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Climate-Induced Tree Mortality: Earth System Consequences

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 [*Raffa 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 (CO_2) necessary for photosynthesis. Isohydric plants must then outlast 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 piñon pine, 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 [*Raffa 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

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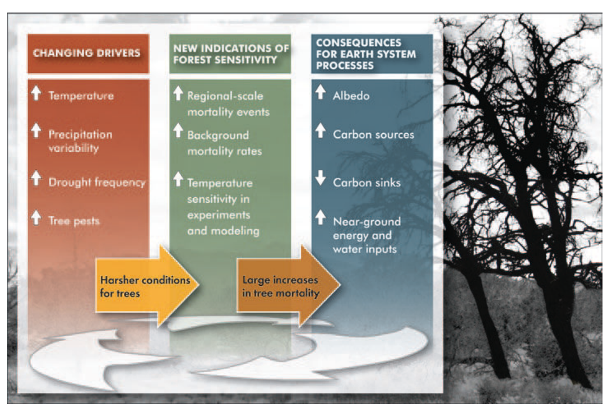

*Fig. 1. Climate change can affect tree mortality both directly (such as through drought) and indirectly (such as by favoring tree pests). Recent observations have revealed apparent warming-induced increases in both background tree mortality [*van Mantgem et al., *2009] and regional-scale forest die-off [*Allen et al., *2010]. Observations, theory, and experiments have begun to unravel sensitivities and mechanisms driving these events [*McDowell et al., *2008;* Adams et al., *2009a]. Accelerating tree mortality resulting from ongoing climate changes could have potentially profound effects on Earth system processes, providing positive feedbacks that further enhance climate change.*

ABOUT AGU

New Executive Director Selected

Christine W. McEntee will join AGU on 30 August as the Union's third executive director. She has been executive vice president and chief executive officer of the American Institute of Architects (AIA) since February 2006.

We are very fortunate to have McEntee join us at this stage in AGU's transformation to an inclusive, participative organization. We are also excited about her outreach expertise and ability to help AGU become an authoritative voice of Earth and space science. She is definitely up to the challenge after having successfully accomplished a similar result at AIA.

McEntee was selected from a large group of outstanding candidates following an extensive international search. AGU was assisted in the process by the executive search firm Isaacson, Miller. Robert Van Hook of Transition Management Consulting, Inc., has served as AGU's interim executive director since the end of January 2009. He will continue in that capacity through August.

In an interview with *Eos,* McEntee outlined some of her goals and priorities and shared her excitement about coming to AGU (see the interview on page 156 of this issue of *Eos*).

—Timothy L. Grove, President, AGU

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are important sinks for anthropogenic CO_2 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 megatons 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, CO_2 released following tree mortality could easily exceed carbon sequestration enhancements from elevated CO_2 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 [*Rotenberg 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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