Meetings

Variability matters: towards a perspective on the influence of precipitation on terrestrial ecosystems

Effects of Precipitation Change on Ecosystems (EPRECOT) – a Terrestrial Ecosystem Response to Atmospheric and Climatic Change (TERACC) and European Commission sponsored precipitation workshop, Elsinore, Denmark, May 2006

The availability of water influences ecosystem structure and function in nearly all terrestrial biomes. Precipitation is the primary input of this limiting resource, which drives both biotic and abiotic processes. As a consequence of global warming, precipitation patterns are expected to change around the world, and data sets from both the USA and Europe demonstrate that changes in rainfall patterns attributable to human activity have already occurred within the last few decades. General circulation models (GCMs) predict changes in the spatial and temporal patterns of precipitation, including shifts in the frequency, intensity and magnitude of precipitation events (IPCC, 2001). Through the use of proxy data, observational studies, experimental manipulations and modeling, scientists are investigating how such changes in precipitation regimes may affect the structure and function of the Earth's ecosystems and biomes. In May 2006, researchers met in Elsinore, Denmark for a workshop on the Effects of Precipitation Change on Terrestrial Ecosystems (EPRECOT; http://www.climaite.dk/eprecot/eprecot.html). The meeting focused on reviewing the current state of knowledge, identifying knowledge gaps for future research activities, and generating testable hypotheses about expected outcomes of precipitation change through the use of ecosystem models. Three central questions formed the foundation for presentations and discussions at the workshop.

(1) How can ecologists pursue questions relating to precipitation change in terrestrial ecosystems in a synthetic way? Is it possible to achieve an understanding of precipitation as an ecosystem driver that spans multiple regions of the globe and biome types?

(2) What are the important response variables in assessing the impacts of precipitation change? How can we conduct research that accounts for responses across ecological, spatial, and temporal scales?

(3) How can experimental design and model development be better integrated? What are the major limitations that exist in interpreting results from both models and experimental research?

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The complexities associated with precipitation research

One of the grand challenges associated with studies of precipitation change is the inherent variability in precipitation itself. This variability, coupled with the complexity inherent to natural ecosystems, complicates simple understanding of effect–response relationships, particularly when feedbacks among the atmosphere, biosphere and geosphere are involved. Precipitation drives many biotic processes, which are the response variables of interest to many ecologists. However, precipitation is most proximally coupled to abiotic characteristics of ecosystems such as soil moisture, the depth of soil wetting and soil moisture recharge, soil temperature, and evaporation (all of which control ecosystem water and energy balance). It is these characteristics that translate the effects of precipitation events and patterns on plant, animal and microbial processes. Biologists and ecologists must therefore incorporate aspects of hydrology into their research and track the movement of water through the atmosphere, soils, and ultimately living organisms.

When attempting to understand and characterize ecosystem function, the most simple and parsimonious explanations tend to be the most useful; mean annual precipitation is thus frequently used to describe the availability and influence of water as a resource. However, increasing evidence suggests that treating precipitation as a black box ecosystem driver in terms of mean inputs is inadequate, and that variability and extremes in precipitation (e.g. size and intensity of event, extended drought or wet periods, seasonality and antecedent conditions) are more important drivers of ecosystem function than are mean conditions. For example, in the Rain Manipulation Plots (RaMPs) experiment at Konza Prairie Biological Station in Kansas, USA, changes in the relative frequency of rain events during the growing season reduced above-ground net primary productivity (ANPP), increased soil nitrogen (N) availability, changed plant community composition, and shifted allocation of carbohydrates from shoots to roots (Knapp *et al.*, 2002). These changes resulted solely from extending the dry interval length between storms (thereby creating a situation of fewer but more intense storms) (Alan Knapp, Colorado State University, Fort Collins, CO, USA).

For many ecosystems, GCMs predict soil moisture deficits and/or greater variability in soil moisture, both of which may affect not only the quantity of water available for uptake by plants, but also the availability and mobility of soil N. Soil N is tightly coupled to soil moisture, both spatially and temporally; consequently, alternate wetting and drying of the soil that will accompany increasingly variable precipitation patterns may give rise to pulses in resources (e.g. water and N). Melany Fisk (Appalachian State University, Boone, NC, USA) described the synchrony between plant nutrient demand and microbial release of resources, and their potential sensitivity to low water availability, which can occur even in temperate forest ecosystems. Reductions in soil moisture are hypothesized not only to restrict movement of nutrients to root zones for uptake, but also to limit the movement of labile carbon (C). Further, the accumulation of C substrates during dry periods may cause a flush of resources upon soil re-wetting, elevating rates of biological activity, nutrient leaching and the transfer of nutrients to unavailable pools (Austin *et al.*, 2004). Ultimately, nutrient limitations could become more important than water limitations. More research is needed to better understand the effect of this interdependent coupling of resources on ecosystem function, as it could have important feedbacks to the climate system by influencing carbon fluxes and storage as well as nutrient cycling.

Another aspect of precipitation regimes that adds complexity to interpretation of biological responses is the role of time lags, wherein effects of particular rainfall events or regimes impact biological activity at a later time. Because of the long time-scales involved, the role of previous precipitation can be readily evaluated through the use of proxy data. In the eastern Mediterranean, declines in rainfall since the late 1970s have reduced the annual stem increment of *Pinus brutia.* Analysis of tree rings has revealed that effects of drought may be manifest several years after the drought; storage of water in the soil during previous years may therefore be a better predictor of growth than current-year precipitation (Dimitris Sarris, University of Patras, Patras, Greece). Time lags can also be demonstrated on smaller spatial and temporal scales more amenable to experimental investigation. For example, Osvaldo Sala (Brown University, Providence, RI, USA) described how experimental reductions in precipitation on the Patagonian Steppe revealed that annual production was reduced in a year of average annual precipitation when the previous 3 years were characterized by relatively low inputs of precipitation.

Interactions with other global change phenomena

Because many global changes are occurring simultaneously, an increasing number of experiments are focusing on the interaction of precipitation change with other potential abiotic or biotic driving variables. In many cases, these multifactor experiments are producing unexpected results and demonstrating complex interactions (Shaw *et al.*, 2002). Atmospheric CO_2 concentration and N deposition are two human-induced chronic drivers of change that have increased during the last century. As essential inputs to photosynthetic processes, their increase drives ecosystem structure and function; however, the effect of CO_2 and N may be enhanced or diminished depending on the availability of water. For example, in the Mojave Desert, annual precipitation determines the relative responsiveness of the ecosystem to CO_2 (Smith *et al.*, 2000). In El Niño years, which bring relatively wet winters to south-western North America, primary productivity increases, with both annual and perennial species responding to the combined effects of these global change drivers (Stanley Smith, University of Nevada, Las Vegas, NV, USA). In contrast, primary productivity is unaffected by elevated CO_2 in La Niña (or 'dry') years. The importance of a secondary driver was similarly observed in serpentine grasslands in western North America, where increases in plant biomass under greater precipitation have been linked to elevated deposition of N (Jeffrey Dukes, University of Massachusetts, Boston, MA, USA). Finally, results from a study in Central Europe suggest that elevated CO_2 may effectively buffer trees from droughts, which are predicted to become more common in the future. In a year when annual precipitation was reduced by > 50% (relative to the long-term mean) and ambient temperatures were elevated by 2–4°C, trees growing under conditions of elevated CO_2 had improved water relations and higher photosynthetic rates than trees growing at ambient CO_2. A reduction in transpiration rates was observed in all species, which suggests that greater water-use efficiency may alleviate conditions of moisture stress for trees in this region (Sebastian Leuzinger, University of Basel, Basel, Switzerland).

While global-scale processes are important drivers of change, the role of regional-scale processes (i.e. land use and management) should also be considered when evaluating the effects on precipitation change on ecosystems. In the UK, sheep currently graze the large tracts of grassland that dominate the landscape. Recent evidence suggests that infiltration of rainfall is correlated with grazing intensity, and that halving the stocking density of sheep doubles rates of rainfall infiltration (Bridget Emmett, Centre for Ecology and Hydrology, Bangor, UK). In western North America, regional cycles of moisture and drought are tightly coupled with fire (Swetnam & Betancourt, 1990). Fire scars in tree rings are correlated with El Niño and La Niña events, which produce cycles of plant productivity followed by intense drying – conditions that encourage fire (Steve Leavitt, University of Arizona, Tuscon, AZ, USA).

Multifactor experiments have been instrumental in demonstrating the importance of interactions among global- and regional-scale drivers (Norby & Luo, 2004); however, they have also demonstrated the complexity of articulating mechanisms when drivers interact in additive or negative ways (Aimée Classen, Oak Ridge National Laboratory, Oak Ridge, TN, USA). During the meeting, Dieter Gerten (Potsdam Institute for Climate Impact Research, Potsdam, Germany) presented model output for several sites where there are ongoing multifactor experiments, which have allowed researchers to compare empirical and modeled results. This generated considerable discussion of model sensitivities, source and sink processes, and ecological processes that may need to be included in models as they continue to be refined.

Cascading responses to precipitation change

Because the response of any given ecosystem to a change in precipitation is likely to be complex, experimental research should consider all levels in the ecological hierarchy (i.e. genetic, population, community, and ecosystem) to identify mechanisms or adaptations and compensatory responses to changes in driving variables. During the meeting, a number of studies described an 'organization' or progression of events that characterizes the temporal response of ecosystems to changes in precipitation patterns. Because plant water status (and subsequently carbon uptake) is closely linked to availability of soil water, reductions in soil moisture influence the physiologic activity of individual plants with ramifications for integrated ecosystem processes such as ANPP. Similarly, reductions in microbial activity may constrain N availability for plant uptake. As a result, interspecific variability in plant physiology (e.g. water and nutrient relations) may ultimately lead to shifts in the relative abundances of species in response to episodic or chronic directional changes in precipitation patterns. In herbaceous systems such as grasslands, community re-ordering can take place in less than 10 years if changes in precipitation are persistent (Alan Knapp).

Under a new climatic regime, either experimental or natural, there are certain to be some 'winners' and some 'losers' in all ecosystems. While this may be evinced in subtle shifts in community composition or dominance (e.g. one species of a C_4 grass replacing another) it may also result in more dramatic community type changes (e.g. grassland to shrubland), functional group substitutions (e.g. C_4 to C_3 species) and/or species losses (Bachelet *et al.*, 2001). Many of the biotic changes will be contingent upon the magnitude of the change in precipitation (and its interaction with other global change drivers) in addition to the buffering mechanisms and thresholds that characterize individual ecosystems. At local scales, communities are composed of multiple species that differ in such characteristics as rooting depth, growth rate, and physiology or morphology, which affect their ability to utilize different resource pools or to conserve water. Josep Peñuelas (Universitat Autònoma de Barcelona, Barcelona, Spain) emphasized the role of phenotypic and genotypic variability as controls over community adaptation to precipitation change, as well as the role of plant species migration. In the Montseny Mountains of Spain, beech trees have migrated to higher elevations from lower elevations commensurate with changes in temperature and aridity. Further, while evolution will lag behind climate change, it is an important aspect of ecosystem response that is difficult to predict.

Need for experimental protocols

It is clear that the number of experiments designed to determine the effect of potential changes in precipitation on terrestrial ecosystems has increased from few to many over the course of the last decade. It is equally clear, based on the presentations at the meeting and the current literature, that there are probably as many methodologies in use as there are experiments (Weltzin *et al.*, 2003). This phenomenon probably arises for several reasons. First, by their nature, experiments are hypothesis-driven, and the plethora of sites and questions across a variety of spatial and temporal scales requires a multiplicity of approaches and techniques. Second, simulation of a current precipitation regime, not to mention potential future regimes, is fraught with uncertainty because of the highly variable (and thus uncertain) nature of the various components of this factor: should one manipulate means, extremes, intensity, frequency, serial correlation, etc.? Once this is decided, what is the best technique to catch and store or deliver, and then apply, water to experimental plots?

Thus, a theme recurrent in discussion was whether a particular protocol could or should be adopted to facilitate synthesis among precipitation manipulation experiments (e.g. free-air CO_2 enrichment experiments that target a CO_2 of 550 ppm). Although this issue was unresolved, it was generally agreed that regions of sensitivity to particular aspects of precipitation change should be identified for additional study, and that manipulations need not necessarily be tied to a specific GCM (or more local or regional model), particularly when research questions are mechanistic (e.g. focusing on identification of critical thresholds or the role of infrequent extremes in driving ecosystem structure or function). In addition, new projects should carefully consider the role of droplet size, runoff, water chemistry, etc. from an ecohydrological perspective, as these 'details' may influence biotic responses. Regardless, a diversity of approaches and methodologies may be required to fully address the diversity of characteristics of contemporary or potential future precipitation regimes.

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