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Review and synthesis

Physiological and ecological factors influencing recent trends in United States forest health responses to climate change

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ABSTRACT

The health of United States forests is of concern for biodiversity conservation, ecosystem services, forest commercial values, and other reasons. Climate change, rising concentrations of CO_2 and some pollutants could plausibly have affected forest health and growth rates over the past 150 years and may affect forests in the future. Multiple factors must be considered when assessing present and future forest health. Factors undergoing change include temperature, precipitation (including flood and drought), CO_2 concentration, N deposition, and air pollutants. Secondary effects include alteration of pest and pathogen dynamics by climate change. We provide a review of these factors as they relate to forest health and climate change. We find that plants can shift their optimum temperature for photosynthesis, especially in the presence of elevated CO_2, which also increases plant productivity. No clear national trend to date has been reported for flood or drought or their effects on forests except for a current drought in the US Southwest. Additionally, elevated CO_2 increases water use efficiency and protects plants from drought. Pollutants can reduce plant growth but concentrations of major pollutants such as ozone have declined modestly. Ozone damage in particular is lessened by rising CO_2. No clear trend has been reported for pathogen or insect damage but experiments suggest that in many cases rising CO_2 enhances plant resistance to both agents. There is strong evidence from the United States and globally that forest growth has been increasing over recent decades to the past 100+ years. Future prospects for forests are not clear because different models produce divergent forecasts. However, forest growth models that incorporate more realistic physiological responses to rising CO_2 are more likely to show future enhanced growth. Overall, our review suggests that United States forest health has improved over recent decades and is not likely to be impaired in at least the next few decades.

Contents

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1. Introduction

Forests are one of the most important ecosystems on Earth. They cover approximately one-third of the world's land mass, are a significant source of commercial products, food, and shelter, and exert a powerful influence on the global carbon cycle. As a precious natural resource, they benefit nature and society in a multitude of ways.

The fate of these and other benefits, however, are of increasing concern among scientists and policymakers, including the United Nations Intergovernmental Panel on Climate Change (IPCC), which has projected that CO_2-induced climate change will adversely impact forests in the years and decades to come due to rising temperatures and drought (e.g., Allen et al., 2010; Carnicer et al., 2011) and that many species will therefore be driven to extinction, some in the next few decades (Settele et al., 2014). Joyce et al. (2014), Groffman et al. (2014), and Peterson et al. (2014) project considerable disruption and adverse consequences for forests due to climate change. For example, based on projected temperature increases of 3–5 °C, Peterson et al. (2014) project forest growth declines, range shrinkage for many species, and increases in pest outbreaks. They cite niche-based analyses that show very large changes in equilibrium forest composition but also models showing increased forest growth for the same regions. The time it might take to achieve this new equilibrium is not discussed, and could be much longer than decades (Loehle, 2014). There is little discussion in these studies of how rising CO_2 might affect tree physiology and growth.

A proper understanding of forest health and future impacts, however, must also include consideration of the historical context for recent trends, the physiological tolerances of trees, and the effect of rising CO_2 on tree growth rates and responses to stressors. Here we evaluate evidence on these issues based on an extensive review of the literature. Our approach was to first examine the findings and literature cited in the IPCC Fifth Assessment Report and in major government (e.g., Forest Service) reports. We then evaluated key literature covering a range of views on the various issues. We do not attempt to summarize the entire vast literature on this topic.

1.1. Temperature

Some authors have predicted that CO_2-induced warming will lead to declines in forest growth and productivity, and in extreme cases to local extinctions, as trees may not be able to migrate fast enough to keep up with the poleward-shifting thermal environments to which they are currently accustomed (e.g., Joyce et al., 2014; Groffman et al., 2014; Peterson et al., 2014; Settele et al., 2014). For climate niche models, this prediction is based on the assumption that tree growth rates can be calibrated based on the current geographic range, with slower growth at the geographic extremes of the range, as for example, modeled by Ehman et al. (2002). Loehle (1998), however, demonstrated that the southern boundary of a tree's natural range is determined less by temperature than by competition between northern species and more southerly-adapted species that have inherently greater growth rates. Loehle (2014) argued that niche-based models do not provide reliable forecasts of tree decline because they show mainly the equilibrium response. We therefore focus here on experimental and historical studies of forest response to temperature.

In contrast to the above studies, multiple studies show that even large increases in temperature do not negatively affect growth of most plants. For example, Way and Oren (2010) found that up to a 13 °C increase in growing season temperature led to increased growth for multiple temperate and boreal trees and little change for tropical trees. Booth et al. (2015) found from data on globally distributed plantings of Eucalypt species that at least some are much more tolerant of warmer temperatures than their current ranges in Australia would indicate. Dick et al. (2012) found that tropical trees evolved under substantially warmer temperatures than today and similar to those predicted for 2100 by models. Trees have also tolerated large swings in temperature across multiple glacial/interglacial climate cycles as well as during the present interglacial when global temperatures have been warmer than present (Behling, 1998; Büntgen et al., 2014; MacDonald et al., 2000; Maley, 1996). We were unable to locate any empirical studies suggesting that trees are as sensitive to warming as niche models assume or that any negative consequences have been found for a few degrees of warming. In fact, a survey of field studies of terrestrial ecosystem responses showed that warming and increased precipitation both increased plant growth (Wu et al., 2011). In the later section on trends in forest growth we discuss several studies showing a correlation between recent rising temperatures and increased tree growth.

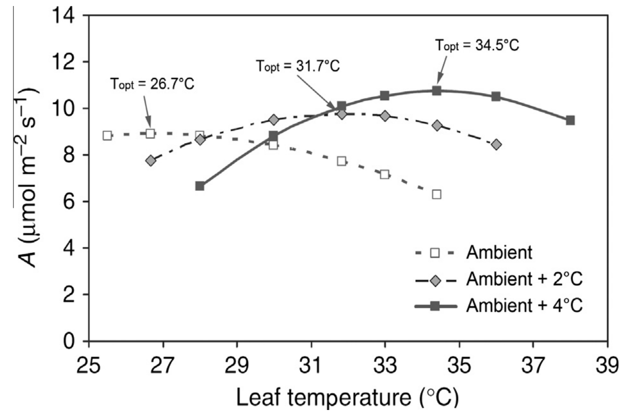

Fig. 1. Net CO_2 assimilation rate (A) vs. leaf temperature in *Quercus rubra* seedlings during June 2003 in ambient temperature (TA) and elevated temperature (TA + 2 °C and TA + 4 °C) treatments. Adapted from Gunderson et al. (2010).

Tree species have been shown to acclimate to changes in temperature. Gunderson et al. (2010) found that "warming treatments resulted in a shift in the temperature response curves for CO_2 assimilation, such that tree leaves in warmer treatments had higher temperature optima [T_{opt}]." As illustrated in Fig. 1, trees growing in warmer environments had higher T_{opt} values and there was a tendency for net CO_2 assimilation rates at higher T_{opt} values to be higher as well. They confirmed this adjustment of thermal optima in all species, "whether temperatures varied with season or treatment, and regardless of climate in the species' range or provenance of the plant material." Furthermore, they observed "responses to the temperature manipulation were not different from the seasonal acclimation observed in mature indigenous trees," which they also investigated locally. This acclimation response is not usually incorporated into forest growth models, which commonly use a single temperature curve.

Rising CO_2 levels also enhance adaptive responses to higher temperatures. It is well-known that atmospheric CO_2 enrichment tends to alleviate high-temperature stress in plants (Faria et al., 1996; Nijs and Impens, 1996; Vu et al., 1997); and when temperatures are high enough to cause plants to die, atmospheric CO_2 enrichment may actually enhance survival (Baker et al., 1992; Idso et al., 1989, 1995; Rowland-Bamford et al., 1996; Taub et al., 2000), and can ameliorate drought conditions (Hamerlynck et al., 2000; Keenan et al., 2013; Polley et al., 2002; Tuba et al., 1998).

In addition, the optimum temperature for plant growth generally rises with atmospheric CO_2 enrichment (Berry and Bjorkman,