 2008]. Determining the future of this sink is vital to projecting future climate change, as accelerating climate-induced tree mortality and subsequent decomposition could switch forests from carbon sinks to sources for several decades following extensive tree mortality. This has occurred in British Columbia, where mortality associated with recent beetle outbreaks reduced carbon sinks by 270 megatonnes over 20 years. This event reversed the carbon sequestration gains of the previous 20 years across millions of hectares of forest [Kurz et al., 2008a] and influenced Canadian climate change policy [Kurz et al., 2008b]. Further, CO₂ released following tree mortality could easily exceed carbon sequestration enhancements from elevated CO₂ promoting forest growth [Chapin et al., 2008].

Tree mortality also is expected to have strong feedbacks on local and regional climate by altering surface albedo and energy exchange between the land surface and atmosphere. Albedo increases, which help mitigate warming, occur when tree loss exposes a lighter land surface, an effect that may be particularly important for boreal and semiarid ecosystems. In boreal forests, large increases in albedo due to tree loss and exposure of snow-covered ground could partially offset climate forcing due to carbon releases [Bonan, 2008; Chapin et al., 2008]. In coniferous semiarid forests, even small increases in albedo due to tree loss could also result in significant negative feedbacks to global warming because the total incoming energy available in these systems is so high [Rosenberg and Yakir, 2010]. Changes in hydrology also are expected, as a loss of tree cover can decrease transpiration while increasing surface evaporation through near-ground inputs of energy and water [Chapin et al., 2008].

**Future Research, Assessment, and Modeling Needs**

The links between global carbon, energy, and water cycles and forest dynamics reveal the critical need for forecasting the extent and patterns of changing forest properties as affected by tree mortality, disturbances, and regeneration under climate change (Figure 1). An improved network of observations, both ground-based and remotely sensed, is needed to document tree mortality annually [Allen et al., 2010]. Improved experiments assessing mechanisms of tree mortality in relation to climate drivers are needed for more biomes. Both observations and experiments must be linked to modeling efforts to improve forecasts. Future needs also include assessment of management actions, such as forest thinning, that might increase the resistance of forested ecosystems to climatic changes.

Last, extensive observations of the effects of increasing tree mortality on fluxes of carbon, energy, and water are needed. Such observations need to quantify not only the magnitude and direction of these responses but also the effects of subsequent forest regeneration and recovery, which ultimately will influence the persistence of impacts. Addressing these information gaps will improve our understanding of climate-induced tree mortality and associated
shifts in Earth system feedbacks, helping researchers to project global changes and anticipate their effects on society.

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MEETINGS

European Biospheric Network Takes Off

Opening Symposium of the TERRABITES Network: Hamburg, Germany, 9–11 February 2010

The huge amount of recently acquired information about the functioning of the terrestrial biosphere and the ever increasing spatial resolution of Earth system models call for a new level of integrating efforts among biosphere modelers, developers of ecological theory, and data-gathering communities. Responding to this call, a new European network, Terrestrial Biosphere in the Earth System (TERRABITES), held its opening symposium in Germany.

The meeting was organized jointly with another recently founded European network, Advancing the Integrated Monitoring of Trace Gas Exchange Between Biosphere and Atmosphere (ABBA). Almost 100 scientific contributions covered the latest advances in modeling ecophysiological and biogeochemical processes; analyses of model constraints set by measurements of water and carbon dioxide (CO2) fluxes, including carbon isotope; and new perspectives in using remote sensing data for evaluation of global terrestrial biosphere models.

Several presentations underlined challenges in using the growing amount of ground-based ecological observations for better quantification of vegetation processes on different scales. A key talk introduced the TRY database, which currently contains more than 2.4 million plant trait records with a focus on 47 key traits such as leaf nitrogen content and litter decomposition rates. Subsequent presentations demonstrated how accounting for trait variability within plant functional types affects the behavior of dynamic global vegetation models and forest gap models. Other presenters took a more radical approach and showed how optimality analysis could predict trait values for a given set of environmental conditions and how trait values could be applied to predicting plant functional types.

Implementing fire occurrences into the global biosphere and Earth system models is another challenging task. Recent results from the Spread and Intensity of Fire (SPITFIRE) model suggest that changes in wood usage for fuel by humans could alter the future trend in fire-related CO2 emissions. Another modeling study found a weak upward trend in twentieth-century fire emissions, in contrast to previous inventory-based estimates that suggested a stronger increase in emissions. Comparison of model results with recent satellite-based products on burned area not only identified regions for model improvement but also stressed remarkable differences among various satellite products.

Presentations of the remote sensing community, organized by specialists from the European Space Agency, focused on the challenge of providing the global modeling community with reliable data. An overview talk highlighted recent advances in...