New Phytologist

# Meetings

## Mucking through multifactor experiments; design and analysis of multifactor studies in global change research

### Ecological Society of America (ESA), 91st Annual meeting, Memphis, TN, USA, August 2006

The composition of the atmosphere and global climate have changed significantly since the start of the industrial revolution and these changes are impacting ecosystem structure and function (Prather *et al.*, 2001). Experimental studies that manipulate atmospheric concentrations of $CO_2$ and $O_3$, nitrogen deposition, or temperature and precipitation regimes, provide evidence that these factors can have significant and sustained impacts on net primary productivity (NPP) (Weltzin *et al.*, 2000; Zavaleta *et al.*, 2003; Hanson *et al.*, 2005; Morgan *et al.*, 2005; Norby & Iversen, 2006). Because of the interactive effects and feedbacks that emerge when factors are applied together, experiments in which only single factors are manipulated may be inadequate to fully predict the impacts of future atmospheric change on ecosystems. With this in mind, many experiments, both empirical and theoretical, have been initiated that examine the effect of multiple global change factors on ecosystems. Despite the knowledge gained from these experiments, many questions remain unresolved and the broad goal of multifactor experiments – to understand the interactions between multiple global change factors and their impacts on ecosystem structure and function – remains elusive. To aid in reaching this goal, the symposium 'Mucking through multifactor experiments; design and analysis of multifactor studies in global change research' was organized by Aimée Classen (Oak Ridge National Laboratory) in cooperation with the NSF Research Coordination Network 'Terrestrial Ecosystem Response to Atmospheric and Climatic Change' (TERACC) and the *New Phytologist* Trust at the 91st annual meeting of the Ecological Society of America in Memphis, Tennessee.

*'… although a single factor may have striking effects on ecosystem function when applied alone, when global change factors are mixed, the physiological and growth adjustments within the ecosystem may dampen the overall response.*

### Using empirical data

A large body of empirical data already exists on the response of ecosystems to global change factors, such as elevated $CO_2$ and $O_3$ applied in isolation (Ainsworth & Long, 2005; Jablonski *et al.*, 2002). By incorporating process-based information from experimental data into multifactor models, Paul Hanson (Oak Ridge National Laboratory, USA) showed how inferences can be made on the response of ecosystems to more realistic global change scenarios. Using empirical data from many single factor experiments, Hanson *et al.* (2005) simulated the interactive effects of elevated $CO_2$ and $O_3$, and changes in precipitation and warming on the growth of upland oak forests in south-eastern United States. By generating alternative climate scenarios and using key physiological and growth responses in a probabilistic framework, the authors were able to generate predictions of forest response to a variety of conditions in 2100. One of the key findings was that, with physiological adjustments to elevated $CO_2$ and temperature, a growth response of 20% may be maintained for south-eastern forests in 2100. Additionally, they were able to rank the global change factors in order of importance, e.g. temperature, $O_3$ and precipitation. This exercise also highlighted the fact that although a single factor may have striking effects on ecosystem function when applied alone, when global change factors are mixed in, the physiological and growth adjustments within the ecosystem may dampen the overall response. Jeff Dukes (University of Massachusetts, Boston, USA) also presented a similar result for California grasslands (Shaw *et al.*, 2002).

Empirical experiments are limited by their duration, but many of the important effects of global change will become evident only over large spatial and temporal scales. By assembling short-term data from a variety of ecosystem types, Steve Del Grosso (Colorado State University, USA) was able to simulate the effects of multifactor global change on large scale and long-term processes such as decomposition, carbon storage and nitrogen leaching. Using DAYCENT, the daily time-step version of CENTURY (Parton *et al.*, 1987, 1998), a gradual increase of 3°C in nightly minimum temperatures and a more conservative increase of 1°C in daily temperatures were simulated over 100 yr, for shortgrass steppe, tallgrass prairie, boreal forest, temperate coniferous and deciduous forest. The authors found that NPP and soil organic carbon increased in most systems, but in the boreal forest, soil carbon stocks decreased after 100 yr. Focusing on the temperate deciduous *Liquidambar styraciflua* forest at Oak Ridge, Tennessee, they found a good agreement between measured and simulated NPP. However, their simulation of root NPP was less reliable and underestimated NPP in elevated $CO_2$. Ross McMurtrie (University of New South Wales, Australia) offered a simpler model that could also be applied across large spatial and temporal scales. To answer 'Why the plant-growth response to rising $CO_2$ is amplified when water is limiting, but diminished when nitrogen is limiting?' he showed that optima exist for leaf N, stomatal conductance and leaf area index in a variety of global change scenarios. Like the model of Del Grosso *et al.*, McMurtrie's model confirmed much of the experimental work that has gone before, e.g. larger relative response to $CO_2$ in drier conditions. Both of these models are widely applicable and highlighted significant knowledge gaps and testable hypotheses for future empirical studies.

## Multifactor experiments

Although they are expensive and often difficult to implement, experiments that expose ecosystems to a range of global change factors are necessary to understand the mechanisms and interactions that drive responses to global change. At the OCCAM (Old-Field Community Climate and Atmospheric Manipulation) experiment in eastern Tennessee, an old field ecosystem was exposed to elevated $CO_2$, warming and altered precipitation. Aimée Classen (Oak Ridge National Laboratory, USA) showed that water availability, but not elevated $CO_2$ or warming, was the major driver of above-ground biomass in this system. However, this effect varied across years, and in 2005, the effects of soil moisture on biomass were reduced by elevated $CO_2$ and increased by warming. Dukes *et al.* also found a minimal role for elevated $CO_2$ at a grassland in Jasper Ridge, Northern California; there, the major driver of ecosystem biomass was an increase in nitrogen deposition. Teis Mikkelsen (Risø National Laboratory, Denmark) described a new experiment in which $CO_2$, temperature, and precipitation are being manipulated in a semi-natural grass and shrub ecosystem.

Many multifactor experiments have been set up to take advantage of a traditional ANOVA framework and often deal inadequately with interannual variation and 'surprises'. By focusing on the probabilities of seedling recruitment in forest gaps, Brian Beckage (University of Vermont, Vermont, USA) showed how abrupt ecological responses to climate change may be modelled using hierarchical Bayesian analysis. Classen *et al.* are exploring how path analysis may offer a more complete analysis than the traditional ANOVA framework. By employing non-parametric approaches, it may be possible to model abrupt ecological responses to global change and to take full advantage of data from empirical and observational studies.

## Applying our knowledge

Ultimately, experimental data should aid policymakers and other stakeholders in predicting the response of ecosystems to future climate scenarios. The extensive datasets that exist from long running global change experiments may aid in this goal. The aspen-FACE experiment in northern Wisconsin has been operating for nine years, and exposes aspen and birch to elevated $CO_2$ and $O_3$ in a fully factorial design. At levels already occurring across much of the globe, elevated $O_3$ offsets the gains in productivity seen in elevated $CO_2$ in *Populus tremuloides* (King *et al.* 2005). Given the ecological and economical importance of *P. tremuloides*, there is an urgent need to determine the regional implications of this result. As well as accumulating data on the physiological and growth responses of the ecosystem to $CO_2$ and $O_3$, Kevin Percy (Canadian Forest Service, New Brunswick, Canada) has also compiled extensive data on many environmental parameters coupled over space and time. By regressing growth against environmental and expected dose parameters for $O_3$, Percy *et al.* determined that the $O_3$, wind speed and growing degree days predicted about 88% of the variation in tree growth across the duration of the experiment. This analysis was extended to show the predicted growth change in *P. tremuloides* across a wide range of sensitivity to $O_3$ exposure. Thus, empirical data from a multifactor experiment provided predictor variables extending important results into the public domain, and contributing to the scientific literacy of stakeholders.

## Perspectives

Ecosystems across the globe are already being exposed to changing atmospheric composition, temperature and precipitation. Many gaps remain in our knowledge of the impacts of these changes on ecosystems, e.g. the role of below-ground processes, disturbance, and invasive species. To address these gaps, one single approach will not be sufficient. Multi-factor modelling must be utilized in conjunction with factorial experiments, to generate hypotheses and expand empirical findings, particularly across broader spatial and temporal scales. At this symposium there was a strong bias towards temperate natural systems; more information is required from under-represented ecosystems, especially those in the tropics and northern latitudes. Factorial experiments are costly and complicated: to maximize their relevance, sound statistical procedures must be applied, and non-parametric statistics may offer new insight into feedbacks and interactions between processes within ecosystems. By continuously measuring ancillary variables such as $O_3$ and precipitation, it may be possible to retrospectively understand and extrapolate results from simple experiments to more complex scenarios. To this end, it is encouraging that these issues were addressed by an international team, who no doubt will continue to expand and improve on the information presented at this symposium.

**Orla Dermody**

University of Tennessee, Knoxville, Tennessee, USA
(tel +1 865 974 4226;
fax +1 865 974 3067;
email odermody@utk.edu)

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# More complexity in the mycorrhizal world

## 5th International Conference on Mycorrhiza, Granada, Spain, July, 2006

The 5th International Conference on Mycorrhiza (ICOM5) was held in Granada (Andalucia, Spain), a multicultural city with a heritage that is both Arabic and European. Over 650 mycorrhizal scientists from more than 50 countries attended the meeting and took part in the varied social events, such as the night visit to the Alhambra (Fig. 1) and the traditional 'Wines of the World' contest. All of which contributed towards making this an open and friendly meeting, enhancing exchange and discussion of the current progress in this fast-moving field. This ICOM edition was thus very successful.

> *'The* Laccaria *genome is thus strikingly multifaceted, with Martin comparing it to the two-headed roman god Janus'*

As the conference opened, the Joint Genome Institute (JGI, Walnut Creek, CA, USA; US Department of Energy, USA) launched the genome sequence portal (http://genome.jgi-psf.org/Lacbi1/Lacbi1.home.html) for the mycorrhizal fungus, *Laccaria bicolor*. This being the official release of the first complete genome for a mycorrhizal fungus made it one of the major breakthroughs widely discussed during this meeting. Ecology and evolution dominated among the posters as well as in the sessions and workshops and, as usual, most talks focused on arbuscular mycorrhizas (AMs, involving Glomeromycetes that form arbuscular haustoria in host cells) and ectomycorrhizas (ECMs, associating Ascomycetes and Basidiomycetes with trees and shrubs). ECMs only half as popular as AMs among talks on cellular, molecular and genomic aspects of the symbiosis, but both were equally represented among talks on ecology and evolution. Such an overrepresentation of ECMs, as compared with their relatively smaller host

 