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The many faces of climate warming

Ecosystem responses to experimental warming and other global climate change factors: Organized session at the Ecological Society of America (ESA) 92nd Annual Meeting, San Jose, CA, USA, August 2007

The release of the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC) this past February raised the stakes on role of climate warming in our planet's future. Within the next century our climate is likely to warm by 1.1–6.4°C in concert with rising concentrations of greenhouse gases, largely reflecting human influences on radiative forcing (IPCC, 2007). The prospect of climate warming coupled with elevated atmospheric concentrations of carbon dioxide, altered precipitation patterns, and increased nitrogen deposition presents a tangled array of global change drivers and the

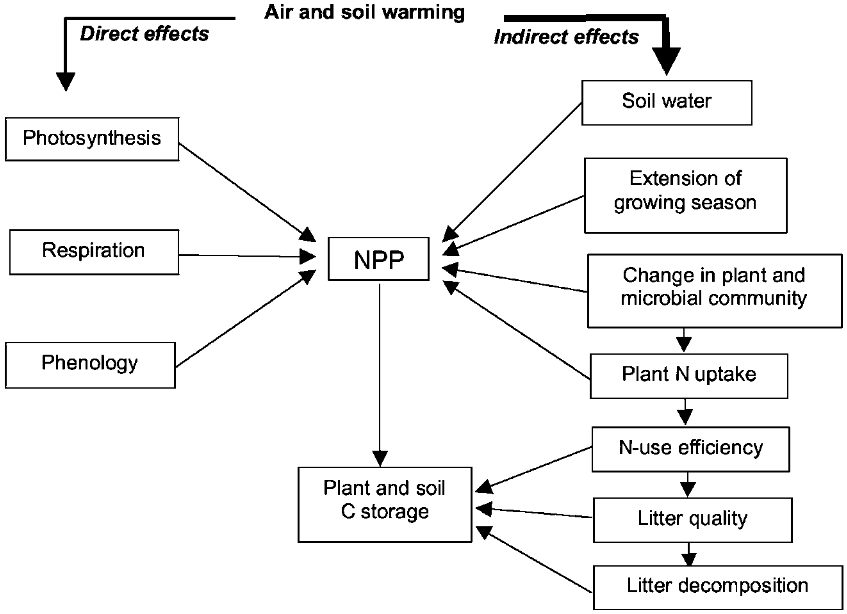

Fig. 1 The major factors controlling the response of net primary production (NPP) and carbon (C) storage to the effects of climate warming in terrestrial ecosystems.

potential for complex effects on the structure and function of terrestrial ecosystems.

Over the past decade, much progress has been made in experimental research and long-term observational studies quantifying the nature and magnitude of climate-warming effects on terrestrial ecosystems and linking them to coupled atmosphere-biosphere processes. Disentangling the direct and indirect effects of warming on ecosystems remains a key conceptual and experimental challenge. To this end, multifactorial experiments and modeling efforts will be key to developing science-based predictions of ecosystem responses to warming (Norby & Luo, 2004). A session organized by Xuhui Zhou and Yiqi Luo (University of Oklahoma, OK, USA) at the 92nd Annual Meeting of the Ecological Society of America in San Jose, CA, USA, in August was aimed at summarizing the findings to date concerning the multiple roles of climate warming in a variety of ecosystems.

> *'... in the coterminous United States, the frost-free period has extended by as much as 25 d over the past 50 yr'*

How important are the direct effects of temperature?

Although temperature affects many terrestrial ecosystem processes, one of the most striking observations to date and prima facie evidence of climate-warming effects has been the extension of the growing season in various climatic zones. For example, in the coterminous United States, the frost-free period has extended by as much as 25 d over the past 50 yr. As Christopher Field (Carnegie Institution of Washington, Stanford, CA, USA) noted at the outset of the morning session, warmer temperatures coupled with a longer growing season should increase net primary production (NPP) as climate warming may directly enhance photosynthetic carbon assimilation (Fig. 1). Indeed, increased NPP in response to warming is observed in a number of experiments, but not always (Rustad *et al.*, 2001; Dukes *et al.*, 2005).

Further studies should enable a critical test of whether or not warming effects on NPP are, as a rule, greater in cooler than in warmer climates, where temperature limitations on productivity are thought to be larger. In warmer climates limitations imposed by water balance may constrain NPP responses to warming and amplify the indirect effects of increased temperature on reducing soil water content via increased evapotranspiration (Fig. 1). Indeed, in tallgrass prairie exposed to climate warming in combination with altered precipitation distribution, reported by John Blair and colleagues (Kansas State University, Manhattan, KS, USA), warming reduced above-ground NPP and soil CO_2 efflux, supporting the notion of water deficit-mediated responses to climate warming.

Given the fundamental nature of the relationships between temperature and plant metabolism, predicting direct temperature effects on photosynthesis and respiration might seem straightforward. Yet we have long known that temperature acclimation modulates the direct effects of temperature on carbon exchange rates in plants (Atkin & Tjoelker, 2003). Recent studies suggest that temperature acclimation may also be an important modulator at the ecosystem scale in terms of respiratory CO_2 efflux from plants and soils (Luo *et al.*, 2001), mitigating direct temperature effects on changes in carbon pools and fluxes (King *et al.*, 2006), and rendering simple simulations based on first principles (i.e. Q_{10} or Arrhenius functions) problematic at best.

To be sure, experimental climate warming often results in increased respiratory carbon losses, particularly from soil organic carbon pools. At Harvard forest in Massachusetts, USA, and Flakaliden, Sweden, decade-long soil-warming experiments revealed increased CO_2 fluxes from soil to the atmosphere. However, the responses were small and transient or diminished through time (Melillo *et al.*, 2002; Eliasson *et al.*, 2005), likely owing to limited pools of labile soil carbon and perhaps reflecting constraints ultimately set by photosynthetic carbon assimilation. Likewise, Richard Gill (Washington State University, Pullman, WA, USA) reported transient and nonsignificant soil respiratory responses of a subalpine meadow to experimental warming. Sorting out the relative contributions of autotrophic and heterotrophic respiration and soil carbon pool dynamics will continue to be an important research objective in warming studies.

The emergence of indirect effects

The indirect effects of global warming on terrestrial ecosystems are likely more important than direct effects (Shaver *et al.*, 2000; Luo, 2007). This was a recurring theme throughout the session. Climate warming influences ecosystem processes by extending the length of the growing season and changing plant phenology (Harte & Shaw, 1995; Wan *et al.*, 2005), increasing soil nitrogen (N) mineralization and availability (Rustad *et al.*, 2001), reducing soil water content (Wan *et al.*, 2005), and shifting species composition and community structure (Shaver *et al.*, 2000; Wan *et al.*, 2005). Warming-induced changes in soil N transformations can trigger long-term feedbacks on ecosystem carbon balances because N strongly regulates terrestrial carbon sequestration, potentially enhancing carbon storage. Warming and associated drought may stimulate below-ground growth, increase root/shoot ratios, and result in shifts of the plant community to C_4 species, shrubs, and other drought-tolerant species. The experimental evidence on indirect effects and interactive effects of warming certainly provides a challenge to modeling efforts of global carbon-climate feedbacks, moving beyond the kinetics of photosynthesis and respiration (Luo, 2007).

The future faces of warming: state changes in ecosystems

Determining the nature and tempo of successional changes in ecosystems in response to warming remains a key challenge. Changes in ecosystem states through altered species composition and dominance will have profound effects on NPP and biogeochemical cycles, perhaps surpassing the direct effects of global change drivers themselves. In particular, feedbacks between plant functional types and soil processes, including effects on microbial communities, are poorly understood in this context.

Will climate warming and other global change drivers promote certain species or plant functional groups over others? Early experiments by Harte & Shaw (1995) demonstrated warming-induced shifts in species dominance in favor of perennial woody shrubs in a montane meadow ecosystem. Margaret Torn and colleagues (Lawrence Berkeley Laboratory, Berkeley, CA, USA), in a study of California annual grassland, reported altered productivity and species abundances in response to warming and interactive effects with precipitation amount. In an old field community in Tennessee, Amiee Classen and colleagues (Oak Ridge National Laboratory, Oak Ridge, TN, USA) reported complex responses of plant functional groups to the combined effects of warming, elevated CO_2, and water availability, including differences among tree species in seedling establishment. In oak savanna in central Texas, the work of one of us (MGT) suggests that encroachment of invasive *Juniperus virginiana* may increase in future, warmer climates. Further surprises are likely in store, owing to constraints on intraspecific plant adaptation and range shifts in fragmented landscapes (Davis & Shaw, 2001). To date, few if any studies have experimentally tackled these landscape-scale questions in an ecosystem framework.

The future of experimental warming studies

A variety of approaches to experimental warming are available, each with advantages and limitations. Glasshouse mesocosms, open-top field chambers, infrared warming, passive nighttime warming, and soil warming are among the techniques, many of which were reported on in the 3 h session. Yet surprisingly, we know relatively little about forest ecosystem responses to experimental warming. Unlike free-air CO_2 enrichment (FACE) studies, which have approached their golden age, spanning diverse vegetation types in nearly every continent, field-based warming studies to date remain largely restricted to small plots and comparatively short-statured vegetation. The development of methods to warm both the air and soil of large-scale forest plots will be an important technical advance.

Ecosystems across the globe have already been exposed to increased temperatures for almost two decades. Long-term observational data will no doubt contribute further insight into warming effects. Yet many gaps remain in our knowledge of the impacts of global warming on ecosystem processes. For example, long-term observations and model simulations show that daily minimum temperatures have increased at a faster rate than daily maximum temperatures (Easterling *et al.*, 1997). Shuli Niu (Chinese Academy of Sciences, Beijing, China) demonstrated differential effects of day vs nighttime warming in a temperate steppe in China, showing increased carbon uptake in response to night warming compared with day warming and control treatments. In a grassland in Oregon, Jillian Gregg (Terrestrial Ecosystems Associates, Corvallis, OR, USA) is testing whether increased carbon assimilation with warmer mornings will offset the greater respiratory costs with warmer night temperatures. These studies underscore the continuing need to resolve ecosystem responses in terms of underlying photosynthetic and respiratory physiology.

How other ecosystems, such as forests, savanna, and deserts, will respond to the many faces of warming is largely unknown. In the meantime, synthesis and modeling activities remain important tools. Nonetheless, the scientific community appears poised to address these questions in an integrative manner. Given the prospects of rapid climate warming, science-based predictions of ecosystem responses will certainly play an important role in the policy debates concerning adaptation and mitigation strategies.

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Key words: acclimation, carbon cycle, climate change, net primary production, temperature, warming.

Meta-analysis: the past, present and future

Synthesizing ecological studies in a changing world using meta-analysis: Organized session at the Ecological Society of America (ESA) 92nd Annual Meeting, San Jose, California, USA, August 2007

The use of meta-analysis in the field of ecology has increased exponentially since its introduction in the early 1990s. Meta-analysis is a set of statistical techniques that enables researchers to combine the results from a number of independent studies. Meta-analysis is therefore the analysis of analyses, as implied by the name. The techniques for ecological meta-analysis have been borrowed from other disciplines, primarily the medical, physical and behavioral sciences (Gurevitch & Hedges, 1999). These techniques have also been adapted for ecology, and new metrics have been developed specifically for ecological questions (e.g. response ratio; Curtis & Wang, 1998; Hedges *et al.*, 1999). Furthermore, the development of easy-to-use statistical software (e.g. METAWIN, Rosenberg *et al.*, 2000) has rapidly expanded the use of meta-analyses in ecology. An organized oral session (OOS) at the 2007 Ecological Society of America (ESA) meeting focused on the historical evolution of meta-analyses in ecology, the current use in synthesizing results from global change studies and the future of meta-analyses in ecology. In this article, we present some highlights and future challenges proposed in the session.