

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.

**Mark G. Tjoelker<sup>1\*</sup> and Xuhui Zhou<sup>2</sup>**

<sup>1</sup>Department of Ecosystem Science and Management, Texas A & M University, College Station, TX, 77843-2138, USA; and <sup>2</sup>Department of Botany and Microbiology, University of Oklahoma, Norman, OK, 73019, USA  
(\*Author for correspondence: tel +1 (979) 845 8279; email m-tjoelker@tamu.edu)

## References

- Atkin OK, Tjoelker MG. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* 8: 343–351.
- Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292: 673–679.
- Dukes JS, Chiariello NR, Cleland EE, Moore LA, Shaw MR, Thayer S, Tobeck T, Mooney HA, Field CB. 2005. Responses of grassland production to single and multiple global environmental changes. *PLoS Biology* 3: 1829–1837.
- Easterling DR, Horton B, Jones PD, Peterson TC, Karl TR, Parker DE, Salinger MJ, Razuvayev V, Plummer N, Jamason P *et al.* 1997. Maximum and minimum temperature trends for the globe. *Science* 277: 364–367.
- Eliasson PE, McMurtrie RE, Pepper DA, Strömgren M, Linder S, Ågren GI. 2005. The response of heterotrophic CO<sub>2</sub> flux to soil warming. *Global Change Biology* 11: 167–181.
- Harte J, Shaw R. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* 267: 876–880.
- Intergovernmental Panel on Climate Change (IPCC). 2007. Technical summary. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, eds. *Climate change 2007: the physical science basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.
- King AW, Gunderson CA, Post WM, Weston DJ, Wullschlegel SD. 2006. Plant respiration in a warmer world. *Science* 312: 536–537.
- Luo Y. 2007. Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology, Evolution, and Systematics* 38: 683–712.
- Luo Y, Wan S, Hui D, Wallace LL. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413: 622–625.
- Melillo JM, Steudler PA, Aber JD, Newkirk K, Lux H, Bowles FP, Catricala C, Magill A, Ahrens T, Morrisseau S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298: 2173–2176.
- Norby RJ, Luo Y. 2004. Evaluating ecosystem responses to rising atmospheric CO<sub>2</sub> and global warming in a multi-factor world. *New Phytologist* 162: 281–293.
- Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126: 543–562.
- Shaver GR, Canadell J, Chapin FS III, Gurevitch J, Harte J, Henry G, Ineson P, Jonasson S, Melillo J, Pitelka L *et al.* 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience* 50: 871–882.
- Wan S, Hui D, Wallace L, Luo Y. 2005. Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochemical Cycles* 19: GB2014. doi: 10.1029/2004GB002315

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## 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.

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*'Since the early 1990s, there have been over 700 published meta-analyses in ecology and evolution'*

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## A brief history

While meta-analyses have been used for several decades in other disciplines, their use in ecology did not really take off until the 1990s. In their seminal synthesis of field experiments of competition, Jessica Gurevitch (Stony Brook University, NY, USA) and colleagues laid the groundwork for using meta-analysis for ecological data (Gurevitch *et al.*, 1992). They suggested that meta-analyses could fundamentally alter the way that ecologists draw conclusions from the outcomes of experiments. Specifically they suggested that meta-analyses could lessen the focus on so-called 'textbook examples' and instead adjust the focus to the quantitative synthesis of separate, independent studies. Furthermore, meta-analyses allow an alternative approach to traditional, narrative reviews or statistically flawed quantitative approaches such as 'vote-counting' reviews. Meta-analyses offer a number of important advantages, including the ability to calculate effect size estimates (i.e. the overall magnitude of responses) and to discriminate statistically among the effect in different subsets of studies. A goal and an inherent part of the philosophy underlying meta-analysis is that it requires the same rigor in sampling and analysis as is required in primary research. The application and influence of meta-analysis in ecology has continued to expand in recent years. Since the early 1990s, there have been over 700 published meta-analyses in ecology and evolution (reported by Gurevitch and Julia Koricheva, University of London, UK).

## What ecological questions has meta-analysis addressed?

The area in which meta-analysis has had the greatest impact is perhaps global environmental change, particularly in the effects of elevated CO<sub>2</sub> on plant physiology and growth. Meta-analysis was first used to synthesize the results from elevated CO<sub>2</sub> studies on gas exchange variables and leaf nitrogen (N) by Peter Curtis (Ohio State University, OH, USA; Curtis, 1996). The earlier CO<sub>2</sub> meta-analyses, although focused primarily on studies with relatively short experimental durations, provided statistical confirmation of a number of key responses to elevated CO<sub>2</sub> in trees (Curtis, 1996; Curtis & Wang, 1998). More importantly, the work by Curtis and colleagues highlighted the areas of uncertainty in our understanding of the plant response to elevated CO<sub>2</sub> and, in doing so, has had a large influence on subsequent primary research and has changed the complexion of CO<sub>2</sub> study as an ecological subdiscipline. Over the last decade,

approximately 50 papers using meta-analytical techniques have been published to synthesize results of the large number of ecological CO<sub>2</sub> studies that have been conducted.

One important feature of meta-analysis that is lacking in empirical studies or traditional reviews is its ability to synthesize results from independent studies in a manner that is both objective and statistically defensible. This feature makes meta-analysis a powerful tool and has revised some earlier assumptions and findings in ecology. For example, it was hypothesized that plant species with the C<sub>4</sub> photosynthetic pathway would have a lower responsiveness to elevated CO<sub>2</sub> and therefore could lose the competitive advantage to C<sub>3</sub> species as the CO<sub>2</sub> level in the atmosphere continues to rise. Meta-analyses by Wand *et al.* (1999) and Poorter & Navas (2003), however, found a significant increase in the growth of C<sub>4</sub> species at elevated CO<sub>2</sub> and thus called for a critical re-evaluation of the assumption of lower growth responsiveness in C<sub>4</sub> species to elevated CO<sub>2</sub>. In a recent analysis of production of crops grown under free-air CO<sub>2</sub> enrichment (FACE) conditions, Ainsworth & Long (2005) found that crop yields increased far less than anticipated from previous enclosure studies. The important quantitative difference detected by this meta-analytical synthesis (Ainsworth & Long, 2005), as well as the finding of lower levels of proteins and essential minerals in staple crops grown at elevated CO<sub>2</sub>, based on a meta-analysis by Daniel Taub and colleagues (South-western University, TX, USA), will have significant implications for food production and human nutrition in the future.

One trend of CO<sub>2</sub> meta-analysis on plant physiology and growth seems to be the synthesis of studies on multiple environmental changes, particularly elevated O<sub>3</sub> (discussed by Elizabeth Ainsworth, University of Illinois, IL, USA). A comprehensive analysis of the publications of O<sub>3</sub>, alone or in combination with elevated CO<sub>2</sub>, for example, demonstrated significant interactive effects of O<sub>3</sub> and CO<sub>2</sub> on leaf chemistry and some indices of insect performance (Valkama *et al.*, 2007). Another trend in CO<sub>2</sub> meta-analysis is to elucidate mechanisms governing plant responses to elevated CO<sub>2</sub>. In a recent synthesis of 411 CO<sub>2</sub> publications, Wang (2007) found that plant assemblages of single species (population) were more responsive to elevated CO<sub>2</sub> than assemblages of multiple species (communities) in biomass accumulation. The meta-analytical findings led to the formulation of the resource usurpation hypothesis (i.e. competitive compartmentation of growth-limiting resources by less responsive plant species), which may be important in determining the growth response to elevated CO<sub>2</sub> in a community (Wang, 2007).

In addition to synthesizing studies of elevated CO<sub>2</sub> on plant physiology and biomass accumulation, meta-analysis has been used to examine CO<sub>2</sub> effects on plant characteristics that can affect C and nutrient cycling. Nitrogen concentration, for instance, showed a small but consistent decline, whereas leaf lignin increased by 6.5% in leaf litter from elevated CO<sub>2</sub>-grown plants (Norby *et al.*, 2001). It was thus concluded

that litter decomposition would be slower in a higher CO<sub>2</sub> environment. A more recent synthesis of 104 publications demonstrated that elevated CO<sub>2</sub> stimulated net accumulations of C and N in terrestrial ecosystems, which may help to prevent the complete down-regulation of long-term CO<sub>2</sub> enhancement of C sequestration (Luo *et al.*, 2006).

The CO<sub>2</sub> responses of organisms other than plants have also been examined using meta-analytical techniques. The effects of environmental changes on the responses of soil organisms and mycorrhizas have significant implications for global C and nutrient cycling. Soil organisms of different trophic levels (detritivores and herbivores at the second trophic level, bacterivores and fungivores at the third level and predators at the fourth level) have been found to vary in their responses to environmental changes, including higher CO<sub>2</sub> (discussed by Joey Blankinship, Pascal Niklaus and Bruce Hungate, Northern Arizona University, AZ, USA and Swiss Federal Institute of Technology, Zurich, Switzerland). Results from an earlier meta-analysis demonstrated that mycorrhizal abundance decreased with the addition of N and phosphorus (P), but increased by 47% at an elevated level of atmospheric CO<sub>2</sub> (Treseder, 2004). These meta-analytical studies were able to statistically generalize results from a large number of individual studies to reach basic and applied conclusions, e.g., support of the plant investment hypothesis (Treseder, 2004).

The scope of meta-analysis in synthesizing ecological studies on global environmental changes is being expanded beyond CO<sub>2</sub> studies. Analysis of the vegetation response to N addition found that biomass growth and tissue N concentration was affected by multiple factors, including precipitation and latitude (discussed by Shuli Niu, Shiqiang Wan and Jianyang Xia, Institute of Botany, Academia Sinica, China). A recent meta-analysis on the responses of plant communities to experimental warming indicated that warming would have negative effects on tundra biodiversity, which will have far-reaching implications for the functioning of ecologically important tundra systems (Walker *et al.*, 2006). There are a number of other global change areas (e.g. habitat fragmentation, urbanization and spreading of non-native species) that have successfully used meta-analysis to synthesize statistically the ever-increasing number of independent studies (discussed by Jessica Gurevitch, Stony Brook University). These meta-analytical syntheses have made significant contributions to the advancement of ecology as a science.

## Challenges ahead

As meta-analysis has now begun to gain widespread acceptance in ecology, we face the challenge of making sure that meta-analysis is used correctly and to its full potential. This includes the use of better statistical methods as well as the proper formulation of questions that can be answered through meta-analysis.

Statistically, most ecological meta-analyses have a long way to go before they approach the sophistication of meta-

analyses in other disciplines, such as medicine. At present, many ecological meta-analyses consist of sets of contrasts, functionally equivalent to performing multiple sets of single classification analysis of variance (ANOVA) tests. More advanced statistical approaches (e.g. two-way ANOVA, analysis of covariance (ANCOVA), regression, and multivariate analysis) are rarely undertaken in ecological meta-analyses. It is as if ecological meta-analysts have become stuck halfway through a standard biostatistics text, but are unable to read the rest of the book. Some specific challenges for ecologists highlighted in the session (discussed by both Michael Rosenberg, Arizona State University, and Jessica Gurevitch, Stony Brook University) include the use of hierarchical nested analyses, accounting for the effect of phylogenetic relationships within the data, and the use of advanced statistical inference methods, such as maximum likelihood and Bayesian meta-analysis. A demonstration of the power of the Bayesian meta-analysis approach was presented by Kiona Ogle (University of Wyoming, WY, USA).

As global change ecologists rise to these challenges, it is believed that meta-analysis will become an increasingly indispensable tool in ecological studies. The overall response to environmental changes produced by the meta-analytical synthesis of individual studies will not only improve our understanding of ecosystem functioning in a changing world, but also provide the information necessary to proactively plan for the future.

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**Elizabeth A. Ainsworth<sup>1</sup>, Michael S. Rosenberg<sup>2</sup> and Xianzhong Wang<sup>3\*</sup>**

<sup>1</sup>USDA-ARS Photosynthesis Research Unit & Department of Plant Biology, University of Illinois Urbana-Champaign, Urbana, IL 61801, USA; <sup>2</sup>Center for Evolutionary Functional Genomics, The Biodesign Institute, and the School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA; <sup>3</sup>Department of Biology, Indiana University-Purdue University Indianapolis, Indianapolis, IN 46202, USA

(\*Author for correspondence: tel +1 3172785714; fax +1 3172742846; email xzwang@iupui.edu)

## References

Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta analytic review of the

- responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist* 165: 351–372.
- Curtis PS. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant, Cell & Environment* 19: 127–137.
- Curtis PS, Wang XZ. 1998. A meta-analysis of elevated CO<sub>2</sub> effects on woody plant growth, form, and physiology. *Oecologia* 113: 299–313.
- Gurevitch J, Hedges LV. 1999. Statistical issues in ecological meta-analyses. *Ecology* 80: 1142–1149.
- Gurevitch J, Morrow LL, Wallace A, Walsh JS. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140: 539–572.
- Hedges LV, Gurevitch J, Curtis PS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80: 1150–1156.
- Luo Y, Hui D, Zhang DQ. 2006. Elevated CO<sub>2</sub> stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology* 87: 53–63.
- Norby RJ, Cortrufo MF, Ineson P, O'Neil EG, Canadell JP. 2001. Elevated CO<sub>2</sub>, litter chemistry, and decomposition: a synthesis. *Oecologia* 127: 153–165.
- Poorter H, Navas ML. 2003. Plant growth and competition at elevated CO<sub>2</sub>: on winners, losers and functional groups. *New Phytologist* 157: 175–198.
- Rosenberg NJ, Adams DC, Gurevitch J. 2000. *MetaWin: statistical software for meta-analysis*, Version 2.0. Sunderland, MA, USA: Sinauer Associates.
- Treseder KK. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO<sub>2</sub> in field studies. *New Phytologist* 164: 347–355.
- Valkama E, Koricheva J, Oksanen E. 2007. Effects of elevated O<sub>3</sub>, alone and in combination with elevated CO<sub>2</sub>, on tree leaf chemistry and insect herbivore performance: a meta-analysis. *Global Change Biology* 13: 184–201.
- Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Hart MS, Calef MP, Callaghan TV, Carroll AB *et al.* 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences, USA* 103: 1342–1346.
- Ward SJE, Midgley GF, Jones MH, Curtis PS. 1999. Responses of C<sub>4</sub> and C<sub>3</sub> grass (Poaceae) species to elevated atmospheric CO<sub>2</sub> concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* 5: 723–741.
- Wang XZ. 2007. Effects of species richness and elevated carbon dioxide on biomass accumulation: a synthesis using meta-analysis. *Oecologia* 152: 595–605.

**Key words:** carbon cycling, elevated CO<sub>2</sub>, elevated O<sub>3</sub>, global changes, meta-analysis, nutrient cycling, terrestrial ecosystems.

## Mycorrhizas take root at the Ecological Society of America

### Mycorrhizal ecology and related sessions at the Ecological Society of America (ESA) 92nd Annual Meeting, San Jose, CA, USA, August 2007

Mycorrhizal symbioses play an important role in virtually all terrestrial ecosystems (Smith & Read, 1997). They are known to have significant impacts on carbon and nutrient

cycling, soil formation and structure, plant productivity and diversity, and food web dynamics (Van der Heijden & Sanders, 2002). Although the importance of mycorrhizas is widely recognized, the study of these symbioses has historically been divided between two groups of scientists. Ecologists interested in this topic have mainly focused on the above-ground part of the symbiosis (i.e. the plants) and treated the below-ground part of it (i.e. the fungi) largely as a 'black box'. In contrast, mycologists have primarily focused on the fungi themselves and given less attention to the way in which these symbioses affect plants and other organisms. Despite their common interest, a look at the early mycorrhizal literature would indicate that ecologists and mycologists rarely interacted with each other. The division between these two groups, however, appears to be quickly disappearing. This was most recently evidenced at this year's Ecological Society of America (ESA) meeting in San Jose, CA, USA, where a record amount of research on mycorrhizal symbioses was presented. Four oral sessions and a poster session were devoted entirely to mycorrhizal ecology. More significantly, research involving the symbiosis was included in 23 different general sessions and made appearances in many talks devoted to other topics. The meeting was also the first gathering for the Fungal Environmental Sampling and Informatics Network (FESIN: <http://www.bio.utk.edu/fesin/>), which will have alternating meetings over the next 4 yr between ESA and the Mycological Society of America in order to bring these two groups of scientists closer together. Here we summarize a few of the highlights of the mycorrhizal work that was reported at the meeting.

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*'... researchers are increasingly finding new and innovative ways to test questions about mycorrhizal fungi under ecologically realistic conditions.'*

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### Molecular techniques

One fundamental aspect of ecological studies is the ability to identify the number of species present in a given area or sample. Because the active part of the mycorrhizal symbiosis occurs below-ground, researchers have increasingly relied on molecular techniques to assess the number of fungal species in their studies (Horton & Bruns, 2001). While the methods themselves have typically held center stage in research on mycorrhizal assemblages, this year's meeting showed that they have largely become second nature and the focus has shifted to how these techniques can be applied to